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Understanding communities in complex agroforestry systems: methodological advances and ecological implications

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ABSTRACT

Agroforestry, the practice of growing crops beneath a canopy of shade trees, is common in tropical regions, and has the potential to provide habitat for wildlife whilst maintaining agricultural production. However, the increasing demand for commodity crops is driving intensification of agriculture in the tropics, which results in the conversion of agroforestry systems into monocultures. This conversion to monocultures drives declines in biodiversity in these habitats, which may in turn cause a drop-off in yields due to loss of ecosystem services. However, the effects of agricultural management on animal communities and the downstream effects on productivity are poorly understood, especially in the Afrotropics.

This project aimed to study the influence of farm management on wildlife communities, and the potential implications for productivity, in African cocoa agroforestry. My research was based on data of bird and arthropod communities in 28 cocoa farms in southern Cameroon. The study farms varied in their shade cover (a proxy for management intensity), from 20% to 100% cover. In these farms we surveyed arthropods using visual surveys, sweep-netting and malaise traps, and birds using mist-netting and acoustic recorders. I investigated trends in bird and arthropod community composition using several statistical methods, including data integration, hierarchical modelling and community modelling.

My results show that the shade cover of farms had a strong influence on animal community composition. Shady (low-intensity) cocoa farms supported higher densities of vulnerable rainforest bird species such as ant-followers and forest specialists. Shady farms also contained higher densities of potential pollinators and natural enemies, and lower densities of pest insects. I investigated the interplay between shade management and interspecific interactions, and found that both these factors were important in shaping communities in these complex agricultural habitats.

Overall, my results indicate that low-intensity management of agroforestry may be beneficial for both biodiversity conservation and productivity, as it favours populations of vulnerable species and ecosystem services providers, whilst reducing pest burdens. These findings shed light on the risks associated to the current push towards intensification of agriculture in the tropics.

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AUTHOR'S DECLARATION

I declare that, except where explicit reference is made to the contribution of others, this thesis is the result of my own work and has not been submitted for any other degree or professional qualification at the University of Glasgow or any other institution.

Crinan Jarrett

May 2022

LIST OF PUBLICATIONS

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Related to this thesis

Jarrett, C., Powell, L.L., Claire, T.T.R, Tchoumbou, M. and Helm, B. (2021). Moult of overwintering Wood Warblers *Phylloscopus sibilatrix* in an annual-cycle perspective. *Journal of Ornithology*, 162 (3), 645-653.

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Previous publications

Previous publications by the author can be found at: https://orcid.org/0000-0002-7154-0149

Chapter 1 | General introduction

Land sparing vs land sharing in a changing world

Human population will continue to increase in the following decades, likely reaching 10 billion by 2050 (United Nations, 2019). This increase in population will require raising overall food production by approximately 60% (Alexandratos & Bruinsma, 2012). At the same time, the destruction and degradation of natural habitats must be slowed in order to avoid (or, by now) minimise, the irreversible consequences of climate breakdown and biodiversity crisis (Pettorelli et al., 2021). There is therefore an urgent need for strategies that will allow increased food production whilst reducing damage to biodiversity (Tscharntke et al., 2012). Mostly, strategies fall under the two categories of land sparing and land sharing (Tscharntke et al., 2012). Land sparing implies maximising crop yields through agricultural intensification to minimise the amount of land required, therefore allowing more land to be set aside for biodiversity conservation. Land sharing involves low-intensity agricultural management to encourage biodiversity in agroecosystems whilst simultaneously maintaining productivity (Tscharntke et al., 2012).

The land sparing vs land sharing dilemma has been discussed in the scientific literature extensively, with empirical evidence supporting both sides. For instance, Gockowski & Sonwa (2011) show that, had intensified technology, developed in the 1960s, been utilized in Côte d'Ivoire, Ghana, Nigeria and Cameroon, over 21,000 km^2 (equivalent to the size of Belgium) of deforestation and forest degradation could have been avoided as well as the release of nearly 1.4 billion t of CO_2. On the other hand, an extensive study from Indonesia shows that there is no relationship between yields and biodiversity in agricultural landscapes, implying that increasing productivity should not require agricultural intensification and consequent loss of biodiversity (Clough et al., 2011).

The question of land sparing vs land sharing is especially relevant in the Earth's tropical regions, which include some of the areas of highest wildlife diversity and poorest human populations (Laurance et al., 2014). These regions are where human populations are expected to increase most steeply, putting increasing pressure on natural resources (Laurance et al., 2014; Tscharntke et al., 2012). Currently, food production in the tropics consists mostly of low-input small-scale subsistence agriculture carried out by farmers living well below the poverty line (Tscharntke et al., 2012). Whilst a land sparing approach could theoretically be effective in the tropics (Phalan et al., 2011), in practice, lack of start-up capital (both personal and public), limitations in infrastructure (e.g., poor roads) and reduced access to technology make intensifying agriculture in these areas a complex process (Laurance et al., 2014; Tscharntke et al., 2012; Vaast & Somarriba, 2014). Given these restrictions, large scale land sparing is unlikely to be achievable in most cases, at least in the foreseeable future. Land sharing, which would combine the conservation of valuable tropical wildlife with food production and is inexpensive to establish, is a more achievable trajectory.

Agroforestry as a land-sharing approach

A prime example of a land-sharing agricultural system is agroforestry, the practice of planting crops under a canopy of shade trees (Tscharntke et al., 2011). Crops commonly grown in agroforestry include cocoa, coffee and vanilla. Agroforestry offers an opportunity to achieve both biodiversity conservation and agricultural productivity (Clough et al., 2011); its vegetatively diverse forest-like structure makes agroforestry a suitable habitat for many rainforest species, and these in turn can facilitate low-input agricultural productivity by provision of ecosystem services such as pollination, soil nutrient cycling and pest control (Maas et al., 2016; Rice & Greenberg, 2000; Toledo-Hernández et al., 2021; Tscharntke et al., 2011).

Cocoa is one of the main crops grown in agroforestry. It is native to the Neotropics but is cultivated also in the Afrotropics and Southeast Asia (Clough et al., 2009). Cocoa trees produce pods containing beans which are then dried, fermented, and used to make chocolate and derivates. Worldwide, the major producers of cocoa beans are Côte d’Ivoire, Ghana, Indonesia, Ecuador and Cameroon (Clough et al., 2009).

The management-biodiversity-yield triangle

Cocoa can be grown under a wide range of conditions, from shady low-intensity agroforestry to full sun monocultures (Rice & Greenberg, 2000; Tscharntke et al., 2011). In the former, cocoa trees are usually planted under a thinned canopy of existing native rainforest trees, or under a canopy of native and non-native trees planted by farmers (for instance fruit trees, trees planted for timber, or trees with other functions such as medicinal; Rice & Greenberg, 2000). In the latter, the rainforest is clear cut and then cocoa trees are planted in full sun. This wide range of conditions under which cocoa can be grown (0 – 100% shade cover) results in very different biotic and abiotic conditions within the farms (Andres et al., 2016; Ofori-Frimpong et al., 2007; Schneidewind et al., 2018).

The degree of shade cover in a farm drives a cascade of down-stream effects, such as light transmittance, soil biochemistry and humidity (Andres et al., 2016; Niether et al., 2018; Schneidewind et al., 2018). These abiotic conditions in turn influence the biotic community, for instance, low light transmittance through tree canopy results in reduced growth of understorey plants (Niether et al., 2018). Though other management variables also affect farm biodiversity (e.g., trimming of understorey, application of chemicals), shade cover remains the major factor shaping communities in cocoa agroforestry (Niether et al., 2018; Sanderson et al., 2022; Tscharntke et al., 2011).

Additionally, farm shade management may influence agricultural yields, both directly (e.g., low light transmittance may decrease photosynthesis rate in cocoa trees; Beer et al., 1998) and indirectly (e.g., high humidity favours breeding habitats for pollinators, which in turn facilitate fruit set; Toledo-Hernández et al., 2021). We are therefore faced with a three-way relationship between farm management, biodiversity and yield (Fig. 1). Given the current trajectory of increased food demand and dwindling biodiversity, understanding this relationship and identifying scenarios that combine viable outputs of yield and biodiversity (land sharing), should be a top priority for agroforestry research and policy (Niether et al., 2020). However, there are still many important gaps in our understanding of this complex relationship.

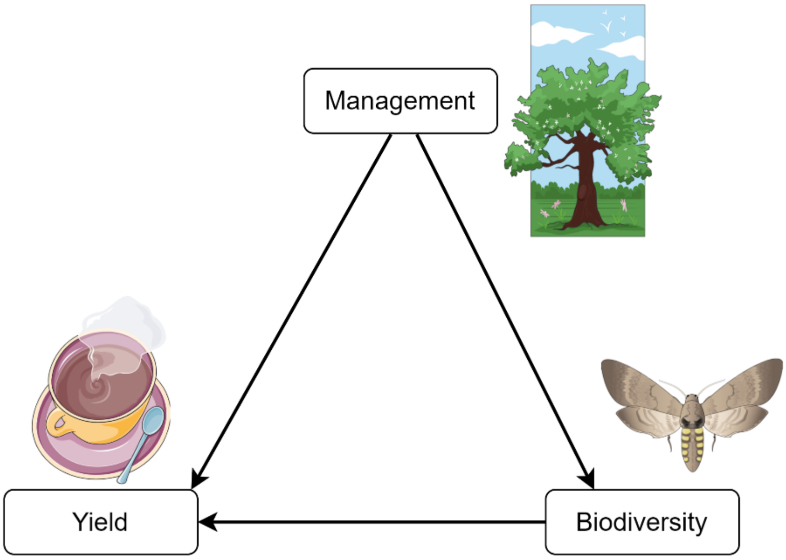

Figure 1. Agroforestry management influences both yield and biodiversity directly, and biodiversity in turn affects yields through the provision of ecosystem services and disservices.

Knowledge gaps

I identified three major gaps in our knowledge that hinder our understanding of the management-biodiversity-yield relationship in African cocoa. These gaps vary in their extent and generality; in some cases what is missing is detailed information on a specific system, whilst in other cases it is a general framework that captures a large-scale process. This combination of detailed information on a specific system with an overarching theoretical framework is the basis of current ecological knowledge, as well as the driving theme of this thesis.

1. *The effect of cocoa farm management on biodiversity in the Afrotropics*

Existing research into the effects of cocoa farm management on biodiversity is extensive but geographically biased. Whilst in the Neotropics and South-East Asia there have been studies covering a wide range of taxa in cocoa farms, in Africa there is a much smaller volume of studies overall (Bennett et al., 2021; De Beenhouwer et al., 2013), and these are almost exclusively focussed on plants and invertebrates. To my knowledge, there are only 2 studies that investigate the effects of farm management on vertebrate fauna in African cocoa (Table 1). The African studies that do exist show a general trend of increasing biodiversity with more shade cover in farms, which agrees with research from the other continents (Blaser et al., 2018; Sanderson et al., 2022; Table 1). Additionally, several studies report higher abundance of pest arthropods in sunny farms compared to shady ones (Babin et al., 2010; Bisseleua et al., 2013; Table 1). However, there is clearly a need for studies that include vertebrate taxa, in order to understand how farm management influences whole-system biodiversity in the Afrotropics (Bennett et al., 2021; De Beenhouwer et al., 2013).

2. *Accounting for observation processes when assessing animal populations in cocoa agroforestry*

Aside from the geographical bias, existing studies into the relationship between management and biodiversity in cocoa are often compromised by methodological bias. In the vast majority of cases, researchers conduct field counts of different animal groups and then attempt to explain these raw data with management covariates. Though the resulting trends form an essential basis for our understanding, this approach is not without issues: in a diverse structurally complex system like agroforestry, surveying animals is complicated (low visibility, high variation in habitat characteristics), and consequently the count data collected may not be representative of the community composition present (Banks-Leite et al., 2014; Kery et al., 2005). In these complex habitats where detection is guaranteed to be imperfect, it can be important to account for detectability and its associated biases (Banks-Leite et al., 2014). Not doing so may mask trends or create false trends when exploring correlations with management covariates, especially when the covariates expected to influence abundance (e.g., vegetation density) may well influence detection (Rodrigues & Prado, 2018). Therefore, there is an additional need for studies that investigate the effects of management on fauna applying robust statistical methods that account for varying detection.

3. *The interplay between management and interspecific interactions in cocoa farms*

An additional limitation in the common methodological approach to understanding management-biodiversity relationships is that studies tend to examine taxa separately, attempting to explain trends in the abundance of each taxon with management covariates. This approach assumes independence between taxa. In a complex habitat there are undoubtedly many links between species, including predation, competition and mutualism, and therefore modelling species separately may overlook important ecological processes (Janssen & Rijn, 2021; Kawatsu et al., 2021; Ovaskainen & Abrego, 2020; Thorson & Barnett, 2017; Tylianakis et al., 2007; Yodzis, 1998). An important development in agroforestry research would be to model the influence of management on animal groups whilst considering interspecific relationships.

4. *The implications of animal community composition for productivity*

Aside from understanding the effects of management on biodiversity, to complete the full picture (Fig. 1), we then need to establish the links with productivity. As mentioned previously, management will influence yield both directly and through biodiversity and so there is a need for a holistic approach to investigate these trends. Until now however, research has tended to address the management-biodiversity-yield issue by assessing sets of correlations. For instance, Blaser et al. (2018) examine correlations between shade cover and yield, animal abundance, and other ecosystem characteristics (e.g., carbon sequestration) and from these draw conclusions about trade-offs between productivity, biodiversity and climate resilience in African cocoa. Whilst the trade-offs presented in this study make sense intuitively and may well be robust to methodological changes, the underlying assumption that these groups react to shade cover independently of each other may overlook ecological processes that could change the shape of the resulting trade-offs (Tylianakis et al., 2007; Yodzis, 1998).

Overall, there is a need for a holistic approach that captures management, biodiversity and yield and the interlinking relationships, that would allow us to identify win-win (and lose-lose) scenarios (Niether et al., 2020). However, these methodological innovations come at a cost; complex community models are data-greedy, and have in the past proven challenging to parameterise (let-alone statistically fit) to field data (Ellner et al., 2002; Yodzis, 1998). In this thesis, I attempt to address the knowledge gaps presented above. Much of the work concerns methodological advances, because whilst my ultimate aim was to understand the ecology of tropical agroecosystems, it was necessary to develop suitable tools that allowed me to infer the underlying complex processes from spatially and temporally constrained, imperfect and taxonomically incomplete data. Such data limitations are pervasive in all community studies, so these methodological advances are beneficial for ecosystem management more broadly.

Table 1. Studies investigating the effect of cocoa farm management on wildlife communities in Africa. I excluded review papers and papers that do not explicitly examine cocoa management covariates (e.g., comparison of cocoa with forest, or land-use gradient that includes a few cocoa plots).

Authors	**Year**	**Taxa**	**Location**	**Main findings**
Kone et al	2014	Ants	Côte d'Ivoire	Ant species richness decreased with increasing management intensity
Tadu et al	2014	Ants	Cameroon	Populations of the most abundant arboreal species, *Oecophylla longinoda, Tetramorium aculeatum*, *Crematogaster spp.*, *Camponotus spp*., were generally aggregated in plantations. Highest densities of *O. longinoda* were sheltered by cocoa trees in the sunniest areas of plots. On the other hand, *Crematogaster* species were usually strongly aggregated in the most shaded areas.
Bisseleua et al	2013	Ants, wasps, spiders and insect pests	Cameroon	Abundance of spiders and wasps and ant species richness increased with increasing shade cover. Abundance of pest insects decreased with increasing shade.
Sanderson et al	2022	Birds	Sierra Leone	Forest-dependent species and Yellow-casqued hornbill (endangered) were more common in abandoned than actively managed farms. A significant interaction indicated that forest-dependent species richness increased with increasing canopy cover when surrounding forest cover was low, but not when forest cover in landscape was high.

Blaser et al	2018	Birds, ants and frogs	Ghana	Agroforests supported higher levels of species diversity than monocultures. Ants and amphibians showed a positive effect of shade trees but no significant relationship with shade-tree cover, suggesting that these taxa benefit from the simple inclusion of shade trees, irrespective of the level of shade cover
Babin et al	2010	Brown capsid (*Sahlbergella singularis*)	Cameroon	Brown capsid populations were aggregated in patches with high light transmittance
Akesse-Ransford et al	2021	Insects	Ghana	Insect abundance and diversity were generally higher in organic farms compared to conventional farms
Gidoin et al	2014	Mirids	Cameroon	Mirid density decreased when a minimum number of randomly distributed forest trees were present compared with the aggregated distribution of forest trees, or when forest tree density was low. Moreover, a decrease in mirid density was also related to decreased availability of sensitive tissue, independently of the effect of forest tree structure.
Felicitas et al	2018	Termites	Cameroon	Termite species richness decreased significantly from the heavy shaded cocoa agroforests (44 species) to the full sun (11 species). Both the richness of termite pests and marketable yield followed a quadratic curve and were found to be lowest and highest in plots with shade cover above 40%.

Djuideu et al	2020	Termites	Cameroon	Complete shade removal or very heavy shade on very old cocoa trees were responsible of the invasion of termites with negative effect on marketable yield. Some tree species, specifically fruit tree species may act as termite attractants and reservoirs by facilitating the building of galleries on cocoa trees. The relationship between yield and the infestation of termites was weak in unshaded systems and very strong under shaded systems.

Thesis structure and contribution

In Chapter 2 (published in *Journal of Applied Ecology*: Jarrett, Smith, et al., 2021), I addressed the limited understanding of the effects of cocoa farm management on vertebrate communities by analysing a historical dataset of bird mist-net captures from forest sites and cocoa farms across Cameroon. First, I compared bird diversity and community composition between primary forest and cocoa farms, and then I investigated the effect of farm shade cover and surrounding forest cover on bird community composition. Whilst I was limited in the types of analyses I could conduct with these data because they were not collected in a standardised fashion (and corresponding effort data were not always possible to find), the extent of the dataset and its novelty in terms of geographical coverage resulted in new insight into trends in vertebrate communities in African agroforestry.

One of the limitations I encountered in Chapter 2 was that I was not able to examine bird population sizes directly, but rather a proxy for abundance (mist-net captures). According to the literature, and to my experience during fieldwork, bird mist-net captures can be a biased index of population size as the habitat in which mist-nets are placed influences detectability (Banks-Leite et al., 2014; Rodrigues & Prado, 2018). In Chapter 3 (accepted in *Ecology*: Jarrett et al., 2022), I tackled this issue by developing a model to estimate bird population size that integrated mist-netting and acoustic data. This method can produce accurate estimates of abundance in scenarios where the same environmental covariates influence detectability and population size. I applied this model to our data from African cocoa to understand the effect of shade management on the population size of different bird guilds.

Continuing with my overarching aim of better understanding the management-biodiversity-yield relationship in African cocoa, I focussed on arthropod communities in Chapter 4. Arthropods are highly important in cocoa agriculture, providing ecosystems services such as pollination and pest control (Akesse-Ransford et al., 2021; Sperber et al., 2004; Toledo-Hernández et al., 2021). Additionally, many arthropod groups are of interest to conservation, such as ecosystem engineers like army ants, dung beetles and termites (Felicitas et al., 2018; Peters et al., 2011; Santos-Heredia et al., 2018). However, several arthropod taxa are pests in cocoa farms, causing severe yield losses of up to 40% (Wessel & Quist-Wessel, 2015). In this chapter, I developed a method to estimate population size of the arthropod community in cocoa farms, and investigated how different groups responded to farm shade cover.

In Chapter 5, I brought together the observation models for birds and insects developed in Chapters 3 and 4: I combined them with a process model that described the dynamics of the bird-arthropod community in cocoa farms. The framework I developed corrects for detection issues (via observation models), considers interactions between species, and considers the effect of shade cover on species' growth. I then assessed the potential outcomes of different shade-induced community compositions in terms of diversity conservation and productivity. I therefore provide a novel and holistic framework to assess trade-offs between biodiversity and productivity in these complex ecosystems.

Study system

This thesis is built upon field data collected over 3 years in 28 cocoa farms in Cameroon (Fig. 2). Cameroon is the fifth largest producer of cocoa beans Worldwide, yet is unique in that the majority of cocoa farming in the country consists in low-intensity agroforests (Rice & Greenberg, 2000). This contrasts with, for instance, Côte d'Ivoire, where fast expansion of highly intensified cocoa plantations has demolished the country's rainforest (Barima et al., 2016). Cameroon, whose large expanse of rainforest contains some of the highest levels of wildlife diversity in the World (Fisher & Christopher, 2007), is at risk of following a similar trajectory to Côte d'Ivoire unless there is a movement towards incentivising low-intensity agroforests. The current recommendation from agricultural policy in general is to intensify cocoa agriculture in the region (Clough et al., 2009; Ordway et al., 2017). This will undoubtedly result in strong losses of biodiversity, and the increase in yield is by no means guaranteed (Clough et al., 2011). The risk is that decisions on management are based on an incomplete picture of these agricultural systems, giving mis-leading expectations about productivity and biodiversity outcomes.

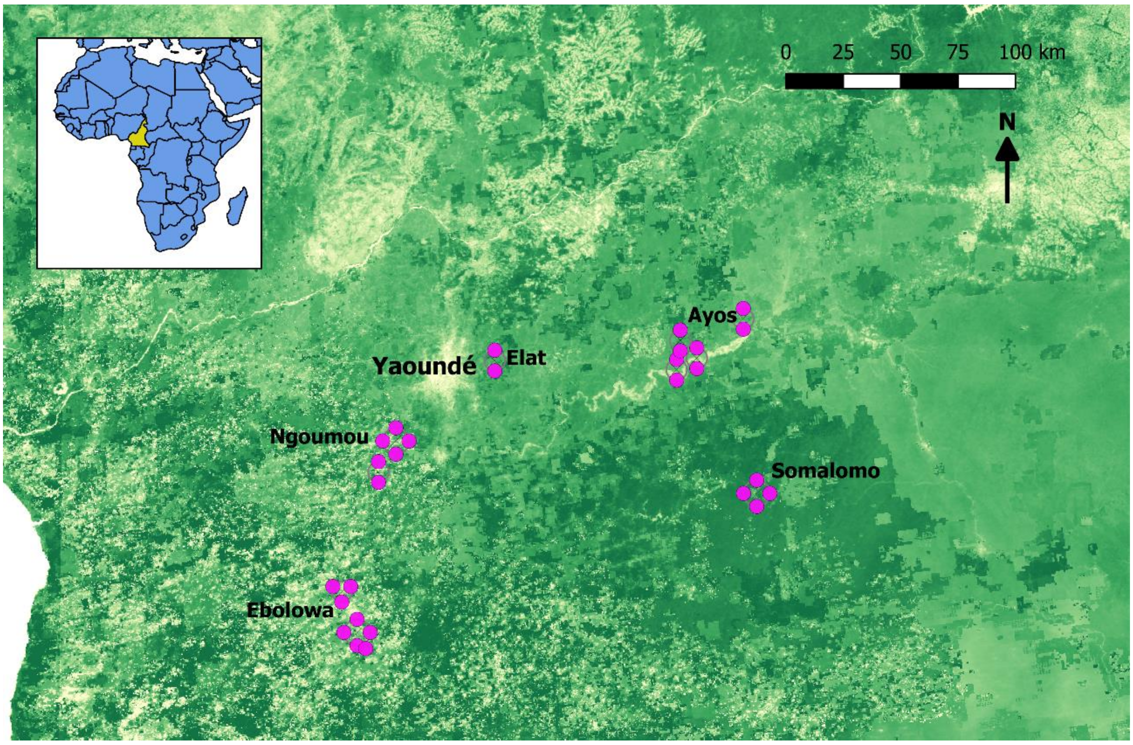

Figure 2. Cocoa farms in southern Cameroon surveyed for birds and arthropods during 2018-2020.

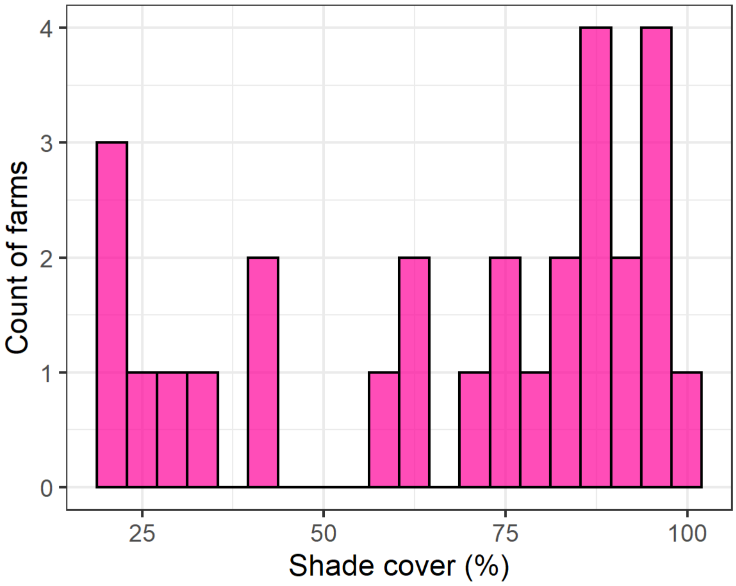

Figure 3. Distribution of shade cover amongst surveyed cocoa farms (*n* = 28).

The study farms for this thesis were on a gradient of shade cover, ranging from intensified cocoa farms with ~20% shade cover, to low-intensity agroforests with ~100% cover (Figs. 2 – 3). We visited these farms in January-February and August-September 2018 – 2020, and during each of these visits we surveyed birds and arthropods. Throughout this thesis, my goal has been to explain patterns in these data using robust statistical techniques that were able to represent the complexity of the system. In doing so, I hope to improve our understanding of animal communities in African agroforestry and contribute to the knowledge of how to manage these systems to achieve viable compromises between biodiversity conservation and productivity.

Chapter 2 | Bird communities in African cocoa agroforestry are diverse but lack specialised insectivores

This chapter has been published in: Jarrett, C., Smith, T.B., Claire, T.T.R., Ferreira, D.F., Tchoumbou, M., Elikwo, M.N.F., Wolfe, J., Brzeski, K., Welch, A.J., Hanna, R. and Powell, L.L., (2020). Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores. *Journal of Applied Ecology*, 58 (6), 1237-1247 https://doi.org/10.1111/1365-2664.13864 (Appendix 11).

ABSTRACT

Forests are being converted to agriculture throughout the Afrotropics, driving declines in sensitive rainforest taxa such as understory birds. The ongoing expansion of cocoa agriculture, a common small-scale farming commodity, has contributed to the loss of eighty percent rainforest cover in some African countries. African cocoa farms may provide habitat for biodiversity, yet little is known about their suitability for vertebrate fauna, or the effect of farm management on animal communities. Here, I report the first in-depth investigation into avian diversity and community composition in African cocoa, by assembling a dataset of 9566 individual birds caught across 83 sites over 30 years in Southern Cameroon. I compared bird diversity in mature forest and cocoa using measures of alpha, beta and gamma diversity, and I investigated the effect of cocoa farm shade and forest cover on bird communities. Gamma diversity was higher in cocoa than forest, though alpha diversity was similar, indicating a higher dissimilarity (beta diversity) between cocoa farms. Cocoa farms differed from forest in community composition, with a distinctive decrease in relative abundance of insectivores, forest specialists and ant-followers and an increase in frugivores. Within cocoa farms, I found that farms with high shade cover in forested landscapes resulted in higher relative abundance and richness of sensitive forest species; shady farms contained up to 5 times the proportion of forest specialists than sunny farms. Sunny African cocoa farms were less able to support sensitive bird guilds compared with shaded farms in forested landscapes. My findings support the notion that certain ecological and dietary guilds, such as ant-followers and forest specialists are disproportionately affected by land-use change. In light of the current push to increase cocoa production in sub-Saharan Africa, my results provide policymakers opportunities for more wildlife-friendly cocoa schemes that maximize avian diversity.

INTRODUCTION

Agricultural expansion is the main cause of terrestrial biodiversity loss worldwide (Newbold et al., 2015). The tropics, particularly sub-Saharan Africa, have the highest risk of biodiversity loss due to limited coverage of protected areas, low conservation spending and high agricultural growth (Kehoe et al., 2017). With agricultural demands projected to double in the next decades (Tscharntke et al., 2012), there is an urgent need for strategies that will combine agricultural production and biodiversity conservation. Trade-offs exist between agricultural production and biodiversity conservation, yet these aims need not be mutually exclusive: high-yield food production and high-biodiversity are able to co-exist in tropical smallholder agroforestry systems, in which agricultural crops are grown among shade trees (Clough et al., 2011; Perfecto & Vandermeer, 2010; Priess et al., 2007).

Cocoa is the fastest expanding export-oriented crop in the Afrotropics (Ordway et al., 2017), driven by a booming market in Europe (Squicciarini & Swinnen, 2016). Cocoa cultivation has caused mass deforestation in countries such as Côte d’Ivoire, where it is now grown industrially in full sun monocultures because of lack of forest land (Maclean, 2017). In other countries such as Cameroon, the 5th top exporter of cocoa worldwide, it is grown in a less intensive manner, usually under a thick forest canopy (Rice & Greenberg, 2000). Though short-term yields may be higher in full sun plantations, there is some evidence to indicate that shaded cocoa farms have a longer productive lifespan and suffer lower pest burdens, making long-term yields comparable (Tscharntke et al., 2011). The Government of Cameroon aims to triple cocoa production by 2035 (Ordway et al., 2017), which may lead to clearing of forested land for monocultures and conversion of shade-grown cocoa to sun monocultures (Andres et al., 2016; Schroth & Harvey, 2007).

Cocoa agroforestry systems often maintain a high diversity of rainforest shade trees, that may resemble the rainforest they replaced (Bisseleua et al., 2013; Sonwa et al., 2007). Partly due to this, several studies have suggested that cocoa agroforestry systems contain considerably higher biodiversity than intensive cocoa plantations

(Bhagwat et al., 2008; Bisseleua et al., 2009; Tscharntke et al., 2011; Vergara & Badano, 2009). However, most studies on cocoa are from the Neotropics and South-East Asia. In their meta-analysis, De Beenhouwer et al. (2013) highlight a lack of research on the capacity of African cocoa agroecosystems to maintain biodiversity. Specifically, we know little regarding vertebrate communities, and how they are affected by farm management practices (Schroth & Harvey, 2007; Sekercioglu, 2012). The notable exception is Sanderson et al (2022), who surveyed birds in African cocoa farms and found that forest-dependent species were more common in abandoned than actively managed farms, and that forest-dependent species richness increased with increasing canopy cover when surrounding forest cover was low, but not when forest cover in landscape was high. Waltert et al. (2005) and Kupsch et al. (2019), who surveyed birds across a gradient of land-use intensification which included some cocoa plots, found that although species richness did not decrease with increasing habitat modification, community composition was significantly affected, with a decrease in abundance of large-bodied frugivores and terrestrial insectivores.

Factors affecting animal diversity in cocoa agroforestry systems occur at two spatial scales: farm level (0.25 – 5 Ha) and landscape level. Within the farm, management actions such as shade tree removal and pruning will affect an animal community. In the Neotropics, farms with dense, structurally diverse vegetation have been shown to support a higher diversity of birds (Cassano et al., 2009), ants (Philpott et al., 2006) and amphibians (Deheuvels et al., 2014). At a landscape-scale, animals are affected by habitat connectivity as has been shown in Brazil where farms in forested areas support higher diversity of birds, bats and frogs than farms in disturbed non-forested landscapes (Cassano et al., 2009; Faria et al., 2006).

Birds are good indicators of habitat quality (Kupsch et al., 2019), with groups such as insectivores showing high sensitivity to habitat degradation (Karp et al., 2011; Powell et al., 2015; Stratford & Stouffer, 2013; Tchoumbou et al., 2020; Wolfe et al., 2015). In the tropics, many bird species depend strictly on microhabitats often only present in pristine forest (forest specialists; Stratford & Stouffer, 2013). Here I focus attention on two additional sensitive guilds of birds: ant-followers and mixed-flock species. Ant-followers are birds that pursue army ants, consuming the invertebrates flushed by the swarm (Peters & Okalo, 2009). Ant-followers are vulnerable to habitat degradation, and they are often the first guild to disappear with habitat conversion (Peters et al., 2008; Peters & Okalo, 2009). Also sensitive to habitat disturbance are mixed-species flocks, assemblages of birds of different species that move through the forest together foraging (Cordeiro et al., 2015).

In this study, I investigated the diversity of ecological bird guilds in African cocoa farms using a dataset collected over 30 years of bird mist-net captures across Southern Cameroon and Equatorial Guinea. I contrasted avian diversity and community composition patterns between forest and cocoa across varying shade and forest cover. Specifically, I asked the following questions: (1) Are bird communities in cocoa farms less diverse than in the forest? (2) Is bird community composition different between forest and cocoa? (3) How do shade and forest cover influence bird communities in cocoa farms?

METHODS

Bird mist-net captures

I considered bird mist-net captures from Cameroonian cocoa farms and mature forest, and from one mature forest site in Equatorial Guinea, between 1990 and 2020 (Fig. 4; Appendix 1). These data were collected for a range of projects, and therefore did not have a standardized methodology or sampling effort. However, the similarities in the overall approach made the data comparable: at each site, 12 to 20 12 x 3 m mist-nets (30 mm mesh) were set up for 6-11 hrs per day (~6:30 to 12.30-17:30; Jarrett, Powell, et al., 2021; Smith et al., 2005). Nets were set up either in a straight transect or in two smaller transects. The number of sampling days per site varied (Appendix 1). I used two methods to account for this unstandardized sampling effort: 1) For diversity analyses, I sampled a standardized number of captures and sites (n = 25 sites per habitat type, n = 30 captures per site) and 2) For community composition analyses I considered only relative abundance and species richness of foraging guilds, calculated for each sampling unit by dividing the number of captures or species of each foraging guild by total captures or species.

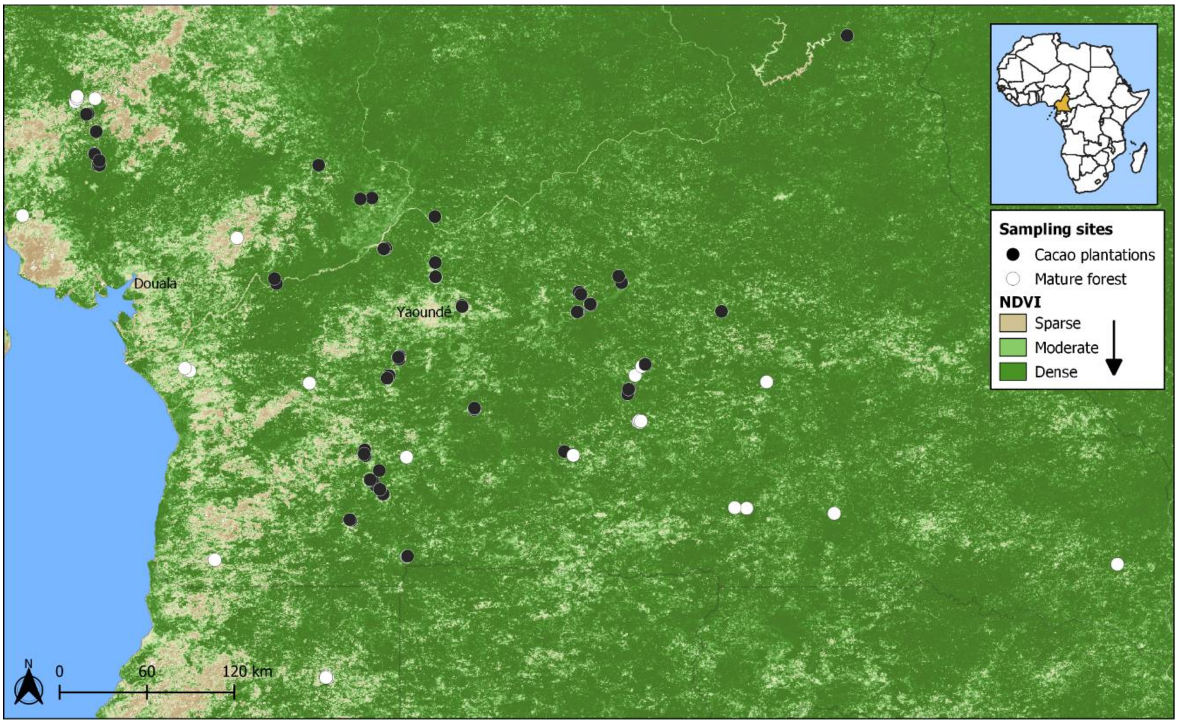

Figure 4. Map of all mature forest (white) and cocoa (black) sample sites across Southern Cameroon and Northern Equatorial Guinea (Appendix 1). The base map shows eMODIS Normalised Difference Vegetation Index (NDVI; October 2018), as an indicator of vegetative land cover (accessed from https://earlywarning.usgs.gov/).

I excluded individual birds that were not identified to species level, except for the commonly caught genera *Criniger*, *Phyllastrephus* and *Terpsiphone*. The resulting database consisted of 9566 birds captured across 83 sites (26 forest and 57 cocoa; Fig. 4; Appendix 1 & 2). I used the Handbook of the Birds of the World (del Hoyo et al., 2019) to classify each species according to its primary food type, its foraging guild and whether it was a forest specialist. Species could belong to more than one category (e.g., insectivorous and forest specialist; Appendix 2). I assessed the conservation status of each species using the IUCN Red List (IUCN, 2020) and I determined species that were geographically restricted to the Congo Basin by consulting distribution maps in Handbook of the Birds of the World (del Hoyo et al., 2019; Appendix 2).

I considered sampling sites independent if they were separated by at least 500 m, those separated by less were pooled. The mature forest sites were at least 1 km from forest edge, had a closed canopy and were considered largely undisturbed by logging activity. Sites were classified into three regions: south, ecotone and west, corresponding to distinct ecoregions in Cameroon (Tamungang et al., 2014). I assigned each sampling visit to a season, either wet or dry, according to rainfall patterns of the corresponding region (Molua, 2006).

Quantifying diversity

I quantified diversity using Reeve et al.'s (2016) framework implemented in the package *rdiversity* (Mitchell et al., 2020), which measures components of alpha, beta and gamma diversity over a continuum of viewpoint parameters, q (for details see Allen et al., 2019; Kirkpatrick et al., 2018; Kumar Sarker et al., 2019). The value of q determines the relative importance attributed to species of differing rarity, giving less importance to rare species as q increases (Appendix 3). Here, I used $q = 0, 1, 2$ and ∞ as they align with commonly used diversity metrics (species richness, Shannon entropy, Simpson diversity and Berger Parker diversity). The framework considers a metacommunity composed of multiple subcommunities, each containing a number of species (Appendix 3). From the framework I calculated: metacommunity gamma diversity, subcommunity gamma diversity, subcommunity alpha diversity and representativeness of subcommunities within the metacommunity (a type of beta diversity; Appendix 3). Representativeness takes a value between 0 and 1; it is smallest when species present in each subcommunity are not present elsewhere in the metacommunity, and largest when all species in the metacommunity are present in the subcommunity (Appendix 3; Reeve et al. 2016).

I standardized number of sites (n = 25 per habitat type) and number of captures (n = 30 per site) for beta and gamma diversity measures. For alpha diversity, I standardized number of captures per site (n = 30) but included all sites, as this measure was calculated for each site in isolation and therefore was not affected by the number of sites. I then repeated each analysis 50 times. I excluded any sites below the capture threshold. I chose this number of individuals as it allowed us to maximize the number of captures while preserving the greatest number of sites. Diversity measures displayed in the results section are an average across the iterations. To improve robustness of my results for subcommunity alpha, I interpolated to 30 captures and extrapolated to 200 captures using the package iNEXT (Hsieh et al., 2016). I conducted all analyses in R version 3.6.3 (R Core Team, 2020).

Shade and forest cover measurements

I investigated the effects of forest cover on birds in a subset of cocoa farms (n = 28; Fig. 2) for which I had canopy measurements. I considered the following spatial scales of forest cover: cover of the farm itself (~1.5 Ha; henceforth shade cover) and mean forest cover in a 1.4, 2.5 and 4 km radius surrounding the farm (henceforth forest cover). Shade cover was an indication of how intensely the farm was managed; traditional or shade farms preserved a mostly intact forest canopy, whilst in intensive or full-sun farms, shade trees were cut exposing cocoa trees to sunlight. Forest cover was a measure of how degraded the landscape was surrounding the farm.

To measure shade cover, I took photographs at 10 locations in each farm, spaced out by 24 m and at minimum 50 m from farm edge. I took photographs using a camera with a fish-eye lens on an extendable pole (5 m). Using the software ImageJ (Schneider et al., 2012), I converted the photographs to black and white, and then calculated the percentage of black (vegetation) in each photograph. The shade cover value used was a mean of the 10 pictures (Fig. 3).

To measure forest cover I used the percent tree cover layer of the MODIS Vegetation Continuous Fields (MOD44B; Townshend et al. 2011), which is published yearly and has a resolution of 250 m. I downloaded the MOD44B layer corresponding to 2018 (birds were captured 2017-2020). In QGIS 2.18.23 (QGIS Development Team, 2018) I created a 1.4, 2.5 and 4 km radius buffer around each farm and extracted the mean percentage tree cover from the pixels within the buffer. Shade cover measurements ranged from 19.6% in the most intensively managed farm to 98.7% in the least, and forest cover ranged from 9.0% in an urbanized area to 65.8% in a farm adjacent to a forest reserve.

To assess scale-dependency in bird responses to forest cover, I used buffers of three different sizes (1.4, 2.5, 4 km radii) centered on each of the 28 sampling sites. Ideally, I would use information on home range or dispersal distance of some of the commonly captured species to determine which spatial scales to use. However, for African rainforest birds these data are lacking, and I therefore selected the buffers based on the following information:

- 1.4 km radius: Peters et al. (2011) investigated the effect of forest cover at a range of spatial scales on the army ant *Dorylus wilverthi* in western Kenya, and found the 1.4 km radius to best predict ant abundance. Army ants are a keystone species in African rainforests, and their abundance drives the presence of ant-following and forest specialist bird species (Peters et al., 2011; Peters & Okalo, 2009).

- 2.5 km radius: Carrara et al. (2015) and Morante-Filho et al. (2015) found that rainforest birds in the Neotropics responded to forest cover at this spatial scale. Additionally, Jackson & Fahrig (2012) found that population abundance was best predicted by forest cover at a radius of 4-9 times the median dispersal distance of a species. Given that rainforest birds (especially insectivores and understory species) have relatively small dispersal distances (e.g., <400m; Powell et al., 2015), a radius of 2.5 km meets this rule of thumb.

- 4 km radius: this is the maximum scale used in Peters et al. (2011).

Data analysis

I used Generalized Linear Mixed Models (GLMMs) with a binomial distribution to investigate the differences in bird community between forest and cocoa, and to investigate the effect of shade and forest cover on bird community composition in the subset of 28 farms for which I had canopy cover data. I grouped visits to a site in the same season and year into one sample unit. I used relative abundance and relative species richness as response variables to allow for varying sample size. For the comparison between cocoa and forest, full models contained an interaction term between season and habitat (forest or cocoa), a fixed effect for region and random factors for site and year. For the cocoa shade and forest cover analyses, full models contained fixed effects for shade cover, forest cover and season, and random effects for site and year. I performed backwards model selection using Likelihood Ratio Tests on fully nested models (LRTs, cut-off probability P>0.05), until reaching a minimal adequate model.

Forest cover values across spatial scales were highly correlated (Spearman’s correlation coefficient 0.86 – 0.95), and therefore I conducted separate analyses for each scale. I used LRTs for backwards selection of minimal adequate models, and in the cases where forest cover was retained in minimal adequate models, I compared final models using Akaike's information criterion corrected for small samples (AICc; cut-off AICc<2). I used AICc for this final step rather than LRTs because models were not nested.

I used minimal adequate models to estimate coefficients; I report estimates and 95% confidence intervals. All GLMMs were ran using the package glmmTMB (Brooks et al., 2017) in R.

RESULTS

Bird diversity in cocoa plantations and mature forest

Metacommunity gamma diversity was higher in cocoa than in forest, though the difference became smaller at increasing values of q (Fig. 5a). At $q = 0$, gamma diversity in cocoa was 90.0 and in forest 71.0, and at $q = 2$ it was 12.8 in cocoa and 11.5 in forest. Subcommunity alpha diversity was similar between cocoa and forest across all values of q; after 30 captures at $q = 0$ cocoa reached 12.4 species and forest reached 12.2 species (Fig. 5b). I found similar results after extrapolating to 200 captures: at $q = 0$ cocoa plots contained 28.9 species (95% CI = 17.3, 40.5) and forest 26.8 (95% CI = 20.2, 33.2). Subcommunity gamma diversity was higher in cocoa than forest at low values of q, but became similar as q increased (Fig. 5c). At $q = 0$, subcommunity gamma in cocoa was 136.7 and in forest 100.2. Subcommunity representativeness was consistently lower in cocoa than in forest over all values of q; at $q = 0$ representativeness in cocoa was 0.61 and in forest 0.64 (Fig. 5d).

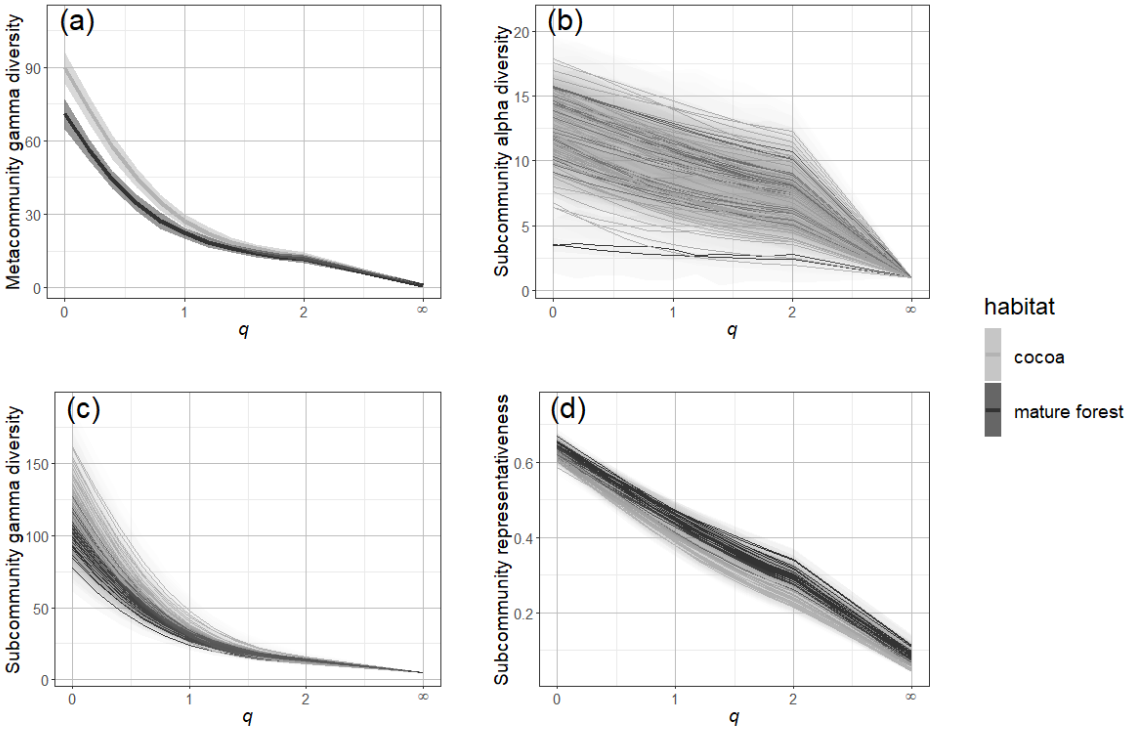

Figure 5. Measures of diversity in cocoa and mature forest sites across varying values of *q*: (a) Metacommunity gamma, (b) Subcommunity alpha, (c) Subcommunity gamma and (d) Subcommunity representativeness (a type of beta diversity; see Reeve et al., 2016*;* Appendix 3). Measures of gamma and beta diversity were calculated over n = 25 sites per habitat type and n = 30 captures per site, and alpha diversity was calculated for n = 30 captures per site. Shaded areas represent 95% confidence intervals derived from the 50 iterations of the analyses.

Community composition in cocoa plantations and mature forest

Bird communities in cocoa and forest differed in their composition (Fig. 6, Table 2, Appendix 4). Habitat was a significant variable in explaining the relative abundance of insectivores, forest specialists, ant-followers and mixed-flock species; these groups constituted a smaller proportion of all captures in cocoa farms than in forest. The largest effect size was for forest specialists, that made up 25% of captures in forest and 3% in cocoa. Frugivores constituted a larger proportion of total captures in cocoa farms than in forest, and occurred in higher relative abundance in the wet season.

Relative species richness of insectivores, ant-followers, mixed-flock species and forest specialists was significantly higher in forest than cocoa (Table 2, Appendix 4). Relative species richness of frugivores and nectarivores was higher in cocoa farms. For mixed-flock species and forest specialists, the effect of season on relative species richness depended on habitat; these groups made up a larger fraction of all captures in the wet season (compared with the dry season) in cocoa, but the opposite was true in the forest.

Species of conservation concern

All species captured were classed as ‘Least Concern’ according to the IUCN Red List, with the exception of Blue-moustached Bee-eater (*Merops mentalis*), listed as ‘Near Threatened’ and caught in mature forest (IUCN, 2020; Appendix 2). Congo Basin restricted birds occurred at higher relative abundance in forest than in cocoa; in forest they constituted 17% of captures (95% CI = 14.5, 20.1) and in cocoa 8% (95% CI = 6.5, 9.0; Appendix 4). Proportional species richness of Congo Basin restricted birds was also higher in forest compared with cocoa; they made up 19% of species in forest (95% CI = 16.9, 21.7) and 13% in cocoa (95% CI = 11.4, 14.5; Appendix 4).

Effect of farm shade on bird communities

Effects of shade cover on bird abundance varied between guilds (Fig. 6, Appendix 4). The only guild that decreased in relative abundance with increasing shade cover was frugivores, from 32% in full-sun farms to 24% in the most shaded farms. Ant-followers increased in relative abundance with shade cover; they constituted 0.2% of captures in sunny farms and 2% in shady farms. Forest specialists increased in relative abundance also with shade cover; shady farms had 5 times the relative abundance of forest specialists than full-sun farms. Mixed-flock species increased from 37% in full-sun farms to 55% in shady farms. Shade cover did not have an effect on the relative abundance of insectivores or nectarivores, or on the relative species richness of guilds.

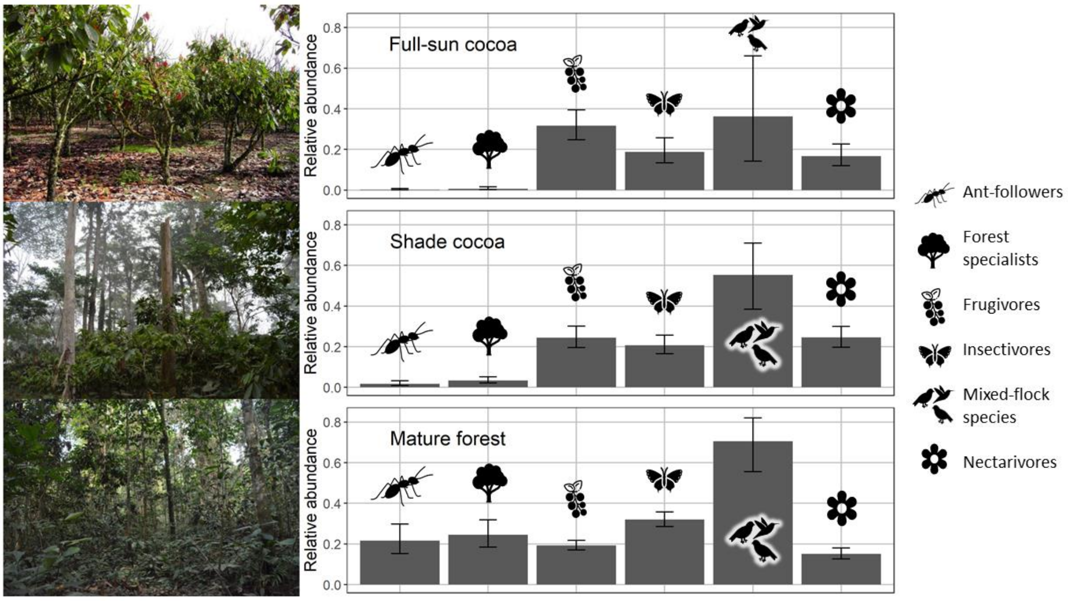

Figure 6. Relative abundance of foraging guilds in full-sun cocoa (20% shade cover), shady cocoa (90% shade cover) and mature forest. Shaded bars and error bars represent the fitted values and 95% confidence intervals from the minimal adequate models. Top photograph: (c) photo by Bea Maas - used with permission.

Effect of forest cover on bird communities

Model selection was consistent across scales, i.e., forest cover was either retained for all three scales or dropped. After selection, forest cover remained in models predicting the abundance and species richness of ant-followers and forest specialists. In every case, models including forest cover at 2.5 or 4 km radii were better at explaining abundance and species richness of these guilds, compared with the model containing forest cover at 1.4 km radius (Table 3). Though in some case the difference in AICc between the 4 km model and the 2.5 km one was < 2, I chose to present results for the 4 km radius because it was overall the better predictor of ant-follower and forest specialist relative abundance and richness.

Table 2. Relative abundance and species richness of feeding guilds in cocoa and mature forest as predicted by minimal adequate models.

		Cocoa			Forest			Dry			Wet		
Type of analysis	Response guild	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper
Abundance													
	Insectivores	0.2[a]	0.19	0.23	0.32	0.28	0.36						
	Forest specialists[b]	0.03	0.02	0.04	0.25	0.18	0.32	0.04	0.03	0.06	0.06	0.04	0.08
	Nectarivores[c]	0.18	0.16	0.21	0.15	0.13	0.18						
	Mixed-flock species	0.49	0.40	0.58	0.70	0.56	0.82						
	Frugivores	0.28	0.25	0.31	0.19	0.17	0.22	0.24	0.21	0.27	0.27	0.25	0.30
	Ant-followers	0.03	0.02	0.04	0.24	0.18	0.31						
Species Richness													
	Insectivores	0.30	0.29	0.33	0.41	0.38	0.43						
	Nectarivores	0.18	0.16	0.21	0.15	0.13	0.18						
	Frugivores	0.22	0.20	0.24	0.11	0.09	0.13						
	Ant-followers	0.11	0.10	0.13	0.26	0.23	0.29						
		Cocoa						Forest					
		Dry			Wet			Dry			Wet		
		Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper	Estimate	Lower	Upper

Species Richness													
	Mixed-flock species[d]	0.31	0.28	0.34	0.34	0.32	0.37	0.44	0.40	0.49	0.41	0.38	0.45
	Forest specialists	0.08	0.05	0.11	0.11	0.08	0.16	0.31	0.24	0.39	0.29	0.24	0.35

[a] Values displayed are the fitted values and 95% CIs predicted by the minimal adequate models. Where only habitat had a significant effect, there are two fitted values.

[b] In cases where both habitat and season had a significant effect on relative abundance, there are four fitted values.

[c] Habitat was not significant in the model predicting relative abundance of nectarivores

[d] For mixed-flock and forest specialist species richness, the interaction between habitat and season was retained in the minimal adequate model.

Table 3. After backwards selection, candidate models to explain abundance and species richness of ant-followers and forest specialists.

Response variable	Explanatory variables	AICc	ΔAICc
Ant-follower abundance			
	Shade cover + Forest cover 4 km	99.88	0.00
	Shade cover + Forest cover 2.5 km	101.72	1.84
	Shade cover + Forest cover 1.4 km	112.70	12.82
Forest specialist abundance			
	Shade cover + Forest cover 4 km	149.00	0.00
	Shade cover + Forest cover 2.5 km	150.84	1.84
	Shade cover + Forest cover 1.4 km	159.36	10.36
Ant-follower species richness			
	Forest cover 4 km	159.57	0.00
	Forest cover 2.5 km	162.40	2.83
	Forest cover 1.4 km	165.66	6.09
Forest specialist species richness			
	Forest cover 2.5 km	128.23	0.00
	Forest cover 4 km	128.44	0.21
	Forest cover 1.4 km	135.97	7.74

Ant-followers increased in relative abundance and species richness with forest cover (Fig. 7); their relative abundance increased from 0.1% to 6% with increasing forest cover, and their relative species richness increased from 5% in farms with low forest cover to 18% in farms with high forest cover. Forest specialists increased in relative abundance and species richness with forest cover (Fig. 7); their relative abundance increased from 0.7% in farms with minimum forest cover to 7% in farms with high forest cover, and their species richness increased from 1% at low forest cover to 19% at high forest cover. Forest cover did not significantly influence the relative abundance or species richness of insectivores, frugivores, nectarivores or mixed-flock species.

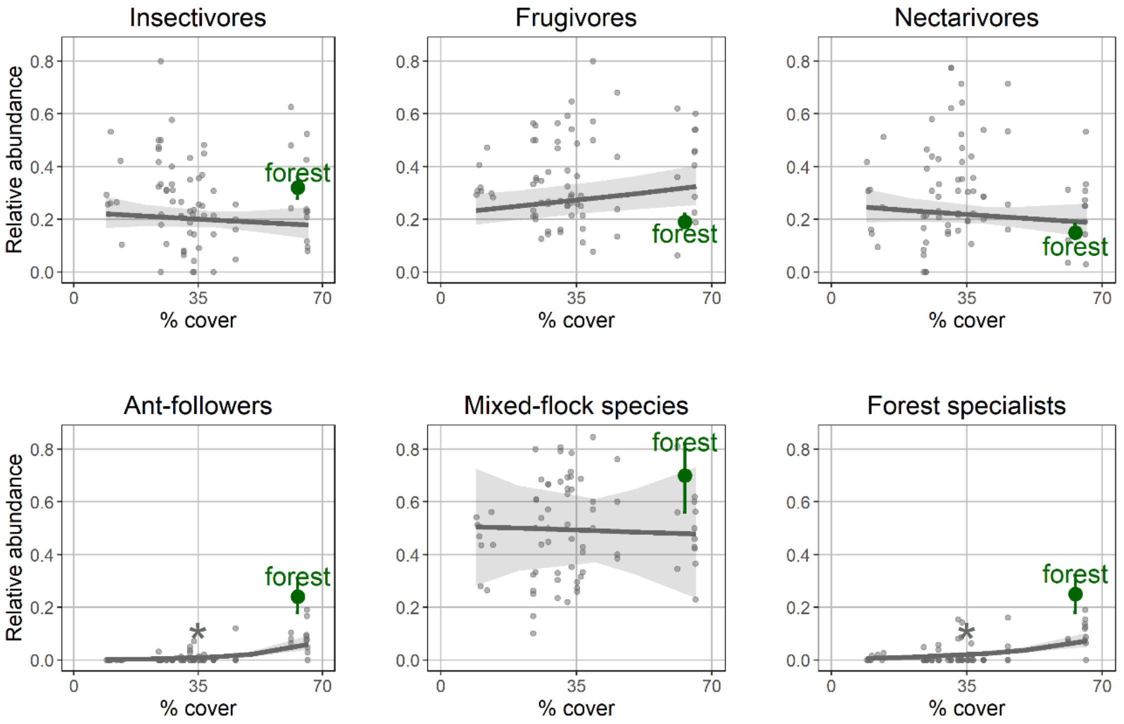

Figure 7. Effect of landscape forest cover (4 km radius) on the relative abundance of foraging guilds. The line indicates the effect size predicted by the minimal adequate model and the shading corresponds to the 95% CIs. The asterisks indicate statistical significance. The point represents the relative abundance of the corresponding foraging guild in mature forest, with associated CIs. The dots correspond to the raw data.

DISCUSSION

My study is the first to specifically examine African cocoa farms as habitat for birds. I found that sensitive guilds such as forest specialists and ant-followers represented a larger proportion of the community in shady farms compared with full-sun farms, and that these groups occurred at higher relative abundance in farms with high forest cover. In the current climate of agricultural intensification, my findings highlight the potential for farmland to be managed in favor of avian communities, and I provide further evidence of the importance of maintaining forested areas in the landscape.

I found that the cocoa-farms bird assemblage comprised more species than the forest assemblage. This could possibly be due to the variability of habitat characteristics in cocoa farms, which can range from full-sun scrubby plantations to shaded farms that are structurally similar to the forest (Sonwa et al., 2007; Tscharntke et al., 2011). Indeed, the lower representativeness of cocoa farms indicates that they were more dissimilar between each other compared with forest sites. These findings support Solar et al. (2015), who report increased beta diversity between secondary forest sites than between undisturbed forest sites. The authors argue that the higher between-site beta diversity of disturbed forests may attenuate species loss at a larger scale. However, though cocoa farms may contain more species that are rare across the metacommunity, these are likely not forest- or range-restricted species (Appendix 2). Indeed, there is an overall trend towards increasing generalist species in disturbed forest landscapes (Rutt et al., 2019). Therefore, whilst cocoa farms may play a role in the conservation of certain bird guilds, we must also prioritize protection of undisturbed primary forests that provide habitat for specialized species that do not frequently occur in modified habitats (Stratford & Stouffer, 2013; Tscharntke et al., 2011).

My results support Waltert et al. (2005), who found that species richness in Afrotropical forest did not differ between mature and agroforest. However, other studies showed different patterns. For example, Reitsma et al. (2001) found lower alpha and gamma diversity of birds in Costa Rican forest compared with managed cocoa, yet De Beenhouwer et al. (2013) found an 11% decrease in bird species richness from forest to agroforestry. Importantly, the diversity patterns I observed were affected by the *q* value. At higher values of *q*, gamma diversity became similar between forest and cocoa, indicating that both habitats contained a similar number of abundant species. Clear examples in forest were Fire-crested Alethe *(Alethe castanea)* and Yellow-lored Bristlebill *(Bleda notatus)*, two forest specialist species, that made up a considerable fraction of the community in almost all forest sites. My results demonstrate how conclusions about diversity can change depending on the measurement parameters. I argue that using a range of metrics and *q* values gives more detailed and useful information about a community's diversity.

The broad differences in community composition that I found between cocoa farms and forest are consistent with literature from across the tropics. The shift from forest to cocoa results in a decrease in insectivores, forest specialists and ant-followers and an increase in frugivores and nectarivores in the Neotropics (Faria et al., 2006; Rice & Greenberg, 2000) and Asia (Maas et al., 2016; Marsden et al., 2006). My findings contribute to a growing recognition that species loss in forested systems is linked to certain ecological guilds. Throughout tropical realms, distantly related species have evolutionarily converged on similar behaviors, such as ant-following and participating in mixed-species flocks, which reduce their resiliency to forest loss and habitat degradation (Powell et al., 2015).

I found that the community composition of birds in cocoa farms was significantly affected by shade and forest cover, with an increased relative abundance of forest specialists, ant-followers and mixed-flock species in shaded farms with high forest cover. Forest specialists are closely tied to vegetation structure (Powell et al., 2015; Stratford & Stouffer, 2013), especially with the understory, which is entirely removed in intensive cocoa plantations (Kessler et al., 2005). Additionally, habitat amount (e.g. proportion of forest in landscape) is important in determining bird abundance and richness, and this effect may be more pronounced in understory or forest specialist species (Carrara et al., 2015; De Camargo et al., 2018), explaining the increased relative abundance and diversity of these taxa with forest cover. Given the current rate of land-use change, forest birds are under severe threat and will likely undergo rapid species loss (Maas et al., 2009; Powell et al., 2015; Sekercioglu, 2012).

Ant-follower abundance is driven by the abundance of swarm-raiding army ants (Peters et al., 2008; Peters & Okalo, 2009). Ants are affected by farm management: Bisseleua et al. (2009) found that ant species richness was significantly higher in structurally diverse, low-intensity cocoa systems compared with intensive systems. Additionally, ants are affected by landscape-level processes, as their sensitivity to temperature limits their ability to move between habitat patches (Rizali et al., 2013). Therefore, shaded farms in forested landscapes likely contain a community of ants like that in the forest, in turn supporting the ant-following bird population. Mixed-flocks have hardly been studied in the Afrotropics (but see Péron & Crochet 2009; Cordeiro et al. 2015), but literature from other regions suggests that this guild is sensitive to disturbance (Goodale et al., 2015; Tien et al., 2005). Mixed-flock frequency and attendance seems to increase with vegetation density and structure, perhaps due to increased prey availability, reduced exposure to predators, and protection from climatic conditions (Tien et al., 2005).

Contrary to expectations, I found no effect of shade or forest cover on relative abundance or richness of insectivorous birds. This could be driven by species such as the Chestnut Wattle-eye *(Platysteira castanea)* and the Paradise Flycatcher *(Terpsiphone sp.)*, which occurred in relatively high abundances in most cocoa farms. Indeed, studies such as Waltert et al. (2005) and Sekercioglu (2012) suggest that small-bodied insectivores respond less to land-use change compared with large-bodied insectivores. From a human perspective, the presence of these small insectivores in cocoa farms could be beneficial due to their role in agricultural pest control (Karp et al., 2013; Maas et al., 2016).

In this study I was able to see general trends in bird communities in forest and cocoa through mist-net capture data. However, given the variable sampling effort, I was only able to consider relative abundance, which may not be representative of absolute abundance. Additionally, the abundance of species' can be a misleading indicator of habitat quality as human-modified habitats can act as population sinks or ecological traps (Johnson, 2007; Robertson & Hutto, 2006). Future studies in Afrotropical cocoa should consider demographic and morphological data to help establish the value of agroforestry systems as buffer habitat and wildlife corridors (Jarrett, Powell, et al., 2021; Schroth et al., 2004).

My study provides strong evidence that African cocoa plantations can be of value for conserving avian diversity. However, plantations need appropriate management if habitat is to be provided for forest bird communities. Low-intensity shaded cocoa not only provides habitat for forest birds and other vulnerable taxa, but can also produce high yields and farmer income, comparable to more intensive systems, thanks to lower pest burdens, longer productive lifespan of trees, and lower input costs (Armengot et al., 2016; Clough et al., 2011; Tscharntke et al., 2011). This dual function of cocoa agroforestry systems aligns with a land-sharing perspective, in which agriculture is managed at low-intensity and in favor of biodiversity. However, my results also demonstrate that even the shadiest cocoa farms are not equivalent to forest, and therefore I argue that within a land-sharing scenario there must be areas of forest preserved on the landscape. In conclusion, to prevent extreme deforestation and biodiversity loss in one of the world's diversity hotspots, policymakers should actively encourage ecologically sustainable agricultural practices such as shaded cocoa agroforestry that employs science-based management.

Chapter 3 | Integration of mark-recapture and acoustic detections for unbiased population estimation in animal communities

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ABSTRACT

Abundance estimation methods that combine several types of data are becoming increasingly common because they yield more accurate and precise parameter estimates and predictions than are possible from a single data source. These beneficial effects result from increasing sample size (through data pooling) and complementarity between different data types. Here, I test whether integrating mark-recapture data with passive acoustic detections into a joint likelihood improves estimates of population size in a multi-guild community. I compared the integrated model to a mark-recapture-only model using simulated data first and then using a dataset of mist-net captures and acoustic recordings from an Afrotropical agroforest bird community. The integrated model with simulated data improved accuracy and precision of estimated population size and detection parameters. When applied to field data, the integrated model was able to produce, for each bird guild, ecologically plausible estimates of population size and detection parameters, with more precision compared with the mark-recapture model. Overall, my results show that adding acoustic data to mark-recapture analyses improves estimates of population size. With the increasing availability of acoustic recording devices, this data collection technique could readily be added to routine field protocols, leading to a cost-efficient improvement of traditional mark-recapture population estimation.

INTRODUCTION

Evaluating trends in species abundance is central to questions of single species and whole ecosystem conservation. Hence, estimating the size of populations remains as critical as it is challenging. At the heart of the issue is that ecological sampling of organisms is rarely exhaustive, and therefore to estimate population size we need to also estimate probabilities of detection (Dorazio, 2014). Detectability may vary according to a wide range of variables, such as weather conditions or observer skill level. To help deal with imprecision and bias in data collection, there has been an upsurge in methods that combine different data sources to generate accurate and more precise estimates of species distribution and density (Fithian et al., 2015; Koshkina et al., 2017; Peel et al., 2019; Williams et al., 2017).

The concept of data integration (combining data types) relies heavily on complementarities between data sources. In general, different methods of data collection will suffer from different detection biases; for instance, it may be more likely that a species is detected by citizen science programs in areas with high human population density (Johnston et al., 2020), and it may be easier to detect animals on visual surveys in open compared to forested habitats (Rodrigues & Prado, 2018). Data integration helps deal with these biases, because shared biological parameters are estimated simultaneously from multiple data types that are not equally vulnerable to the same problems (Miller et al., 2019). Thus far, integrated models have largely focused on spatially explicit landscape-level models of species distribution, often generated using large online datasets. Whether data integration methods will be effective in estimating abundance of species in smaller-scale field-generated datasets is less clear (Isaac et al., 2020).

Mark-recapture has been employed for population estimation across a broad range of taxa including birds, mammals and fish (Schwarz & Seber, 1999). While mark-recapture analyses can provide robust estimates of population size, they can also suffer from biases, for instance when environmental covariates affect both detectability and population size (Banks-Leite et al., 2014; Oyster et al., 2018). Data integration methods can mitigate these problems and estimate the contributions of the different determinants of abundance and detection. In the case of mark-recapture, we could expect a benefit of combining these data with another type of data, ideally one collected using a method whose detectability is not influenced by the same variables.

Acoustic data could provide this opportunity. Acoustic recordings are usually collected using automated devices that are easy to operate, require low levels of effort (installation, collection, and storage), and can generate a wealth of data (Bradfer-Lawrence et al., 2020). However, abundance estimation from acoustics alone, though feasible, can be complicated due to either double-counting (overestimation) or saturation (underestimation) effects (Dawson & Efford, 2009; Doser et al., 2021). Additionally, to estimate abundance from acoustic data it is often necessary to know species' vocalization rates, which is typically not feasible. Combining mark-recapture with acoustics could result in improved estimates, partly because the factors affecting detectability of each method are different (Dawson & Efford, 2009). In a practical sense, simultaneously collecting both mark-recapture and acoustic data in the field is very achievable; mark-recapture protocols are already widespread, and adding an automatic recording unit to these systems is logistically simple and inexpensive (Whytock & Christie, 2017).

A recent study by Doser et al. (2021) combined acoustic data with point counts to estimate the abundance of a bird species and found that the integrated model improved accuracy and precision of results. Here, I build on the ideas of Doser et al. (2021) and take the next natural steps, from point counts to mark-recapture data (as is common in e.g., bird surveys) and from single species to whole communities. My modelling framework integrates mark-recapture data and count data from acoustic recordings to estimate population size of a multi-guild community. This method is widely applicable to any animal community for which mark-recapture and acoustic data are available. My aim was to assess whether the addition of acoustic data to mark-recapture models improved accuracy and precision of population size estimates, and to illustrate the application of the method to a dataset of bird communities in African agro-ecosystems.

METHODS

Model overview & assumptions

My model integrates mark-recapture and acoustic data into a joint likelihood, to estimate population size (N). My focus was on exploring the trade-offs and complementarities of the joint analysis of these two common data types, and I wished to isolate these issues from the wider problems of population change and emigration. Therefore, I assumed throughout that population size remained constant during each sampling period.

Determinants of population size

Throughout these analyses, I considered animal communities made up of several subgroups. I use the term 'guilds' to describe taxonomic groups, which may be species but could also be functional groups, families, etc. I considered site as the discrete area covered by the sampling radius of our mist-nets, and therefore the population size at site *j* is the number of animals whose home ranges overlap with this area. Importantly, I assumed that the detection radius of the acoustic recorder/s was the same or smaller than the mist-net sampling radius, so that the number of individuals detectable by acoustic recorders was proportional (but not necessarily equal) to the number of individuals detectable by mist-nets. I assumed that the population size (N_{ij}) of guild *i* at site *j* was Poisson distributed (but my method is easily adapted to other distributions) with expected number of animals per site D_{ij}.

$$N_{ij} \sim \text{Poisson}\left(D_{ij}\right) \quad \textbf{(3.1)}$$

D_{ij} was modelled as a log-linear function

$$\log\left(D_{ij}\right) = \sum_{q=0}^{Q_f} \nu_{iq} X_{jq} \qquad \textbf{(3.2)}$$

The linear predictor comprised Q_f covariates, X_{jq}, affecting population size, and their respective regression coefficients ν_{iq}, where q refers to the qth covariate (the intercept (ν_{i0}) was included by setting $X_{j0} = 1$).

Mark-recapture

Instead of dividing each survey event into arbitrary discrete time-periods as is commonly done in mark-recapture studies (Schofield et al., 2018), I modelled the capture history of every animal as a Homogeneous Poisson process (HPP) in continuous time. The HPP had a rate of r_{ij} captures per unit time (Xi et al., 2007), and the time period over which sampling occurred was T_j. The HPP process implies that the waiting time to first capture of an individual *k* of guild *i* at site *j* (c_{kij}) follows an exponential distribution with mean $1/r_{ij}$

$$c_{kij} \sim \text{Exponential}(r_{ij}) \qquad \textbf{(3.3)}$$

By definition, if $c_{kij} > T_j$ the animal was not detected. The probability of detection is then $P\left(c_{kij} < T_j\right) = 1 - \exp\left(-r_{ij}T_j\right)$. Therefore, the total number of first captures n_{ij} for the *i*th guild at the *j*th site was

$$n_{ij} \sim \text{Binomial}(N_{ij}, 1 - \exp\left(-r_{ij}T_j\right)) \qquad \textbf{(3.4)}$$

After the animal was caught once, the total number of recaptures (y_{kij}) in the remaining time (conditional on $c_{kij} < T_j$) was a Poisson variate given by

$$y_{kij} \sim \mathrm{Poisson}(r_{ij}(T_j - c_{kij})) \qquad \textbf{(3.5)}$$

Capture rate, r_{ij}, was modelled as a log-linear function

$$\log{(r_{ij})} = \sum_{q=0}^{Q_h} \rho_{iq}\, W_{jq} \qquad \textbf{(3.6)}$$

comprising Q_h covariates, W_{jq}, and their respective regression coefficients ρ_{iq}, with q referring to the q^{th} covariate and where ρ_{i0} is the intercept. This mark-recapture model assumes that capture rate did not vary between individuals of same guild, did not decline with consecutive captures, and marks were not lost. Additionally, I assumed instantaneous sampling (i.e., individuals were immediately available for sampling after capture).

Acoustics

I assumed that it was not possible to identify individuals from acoustic data (but see Dawson & Efford, 2009). Additionally, non-automated counting of vocalizations over a whole community from acoustic recordings would require large amounts of processing time. Therefore, to simplify data extraction, I considered a set of L_j discrete listening periods each lasting *M* time units, during which guilds may be heard and thus recorded as present. I modelled vocalizations as a HPP in continuous time with rate $\lambda_{ij}N_{ij}$ per unit time, where λ_{ij} was a site/guild-specific per-capita vocalization detection rate. The probability that at least one vocalization was recorded in any given listening period was the probability that the time to the first vocalization was less than *M*. I modelled the total number of detections a_{ij} over L_j listening periods as

$$a_{ij} \sim \mathrm{Binomial}(L_j,\ 1 - \exp{(\lambda_{ij}N_{ij}M)}\,) \qquad \textbf{(3.7)}$$

Vocalization rate, λ_{ij}, was modelled as a log-linear function

$$\log{(\lambda_{ij})} = \sum_{q=0}^{Q_r} \psi_{iq}\, G_{jq} \qquad \textbf{(3.8)}$$

comprising Q_r covariates, G_{jq}, and their respective regression coefficients ψ_{iq}, with q referring to the *q*th covariate, and ψ_{i0} the intercept.

I assumed that the probability of capturing an individual bird was independent of the probability of it being detected by the acoustic recorder, and consequently the mark-recapture and acoustic models were independent, both conditional on the true latent population size N_{ij} (Miller et al., 2019). I fit my 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, 2020). For each model, I ran three chains of 100,000 iterations with a burn-in period of 5,000 iterations. Model convergence was assessed by visually inspecting chains and with the Gelman-Rubin R-hat diagnostic, with convergence presumed when R-hat < 1.1.

Simulation study

To assess whether the integrated model produced more accurate and precise estimates compared with single-dataset models, I compared it with a model that used just mark-recapture data (Equations 3.1-3.6). I applied each model to simulated data from 20 sites each assumed to contain 3 guilds (labelled A, B and C), and to have been visited twice. This represents a minimally realistic design for a mark-recapture study, given the number of guilds and parameters involved. I included several environmental covariates: the first was a site-specific covariate that affected both population size and capture rate (Equations 3.2 & 3.6). I added this covariate because previous models have encountered identifiability issues when retrieving covariates that affect both population size and detectability (Fithian et al., 2015; Simmonds et al., 2020). The second covariate affecting population size was shared across guilds and sites but varied with visit (Equation 3.2). I generated data using the model statements above and used the same priors for both models (see Table 4 for parameter values and priors). At each site, capture period T_j was set to 6 hrs, and I assumed 20 listening periods (L_j) each lasting 0.03 hours (2 mins; M). For both models I examined accuracy and precision by recording the mean and 95% Bayesian credible intervals (BCIs; calculated for the highest posterior density intervals) from each posterior.

Effort analysis

I investigated the effect of sampling effort (both in mist-netting and acoustic recording) on model performance. Using the same population size and detection parameters as in the simulation study, I generated data corresponding to a range of 1 – 30 sampling hours (at intervals of 5 hrs) both for mist-netting and acoustic recordings. For mist-netting, the effort hours corresponded to the hours during which mist-nets are open. For acoustic recording, as processing the recordings can be time-consuming, I assumed that for every 1hr of recording I would need 2hrs of processing (this is a conservative estimate, our experience is more in the range of 1.4hrs of processing per recording hour). In other words, the actual field sampling hours used in the effort analysis were 1 – 30 for mist-netting and 1 – 10 for acoustic recording. I generated data for 36 combinations of these values and fit the integrated model to the resulting datasets. For each combination of values, I ran the model with three chains of 5,000 iterations with a burn-in period of 5,000 iterations and a thinning rate of 10.

I evaluated the results in terms of accuracy and precision: I examined accuracy by calculating the % bias of the posterior mean (i.e., 100 × (Estimated mean-True mean)/True mean) and I considered precision as the coefficient of variation (i.e., SD/Mean) of the posterior distribution. I used the coefficient of variation (CV) to measure precision (rather than BCIs as above) to make the measures comparable across different scenarios.

Model verification

To understand the sensitivity of the integrated model to variation in the main data generating parameters (linear predictors for capture and vocalization rate ρ_{i0} and ψ_{i0}), I simulated 121 combinations of parameters ρ_{i0} and ψ_{i0} ranging from -8 to -2 and -3.9 to 2 respectively, corresponding to rates in the range ~0 and 0.14 per capita captures per hour, and 0.02 and 8 detected vocalizations per hour. From each parameter combination I simulated 100 datasets, resulting in a total 12100 datasets. For this analysis, I used a simplified version of the simulation, looking at one site containing one guild, removing the covariates affecting N, ρ_{10} and ψ_{10}. I set the underlying population size N to be 50 in every case. For model fitting I set normally distributed priors N(0, 4.5) and N(-5, 4.5) for ρ_{10} and ψ_{10} respectively (mean and SD), and N(4.4, 4.5) for ν_{10}. For each combination of parameters, I ran the model with three chains of 5,000 iterations with a burn-in period of 5,000 iterations and a thinning rate of 10. I evaluated the results in terms of accuracy and precision: I calculated accuracy as a percentage (as above) and I considered precision as the CV.

Case study

Field methods

Mist-netting and acoustic data were collected from birds in 28 cocoa farms and 4 primary forest sites in Cameroon over 4 years (2017 – 2020; Fig. 2). Each of the 32 sites was visited between 2 and 6 times, in two different seasons. Sites were separated by at least 500 m and farms were at least 1.5 ha. Mature forest plots were in the Dja Faunal Reserve (3.19 N 12.81 E) and were at least 1 km from forest edge, had a closed canopy and no logging activity. Sites had varying canopy cover, which I predicted could influence both capture rate and population size (Fig. 3). In cocoa farms, canopy cover is an indication of farm management; more intensively managed farms tend to have open canopies, whilst traditional agroforest farms have closed canopies.

At each site 20 12 x 3 m mist-nets (30 mm mesh) were set up, placed in a "T", "L" or "+" layout to fit the site boundaries (for farms). They were opened for 6 hrs (~6.20 am to 12.20 pm; T_j = 6), during which captured individuals were identified, ringed and then released. The Handbook of the Birds of the World (del Hoyo et al., 2019) was used to classify each species according to its primary food type, resulting in 6 mutually exclusive categories: insectivores, frugivores, nectarivores, ant-followers, granivores and other (including carnivores and piscivores; Jarrett, Smith, et al., 2021). Though the categorization of species into guilds may mask some variability between species, it also makes parameter estimation a lot more feasible given the low number of captures for some species. I excluded any birds caught outside the 6hr sampling period. I considered recaptures as birds caught more than once during the same visit, but I excluded recaptures caught within 20 mins of release as this could indicate birds that flew straight back into nets due to disorientation or stress.

On the same day as the mist-netting, one automatic recording unit (ARU; Song Meter SM4, Wildlife Acoustics) was set up approximately at the center of mist-net transect, and programmed to record 6.30-6.40 am and 7.30-7.40 am. Due to the short time window over which acoustic data were extracted, I did not expect vocalization rate to vary temporally (as would be commonly expected if recordings covered e.g., whole day). The 20 min period was then divided into 1 min intervals (L_j = 20, M = 0.03; Equation 3.7), during which each species was recorded either as present (when a call was heard) or absent. The acoustic data processing was done manually by one listener. The use of intervals was to facilitate data extraction from continuous recordings. I clumped species into the same 6 guilds applied to mist-net captures, and I excluded from the dataset any species that had never been caught in mist-nets (e.g., canopy species).

To measure canopy cover, photographs were taken at 10 locations in each site (corresponding to the center of every second mist-net), spaced out by 24 m and at minimum 50 m from farm edge. Photographs were taken using a camera with a fish-eye lens on an extendable pole (5 m) in order to extend above the cocoa trees growing in the understory. Using the software ImageJ (Schneider et al., 2012), I converted the photographs to black and white, and then calculated the percentage of black (vegetation) in each photograph. The shade cover value used was a mean of the 10 pictures. Sites were on a gradient of canopy cover, with values ranging from 19.6% to 100% (Fig. 3).

Model structure

Population size of each of the 6 bird groups at each sampling event z was modelled with a guild-specific intercept (ν_{i0}) and two covariates ($Q_f = 2$): a guild-specific effect of canopy cover (continuous variable, centered and standardized) on population size ($\nu_{i1}X_{j1}$) and a seasonal categorical covariate shared between guilds ($\nu_2 X_{z2}$, where $X_{z2} = 1$ if Dry and 0 otherwise; Equation 3.10).

$$N_{ijz} \sim \text{Poisson}\left(D_{ijz}\right) \quad \textbf{(3.9)}$$

$$\log\left(D_{ijz}\right) = \nu_{i0} + \nu_{i1}X_{j1} + \nu_2 X_{z2} \quad \textbf{(3.10)}$$

I modelled total captures for each sampling unit as in Equation 3.4 and individual bird capture histories with Equation 3.5. I considered capture rate r_{ij} to be guild-specific and to vary between sites according to canopy cover ($Q_h = 1$; Equation 3.11), and I considered vocalization detection rate to be guild-specific but not influenced by detection covariates ($Q_r = 0$; Equation 3.12).

$$\log\left(r_{ij}\right) = \rho_{i0} + \rho_1 W_{j1} \quad \textbf{(3.11)}$$

$$\log(\lambda_i) = \psi_{i0} \quad \textbf{(3.12)}$$

I modelled number of vocalizations with Equation 3.7.

Priors used for model fitting were normally distributed (Appendix 6). To compare the performance of integrated vs single-dataset models, I fit a model that used only mark-recapture data. For both models I recorded parameter estimates and BCIs to assess posterior precision of one method relative to another.

RESULTS

Simulation study

The results from testing my model on simulated mark-recapture and acoustic data demonstrated that overall, the integrated model more accurately estimated all relevant parameters: capture rates, vocalization rates, detection covariate and covariates affecting population size (Fig. 8; Table 4). Compared with the mark-recapture model, the estimates of population size from the integrated model were more accurate and precise (Appendix 5). The simulation also confirmed that the parameter estimates from the integrated model were more accurate and more precise (Fig. 8; Table 4). The single-dataset mark-recapture model estimated with low precision the coefficients corresponding to the covariate that affected both population size and capture rate (ν_1 and ρ_1). For these two coefficients, the integrated model was >2 times more precise than the mark-recapture model (Fig. 8).

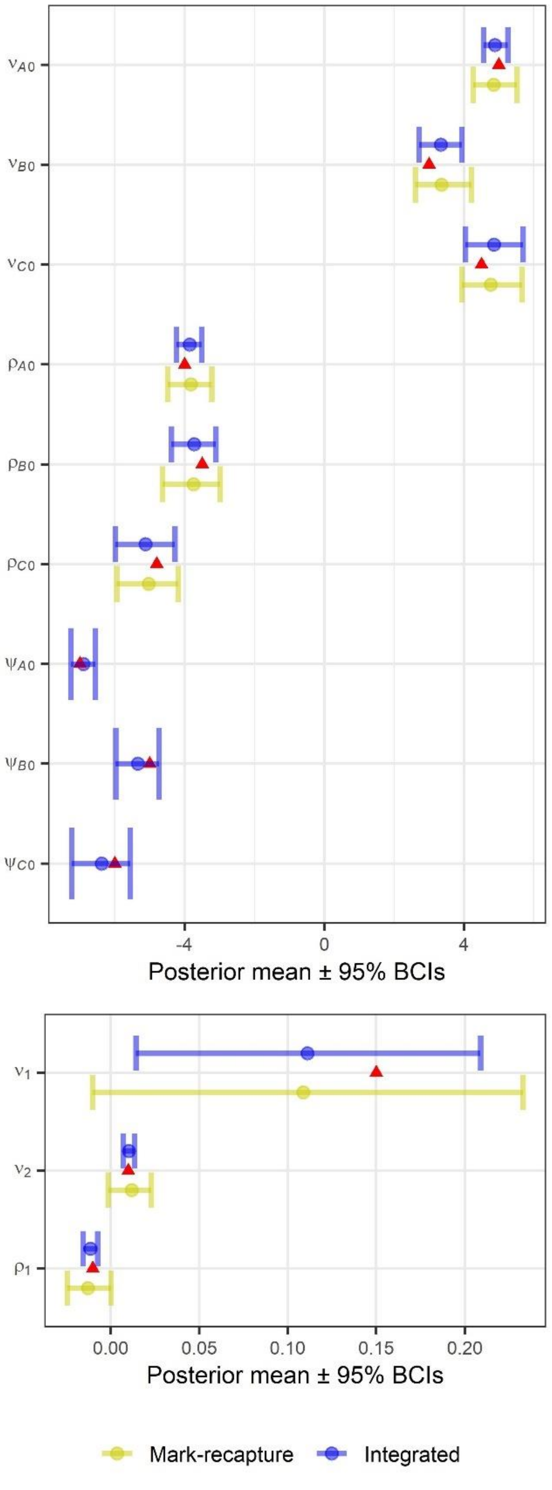


Figure 8. Mean of posterior distribution (and 95% BCIs) for population size and detection parameters from mark-recapture only model and integrated model under simulation. Only the integrated model (with acoustic data) calculated vocalization rates. The triangles represent the simulation values. For parameter definitions see Table 4.

Table 4. For each parameter in model: true value used to simulate data, prior (standard deviation), and mean (95% Bayesian Credible Intervals) of parameter estimates from model with only mark-recapture data and integrated model. The distribution of the priors was normal, in every case. See Equations 3.1-3.8 for further details.

Parameter	**Description**	**Simulation value**	**Prior (SD)**	**Capture-recapture**	**Integrated**
ν_{A0}	Intercept of linear predictor of population size for species *A*	5.00	6.00 (0.82)	4.85 (4.26, 5.52)	4.88 (4.55, 5.25)
ν_{B0}	Intercept of linear predictor of population size for species *B*	3.00	6.00 (0.82)	3.36 (2.61, 4.21)	3.34 (2.72, 3.94)
ν_{C0}	Intercept of linear predictor of population size for species *C*	4.50	6.00 (0.82)	4.77 (3.94, 5.65)	4.86 (4.04, 5.70)
ν_{1}	Effect of site-level covariate X_{j1} on population size	0.01	0.00 (1.00)	0.01 (0, 0.02)	0.01 (0.01, 0.01)
ν_{2}	Effects of visit-level covariate X_{2} on population size	0.15	0.00 (0.20)	0.11 (-0.01, 0.23)	0.11 (0.01, 0.21)
ρ_{A0}	Intercept of linear predictor of capture rate for species *A*	-4.00	0.00 (3.16)	-3.82 (-4.49, -3.22)	-3.86 (-4.23, -3.5)
ρ_{B0}	Intercept of linear predictor of capture rate for species *B*	-3.50	0.00 (3.16)	-3.75 (-4.64, -2.98)	-3.75 (-4.43, -3.10)
ρ_{C0}	Intercept of linear predictor of capture rate for species *C*	-4.80	0.00 (3.16)	-5.04 (-5.95, -4.19)	-5.13 (-5.99, -4.28)
ρ_{1}	Effect of site-level covariate W_{j1} on capture rate	-0.01	0.00 (1.00)	-0.01 (-0.02, 0)	-0.01 (-0.02, -0.01)
Ψ_{A0}	Intercept of linear predictor of vocalization rate for species *A*	-7.00	-5.00 (2.00)		-6.9 (-7.26, -6.56)
Ψ_{B0}	Intercept of linear predictor of vocalization rate for species *B*	-5.00	-5.00 (2.00)		-5.35 (-5.98, -4.74)
Ψ_{C0}	Intercept of linear predictor of vocalization rate for species *C*	-6.00	-5.00 (2.00)		-6.38 (-7.24, -5.56)

Effort analysis

Accuracy was highest at >20 mist-netting hrs, with little effect of listening effort. However, at <10 mist-netting hours, increasing listening effort improved accuracy (Fig. 9). A similar trend was true for precision (Fig. 9). Models with <5 mist-netting hours consistently failed to converge, and models with <10 mist-netting hours converged only when there were more than 5 listening hours (Fig. 9).

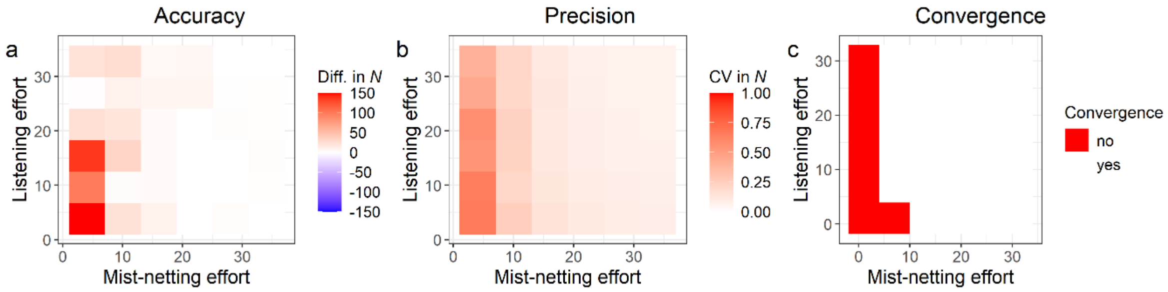


Figure 9. Accuracy (a) and precision (b) of posterior distributions for bird population size (N) across different effort scenarios, and model convergence across those same scenarios. I calculated accuracy (labelled ‘diff.’) of the posterior mean as $100 \times (Mean - Truth)/Truth$), and I considered precision as the coefficient of variation (CV) of the posterior distribution. I considered that a model achieved convergence if the Gelman-Rubin R-hat diagnostic for all model parameters was <1.1.

Model verification

Accuracy in the mean of the posterior distributions for N, ρ_0 and ψ_0 was affected by the parameter values given to ρ_0 and ψ_0 in the simulation. The mean of the posterior distributions deviated from the given value by a maximum of -47.3%, 24.9%, and 25.3% for N, ρ_{10} and ψ_{10} respectively (Fig. 10a-c). Accuracy in the mean of the posterior distribution for N increased with increasing values of ρ_{10} and ψ_{10}, more steeply with the former. N was consistently underestimated, likely due to the priors for the detection rate parameters; these were centered around 0, and an overestimation of ρ_{10} and ψ_{10} would result in an underestimation of population size. The ability of the model to retrieve parameter ρ_{10} remained relatively similar across the range of parameter values, whilst the accuracy in the estimation of ψ_{10} decreased at high values of ψ_{10}. Both parameters were consistently overestimated when at low values, likely due to the influence of their priors (centered at 0).

In terms of precision, the CV of the posterior distributions of N, ρ_{10} and ψ_{10} had maximum values of 0.68, 0.37 and 0.49, respectively (Fig. 10d-f). Precision in the estimate for N was lowest when both ρ_{10} and ψ_{10} were small, and a similar pattern was true for the estimation of ρ_{10}. For ψ_{10}, precision was consistently high until approximately -3.5, after which it decreased. All parameter combinations resulted in model convergence.

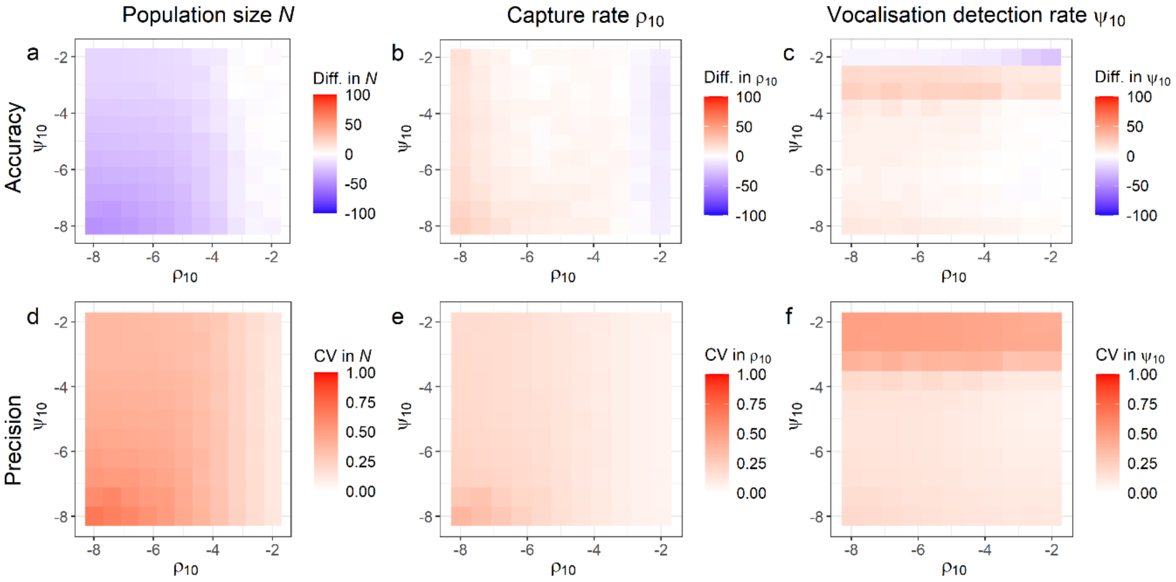


Figure 10. Accuracy (a – c) and precision (d – f) of posterior distributions for bird population size (N), capture rate (ρ_{10}) and vocalisation detection rate (ψ_{10}) from 1150 simulations generated using varying values for ρ_{10} and ψ_{10}, with N = 50, and replicated 10 times. I calculated accuracy (labelled ‘diff.’) of the posterior mean as $100 \times (Mean - Truth)/Truth$), and I considered precision as the coefficient of variation (CV) of the posterior distribution.

Case study

I fit my integrated and single-dataset models to mist-netting and acoustic data from Cameroonian cocoa farms and forest sites. Compared with the mark-recapture only model, the integrated model produced more precise estimates for model parameters and population size (Fig. 11; Appendix 6). The integrated model estimated with ~1.5 times more precision parameters ν_{i1}, which quantify the effect of canopy on population size of each guild. Estimated population sizes of bird guilds were 165 – 233 for frugivores, 67 – 102 for insectivores, 133 – 143 for nectarivores, 3 – 13 for ant-followers, 20 – 41 for granivores and 67 – 83 for other. The effect of canopy cover on abundance was different between groups (Fig. 11); frugivores, insectivores and granivores decreased with increasing canopy cover, whilst ant-followers showed the opposite trend. Nectarivores and other birds were largely unaffected by canopy cover (Fig. 11). Abundance was ~1.3 times higher in the dry season compared with the wet season. Capture rate decreased with increasing canopy cover and vocalization detection rate ranged from 0.003 in nectarivores to 0.02 in granivores.

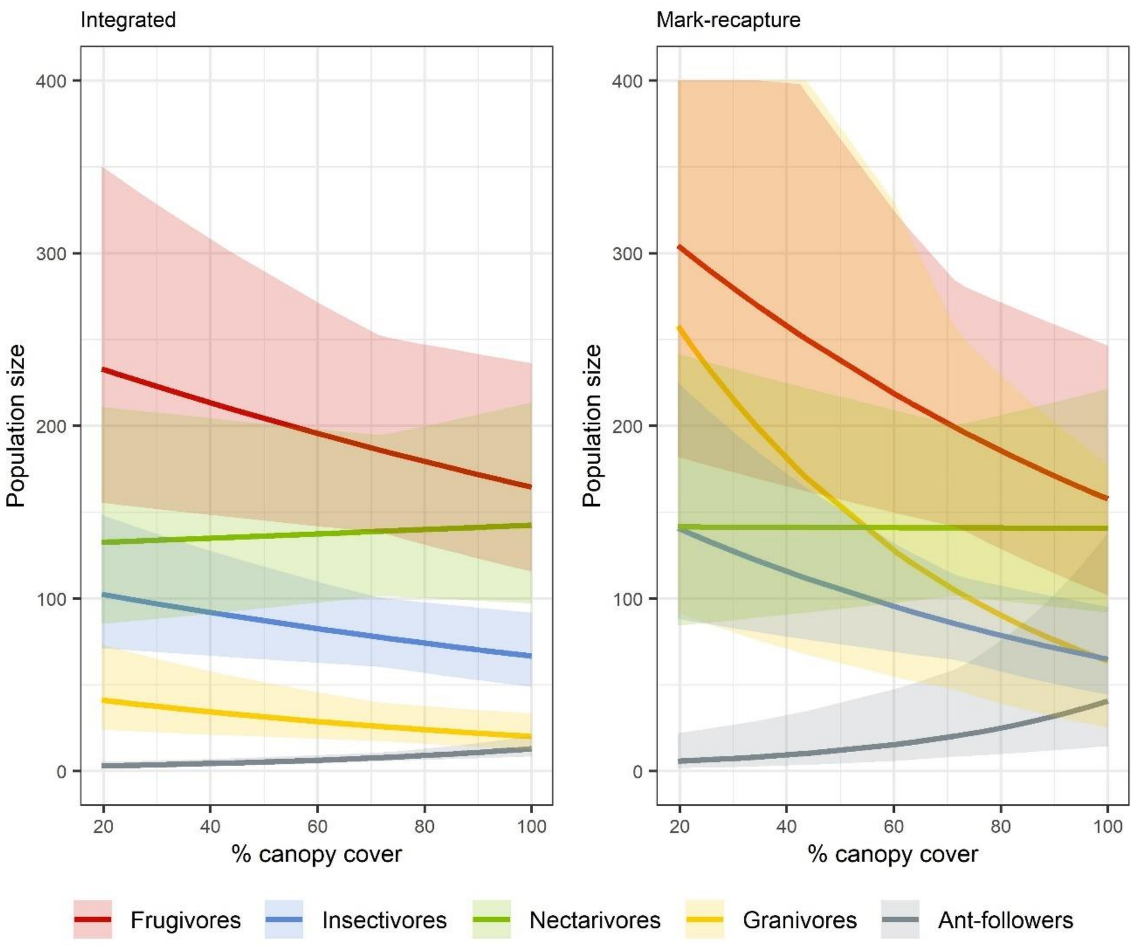


Figure 11. Population size (mean and 95% BCIs) of bird guilds with canopy cover in Cameroonian cocoa farms and forest in the dry season, estimated from both mark-recapture model and integrated model. The guild ‘other’ was excluded from plots for the purpose of visual clarity.

DISCUSSION

The improved accuracy and precision of parameter estimates resulting from my integrated model compared with the simpler model match previous findings using different types of data (Doser et al., 2021; Fithian et al., 2015; Koshkina et al., 2017; Pacifici et al., 2017; Peel et al., 2019). However, the superior performance of integrated models should not be taken for granted, especially in scenarios like my own, where sample sizes are relatively small and there is overlap between detection and environmental covariates (Simmonds et al., 2020). Simmonds et al. (2020) found that when combining simulated presence-only (PO) and presence-absence (PA) data, an integrated model only outperformed a simple model (just PA) beyond a certain sample size threshold. Additionally, they found that the PA-only model was more accurate in predicting an environmental covariate if that covariate also influenced detection probability (Simmonds et al., 2020). In contrast, also using simulated PA and PO data, Peel et al. (2019) found little influence of sample size on accuracy or precision of the estimates from an integrated model. Overall, it appears that the effectiveness of integrated models at estimating parameters is variable and dependent on specific characteristics of the data used.

Doser et al.'s (2021) recent study deftly integrated point counts and acoustic surveys to estimate the abundance of a single bird species. They found that the integrated model produced more accurate and precise results compared with single-dataset models. Aside from the key difference in data types used (count vs mark-recapture) and the single- vs multi-guild element, there were several additional differences between my approach and that of Doser et al. (2021). First, my model allows for covariates that are specific to each sampling instance, and therefore does not assume that populations stay constant between visits. Second, my formulation in continuous time allows for more flexibility in sampling intervals and covariates. Third, the processing of acoustic data was undertaken differently (semi-automatic clustering algorithm vs manual identification), resulting in potential false positives in Doser et al.'s (2021) study but not in mine. Finally, Doser et al. (2021) did not include covariates that simultaneously affected detectability and population size. I conjecture that mark-recapture data may provide a significant advantage when it comes to estimating population size given these confounding covariates.

When applied to a real-life scenario of bird populations, my integrated model produced relatively precise and ecologically plausible estimates. The estimated population size for the different feeding guilds were consistent with other studies from the tropics (Newmark, 2006), and the relative abundance of each guild matched previous knowledge from the system (Jarrett, Smith, et al., 2021). The largest difference between the integrated and mark-recapture models was in the population size estimate for granivores, likely because granivores were not commonly caught in mist-nets, yet had high vocalization rates, and therefore acoustic data for this species were rich.

The integrated model benefitted from borrowed strength between species, both in the observation and process components. In my observation model, species shared the effect of canopy cover on capture rates, and in the process model species shared a seasonal trend. This is a small example of strength borrowing in a multi-species framework – an approach carried out at much greater depth by Ovaskainen & Abrego (2020) amongst others. An additional benefit of my integrated model is that it provides potentially valuable information on species' vocalization rates.

To test the effectiveness of integrating data I wished to remove the additional confounding factors of demographic processes. I therefore assumed that the population remained closed within each sampling period. Given the small sampling intervals used in the survey (6hrs), this assumption is reasonable, but a natural extension of my model would be to consider longer sampling periods over which demographic processes occur. Additional extensions to this model could consider longitudinal effects such as capture shyness, which can be a common phenomenon in active trapping methods such as mist-netting (Marques et al., 2013), and daily fluctuations in bird activity (especially vocalization). Despite these simplifying assumptions, my model provides a practical and expandable way to improve estimates of population size for small-scale field studies. In general, adding an acoustic recording protocol to field surveys requires low effort and is relatively inexpensive (Bradfer-Lawrence et al., 2020; Whytock & Christie, 2017). The addition of acoustic data may be especially beneficial when mark-recapture effort is limited (e.g., small number of visits) or when capture rates are low. While identification of species from acoustic recordings can be a time-consuming bottle-neck, the increase in popularity of acoustic methods is resulting in more and more tools that help with this process (Darras et al., 2020).

In conclusion, the combination of acoustic and mark-recapture data offers an opportunity for more accurate and precise estimates of population size. This method can be applied to any taxa for which these data types are available, including birds, bats, cetaceans, and amphibians. To achieve accurate estimates of population size, we should move towards a modelling approach that accounts for possible biases and makes the most of available data.

Chapter 4 | Fewer pests and more ecosystem service arthropods in shady African cocoa farms: Insights from a data integration study

ABSTRACT

Agricultural intensification is leading to conversion of cocoa agroforestry to monocultures across the tropics. Arthropod communities in cocoa agroforestry 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 (species that consume pests) have the potential to enhance agricultural yields. Understanding how intensification of cocoa farms affects different arthropod groups is therefore important in maximising the abundance of beneficial arthropod groups and reducing pest burdens. However, little is known about the influences of agricultural intensification on tropical arthropod communities, especially in Africa, in which ~70% of the world's cocoa is produced. Additionally, 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 meaningful comparison between arthropod taxa, and therefore the study of community dynamics. Additionally, combining the data from the different methods would increase precision (due to larger pooled sample size). Here, I 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 (a proxy for management intensity). My results show that eight of eleven arthropod taxa responded to farm shade cover; importantly, brown capsid (primary pest of cocoa), Coleoptera pests and Hemiptera pests increased with increasing management intensity, whilst Araneae (natural enemies) and Diptera (potential pollinators) were more abundant in shady farms. My study provides novel insight into management-induced changes in arthropod communities in African agroforestry, and establishes a method to estimate population size of arthropod taxa. My findings shed light on the risks associated with the current push towards high-intensity cocoa farming in Africa.

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; Tscharntke et al., 2012). Currently, 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; Tscharntke et al., 2011). Thus, identifying the optimal approach to sustainable management requires better understanding of the effect of agricultural intensification on arthropod communities (Janssen & Rijn, 2021; Niether et al., 2020).

One aspect of optimising management for improved yields is understanding how to enhance natural provision of ecosystem services (Bisseleua et al., 2013; Toledo-Hernández et al., 2021). Certain arthropod groups provide essential ecosystem services, such as pollination, which have the potential to greatly increase yields (Toledo-Hernández et al., 2020). Understanding how management influences both beneficial arthropod groups and pests is therefore essential to achieve a desirable balance between potential services and dis-services in agroecosystems.

Agroforestry, the practice of growing crops under a canopy of shade trees, is a common form of food production in tropical regions, in part 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; Tscharntke 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). Though cocoa is traditionally grown under shady conditions, recently there has been a noticeable shift towards more intensively managed monocultures, in which cocoa trees are planted in clear-cut patches of land (Armengot et al., 2016; Tscharntke et al., 2011). This expansion and intensification of cocoa agriculture has led to massive deforestation in countries such as Côte d’Ivoire (Barima et al., 2016;

Maclean, 2017). While 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; Tscharntke et al., 2011). However, most of the research into cocoa management and its relationship to biodiversity and productivity comes from the Neotropics and South East Asia (Bisseleua et al., 2013), and the African cocoa belt comprises different common management practices as well as a different arthropod community (Bagny et al., 2018; Bisseleua et al., 2013).

In Africa, the main cocoa pests are the brown capsid *Sahlbergella singularis* (Hemiptera: *Miridae*; Bagny Beilhe et al., 2018), as well as other Hemipteran groups such as Mealybugs (Hemiptera: *Pseudococcidae spp*.) and Mosquito capsids (Hemiptera: *Afropeltis spp*.). These pests are still among the most important factors limiting cocoa production, causing annual crop losses of about 25 to 40% (Wessel & Quist-Wessel, 2015). Hemipteran bugs tend to occur at higher abundances in sunnier farms, though evidence supporting this is still limited (Bagny Beilhe, Babin, et al., 2018). While 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 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 (Toledo-Hernández et al., 2021). Natural enemies such as ants and spiders may provide pest suppression in cocoa agroforestry, and there is some indications that these groups show a preference for shadier farms (Bisseleua et al., 2017).

One major limitation in our current understanding of arthropod communities is that it is almost entirely based on relative measures of abundance, rather than absolute population sizes (Didham et al., 2020). Until now, arthropod surveys commonly involve different methods to target different groups, and then interpret the resulting data as proxies to investigate trends within groups across time or space (Didham et al., 2020; Montgomery et al., 2021). This approach has two main limitations: first, using data from each survey type independently results in smaller effective sample sizes, thus reducing the potential precision of results for a given level of survey effort (Kindsvater et al., 2018). Second, this approach does not involve estimating detection probabilities, and results in proxies for abundance for each group that are not corrected for detectability and therefore not directly comparable between taxa. The use of proxies rather than absolute abundances limits the applications of these data; of special importance is the study of arthropod community dynamics, which requires data on population size comparable between taxa (Curtsdotter et al., 2019). Studying community dynamics is the most effective method to understand the mechanisms driving arthropod community composition and the implications in terms of ecosystem services (Curtsdotter et al., 2019; Janssen & Rijn, 2021; Kawatsu et al., 2021; Tipping et al., 2016). In these complex systems 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). Lack of information on arthropod group population size could lead to ineffective management due to targeting unimportant groups (Janssen & Rijn, 2021), targeting important groups at the wrong time of year (Mahob et al., 2011), or missing opportunities for natural enhancement of yields via arthropod-provided ecosystem services (Janssen & Rijn, 2021; Niether et al., 2020; Tscharntke et al., 2011).

Estimating insect population sizes is challenging, and rarely confronted. The main challenge is that Insecta is a mega-diverse class made up of species with contrasting characteristics, behaviours, and life-history strategies, and consequently survey methods used in the field tend to be biased towards specific groups or characteristics (Didham et al., 2020; Montgomery et al., 2021). Active visual surveys have broad taxonomic coverage (Montgomery et al., 2021) but are more labour-intensive and expertise-demanding compared with passive methods. Commonly surveys favour the latter, perhaps because it allows for more spatial and temporal replicates (Montgomery et al., 2021); passive trapping mostly just involves deployment and collection, and can be done in many sites simultaneously, whilst active surveys require personnel consistently on the ground.

An appealing solution to the problem of insect population size estimation is data integration, which consists of combining different data sources to generate parameter estimates that are typically more robust than any one method alone (Jarrett et al., 2022). This technique has been used to estimate species' abundance and distribution from patchy and biased data, for instance citizen science records or museum specimens, in combination with higher-quality data such as surveys (Koshkina et al., 2017; Miller et al., 2019; Peel et al., 2019). Integrating different data types can provide improved estimates of abundance for two main reasons: first, combining different data types compensates for their respective biases, because shared biological parameters are estimated jointly (Miller et al., 2019). Second, combining these data types results in an increase in the effective sample size (data pooling), thus providing more statistical power (Kindsvater et al., 2018; Matthiopoulos et al., 2022). Data integration methods are especially appealing when applied to arthropods, because they could allow the combination of a small amount of high-quality data (from active visual surveys) with a larger amount of lower quality data (from passive trapping), thus optimising field effort investment. However, until now, these methods have not been applied to arthropod sampling data.

Here, I combine data from three methods (malaise traps, sweep-netting and visual surveys) to estimate the population sizes of arthropods groups. I chose these specific methods for several reasons. First, they broadly represent the three main categories of sampling techniques: passive trapping (e.g., pan traps, light traps, malaise traps), active trapping (e.g., beating sheet, sweep-netting) and visual surveys. Second, these three methods are complementary in terms of target groups and effort: malaise traps are most effective at sampling flying insects and require low effort in the field but higher processing effort, whilst sweep-netting and visual surveys are most effective for stationary insects and require higher effort in the field (Montgomery et al., 2021).

I applied the data integration technique to 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 tend to have open canopies, whilst traditional (‘shady’) agroforests have closed canopies (Tscharntke et al., 2011). Using data collected across this gradient, I aimed to 1) generate comparable estimates of population size across the arthropod community; and 2) investigate the effect of shade management on arthropod groups with a focus on pests.

METHODS

Field sites

We conducted arthropod surveys in 28 cocoa farms in Southern Cameroon (Fig. 2). Farms were separated by more than 500 m and were at least 1.5 ha in size. The shade cover in our farms ranged from 20% to 100%, and was measured following Jarrett, Smith, et al (2021; Fig. 3).

We surveyed arthropods in these farms over 4 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. In Southern Cameroon, rainfall follows a bimodal seasonal pattern with the main dry season spanning November to February, followed by a rainy season from March to June, a short dry season in July, and a second rainy season from August to October (Molua, 2006). Our visits captured both the dry season (Jan-Feb) and the rainy season (Aug-Sept), allowing us to assess the effect of rainfall seasonality on arthropod populations.

Insect surveys

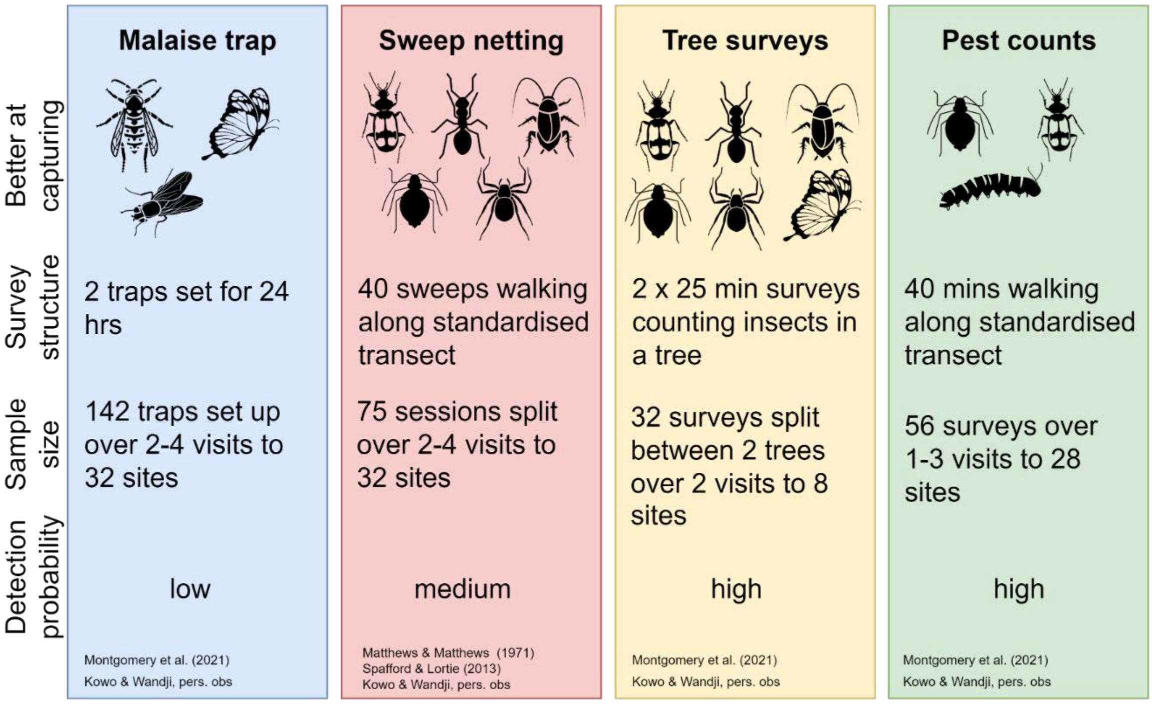
We used 3 different sampling methods to survey arthropods: sweep netting, malaise traps, and visual surveys (summarised in Fig. 12). For all observations of a given survey type, the observer was the same researcher.

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 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. At the end of the session, the observer would transfer 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, the observer removed them from the bag and counted the number of individuals from each arthropod order. For the analyses, I considered the sum of the morning and evening counts. The evening before the dawn sweep netting session, we set up 2 malaise traps at each farm. They were placed at least 20m from the farm boundary and were separated by a minimum of 50m. The malaise traps were unbaited, with the collection jars containing 50% ETOH. The traps were left standing for 24hrs, so that they were collecting at the same time as the sweep netting occurred. At the end of the 24hrs 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 surveys and pest counts (henceforth ‘visual surveys’ refers to both, ‘tree 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 surveys. Whilst sweep netting and malaise traps were used at each visit to each farm, tree surveys were conducted in a sub-sample of farms, due to effort constraints. The tree surveys consisted of a 25 min survey of all arthropods found in a specific cocoa tree (Ferreira et al., n.d.). In each of the 8 farms in which the full tree 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-minute 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 et al., n.d.). The observer used a ladder to reach the higher parts of the crown, and stopped the watch when the count or identification was not instantaneous.

The pest counts (conducted in same 24 hr period as sweep-netting and malaise traps) adopted similar methodology to the tree surveys, but with several important distinctions. First, the pest counts disregarded other arthropods. We considered as pests any arthropods found visibly damaging cocoa trees, whether it be the pods themselves or the leaves, shoots or trunks. This distinction possibly results 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 to species level in the field requires a high level of expertise and increases handling time considerably. Additionally, though the main pests of cocoa in Africa are well known (e.g., brown capsid), other secondary pests are less well documented (Bagny 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 count 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 farm stopping at each tree on-route to identify and count any pest arthropods. The number of trees visited was approximately 50. 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 they re-commenced surveying. The pest counts were conducted at dawn, because brown capsids become less active during the sunniest hours of the day (Bagny Beilhe, Babin, et al., 2018).

To simplify the analyses, I grouped arthropods into the following 11 taxa: Araneae, Blattodea, brown capsid (primary pest of cocoa), Coleoptera non-pest, Coleoptera pest, Diptera, Hemiptera non-pest, Hemiptera pest, Hymenoptera, Lepidoptera non-pest and Lepidoptera pest (Table 5). These groupings represent the orders most captured across trapping methods.



	Malaise trap	Sweep netting	Tree surveys	Pest counts
Better at capturing				
Survey structure	2 traps set for 24 hrs	40 sweeps walking along standardised transect	2 x 25 min surveys counting insects in a tree	40 mins walking along standardised transect
Sample size	142 traps set up over 2-4 visits to 32 sites	75 sessions split over 2-4 visits to 32 sites	32 surveys split between 2 trees over 2 visits to 8 sites	56 surveys over 1-3 visits to 28 sites
Detection probability	low	medium	high	high
	Montgomery et al. (2021) Kowo & Wandji, pers. obs	Matthews & Matthews (1971) Spafford & Lortie (2013) Kowo & Wandji, pers. obs	Montgomery et al. (2021) Kowo & Wandji, pers. obs	Montgomery et al. (2021) Kowo & Wandji, pers. obs

Figure 12. Summary of sampling methods used in the field. Created with diagrams.net.

Table 5. Taxa considered in the model, and taxonomic coverage of each survey method. Sweet-nets, malaise traps and tree surveys did not distinguish pests and non-pests, and therefore considered the sum of both, whilst pest counts only considered pests.

Taxa	**Surveyed by sweep-netting and malaise traps (subscript *j**)**	**Surveyed by tree surveys (subscript *j**)**	**Surveyed by pest counts (subscript *p*)**
Araneae	Araneae	Araneae	
Blattodea	Blattodea	Blattodea	
Coleoptera non-pest	Coleoptera	Coleoptera	
Coleoptera pest			Coleoptera pest
Diptera	Diptera	Diptera	
Hemiptera non-pest	Hemiptera	Hemiptera	

Hemiptera pest			Hemiptera pest
Hymenoptera	Hymenoptera	Hymenoptera	
Lepidoptera non-pest	Lepidoptera	Lepidoptera	
Lepidoptera pest			Lepidoptera pest
Brown capsid		Brown capsid	Brown capsid

Modelling framework

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

Determinants of population size

I considered an arthropod community made up of the 11 taxa listed above (Table 5). My estimates of population size were at the spatial scale of one cocoa tree: N_{jiv} refers to the population size of each taxon *j* at site *i* and visit *v* per cocoa tree. I modelled population size from a Poisson-Gamma (i.e., Negative Binomial) process with rate λ_{jiv} and a scale parameter h_j (Greene, 2008).

$$N_{jiv} \sim \text{NB}(\lambda_{jiv}, h_j) \qquad \textbf{(4.1)}$$

$$h_j \sim \text{Gamma}(\theta_j, \varphi_j) \qquad \textbf{(4.2)}$$

I used a Poisson-Gamma distribution to allow for overdispersion resulting from stochastic variation in species population sizes. I set uninformative priors on h_j, Gamma distributed with shape θ_j = 0.0001 and rate φ_j = 0.0001 (truncated at 0.1 to avoid infinite values). 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 standardized) on population size ($canopy_i$) and a guild-specific seasonal categorical covariate ($season_v$, where $season_v = 1$ if Dry and 0 otherwise; Equation 4.3).

$$\log(\lambda_{jiv}) = \gamma_{j0} + \gamma_{j1} canopy_i + \gamma_{j2} season_v \qquad \textbf{(4.3)}$$

Observation component

During each visit, separated by at least 5 months, I sampled the arthropod community using sweep-netting, malaise traps, tree surveys and pest counts, as discussed above. I assumed 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. I 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 surveys did not distinguish between pests and non-pests. Therefore, groups Hemiptera, Coleoptera and Lepidoptera included both pests and non-pest individuals (henceforth, I use subscript j^* to represent $nonpest_j + pest_j$; Table 1). I modelled the number of individuals found of each taxon by each method m (c_{mj^*iv}) from a Poisson-Gamma distribution with a mean of μ_{mj^*iv} and a scale parameter d_{mj^*iv}. 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(β_{mj^*}) .

$$c_{mj^*iv} \sim \mathrm{NB}(\mu_{mj^*iv},\ d_{mj^*iv}) \quad \textbf{(4.4)}$$

$$d_{mj^*iv} \sim \mathrm{Gamma}(\psi_{mj^*}, \psi_{mj^*}) \qquad \textbf{(4.5)}$$

$$\mu_{mj^*iv} = N_{jiv} \exp\,(\beta_{mj^*}) \qquad \textbf{(4.6)}$$

My model is similar to the Poisson version of an N-mixture model (Kéry & Royle, 2020; Royle, 2004), except that N-mixture models assume that population size *N* remains fixed between survey events, and therefore each survey is a replicated count with the same underlying population size. In my model, *N* did not remain fixed between survey events (i.e., visits), but was proportional between methods. In other words, I assumed that each method was surveying the same latent population.

To ensure that the magnitude of the scale parameter did not dilute all the signal in the data, I implemented a shrinkage tendency towards Poisson dispersion by setting the following prior for ψ_{mj^*}.

$$\psi_{mj^*} = \max\left(10000 - \psi^*_{mj^*}, 1000\right) \text{ where } \psi^*_{mj^*} \sim \text{Exponential } \left(\frac{1}{200}\right) \qquad \textbf{(4.7)}$$

I 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 sweep netting, I set priors of mean = -1, SD = 2 for all groups except Diptera and Lepidoptera, that comprise mostly flying forms and therefore can avoid sweep nets more easily. For these flying groups I centred priors around -2 (SD = 2). For malaise traps I set priors with mean = -1 and SD = 2 for all groups except Diptera and Lepidoptera, which are the groups best captured by this method. For these, I centred priors around 1.2 (SD = 2). I considered visual survey capture rate to be the highest, with a mean of -0.2 (SD = 0.1) for all groups. For visual surveys I assumed a high capture rate, and this essentially calibrated the capture rates of the other methods. While visual surveys were only conducted on a subset of farms, they enabled us to calibrate capture rates for sweep netting and malaise traps.

The pest counts sampled only pests, and therefore only considered the subset of groups (p) that contained this type (Table 5). I modelled the pest count data for each visit (c_{4piv}) from a Negative binomial distribution with a mean of μ_{4piv} and a scale parameter d_{4piv}. The mean μ_{4piv} was given by population size N_{piv} multiplied by a group-specific per-capita capture rate. Per unit area, the capture rates for pest counts were considered the same as the capture rates for tree surveys for the corresponding groups. However, as the pest counts covered a different surface area compared with the tree surveys (for tree surveys 1 entire tree, for pest counts a fraction of 50 trees), I scaled the capture rates β_{j3} by a parameter a which represented the ratio of surface area covered by both methods.

$$c_{4piv} \sim \text{NB}(\mu_{4piv},\ d_{4piv}) \qquad \textbf{(4.8)}$$

$$d_{4piv} \sim \text{Gamma}(\psi_{4p},\ \psi_{4p}) \qquad \textbf{(4.9)}$$

$$\mu_{4piv} = N_{piv} \exp\left(\frac{\beta_{j3}}{a}\right) \qquad \textbf{(4.10)}$$

I set the same prior for ψ_{4p} as described for ψ_{jm}.

Analyses

I fit the integrated model to the field data and evaluated precision of the posteriors using Bayesian Credible Intervals (BCIs). I performed model validation by generating simulated data with known parameters, fitting the integrated model and then comparing simulated and estimated parameters (Appendix 7).

I 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, 2020). I 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.

RESULTS

Estimates of population size

Under simulation, the integrated model was able to accurately estimate model parameters relating to detection rates and population size (Appendix 7). When fit to data from the field, the integrated model was able to estimate ecologically plausible population sizes for each arthropod group (Figs. 13 – 14). The arthropod community in cocoa trees was dominated in abundance by Hymenoptera, followed by non-pest Hemiptera. The least abundant group was Brown capsid, with mean population sizes of 1.6 individuals per tree (95% CIs = 0.52, 3.4).

Effects of management & season

My model detected significant effects of shade cover on the population size of eight out of eleven arthropod groups (Figs. 13 & 15). 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 4 times higher in sunny farms compared to shady farms. Coleoptera and Hemiptera decreased in population size with increasing shade cover, with approximately 2x the number of Hemipteran and Coleopteran pest individuals in sunny farms compared to shady ones.

Season had a significant effect on five out of nine groups (Figs. 14 – 15): Diptera and brown capsid were more abundant in the rainy season, with brown capsids doubling in population size from the wet season to the dry season. Hemiptera were significantly more abundant in the dry season than the wet season, and a similar trend was true for Hymenoptera.

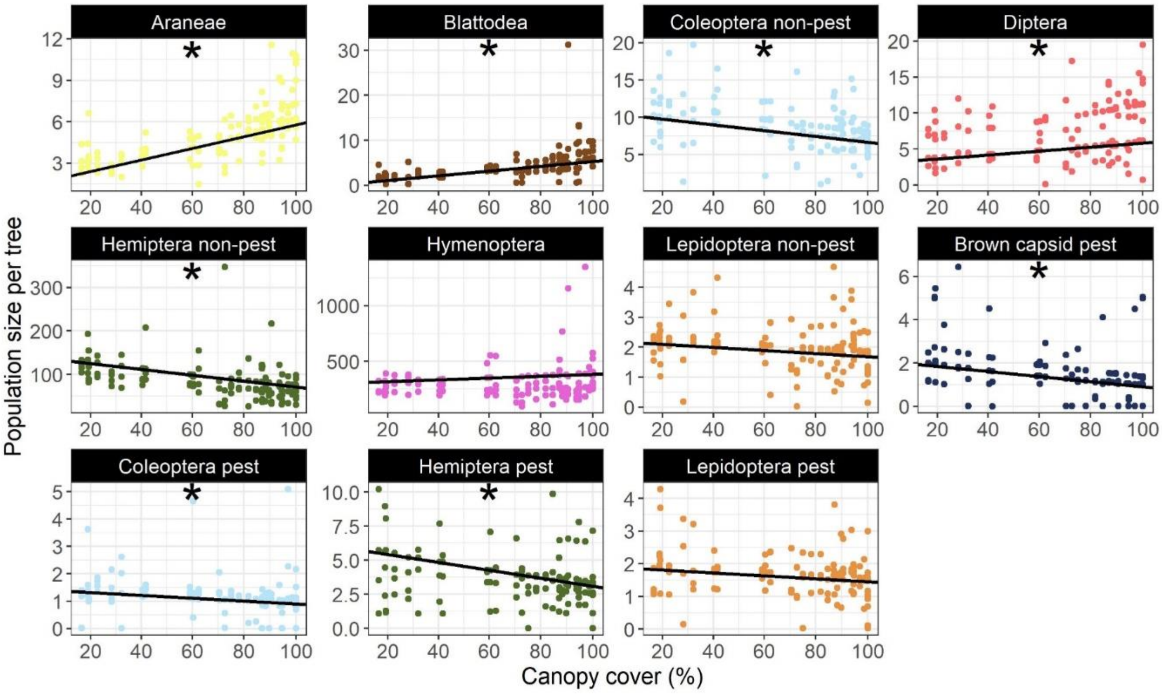


Figure 13. Effect of canopy cover (%) on population size of different arthropod groups. Points are mean of posteriors for population size at each site & visit, and the line is the coefficient describing the effect of canopy cover on population size, as estimated by model (parameter γ_{j1}). Asterisks indicate that the 95% BCIs of the posterior did not overlap 0.

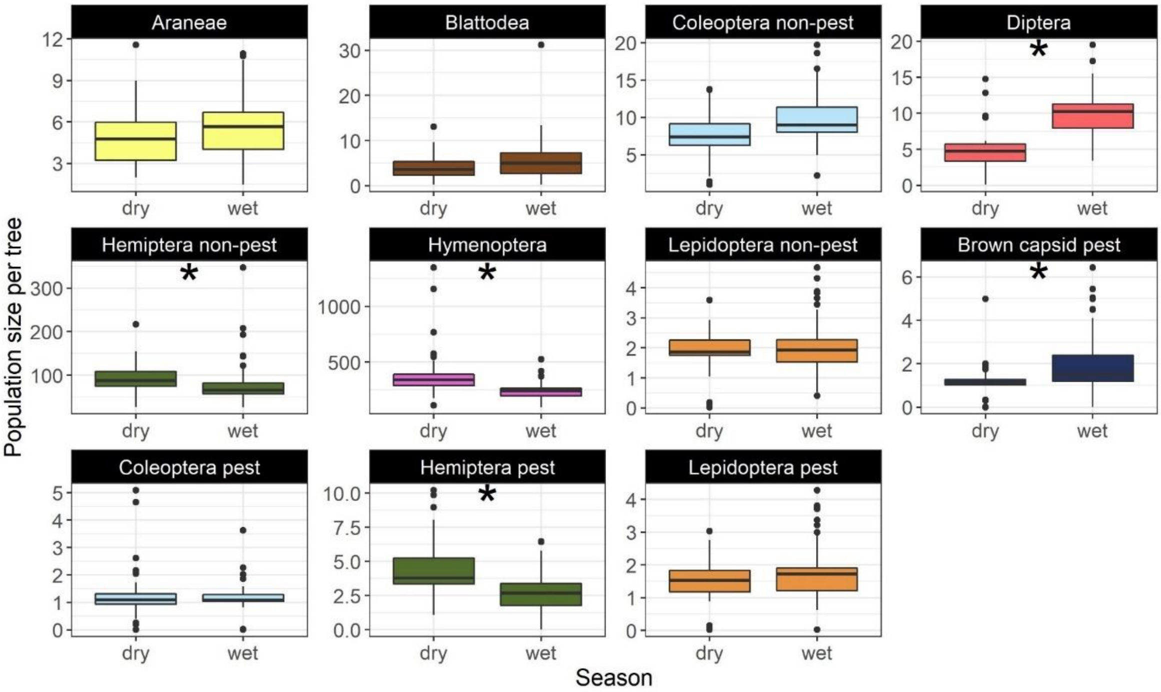


Figure 14. Effect of season (dry or wet) on population size of different arthropod groups. Asterisks indicate that the 95% BCIs of the posterior of parameter γ_{j2} (coefficient for the effect of season on population size) did not overlap 0.

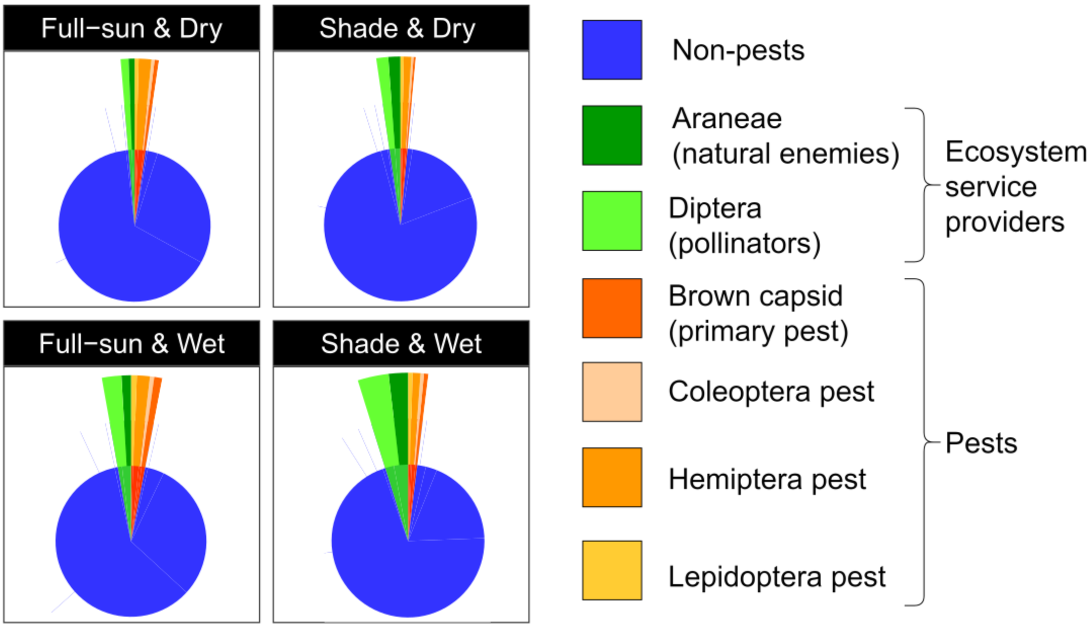


Figure 15. Arthropod community composition in cocoa trees under four different scenarios: full-sun farm (20% canopy) in the dry and wet season, and shade farm (90% canopy) in the dry and wet season. Proportional community composition predicted from model.

DISCUSSION

I used integrated analysis of data from several common arthropod survey techniques, to estimate the population size of arthropod taxa in cocoa agroforestry systems. I investigated the effect of shade cover and season on these groups, finding that 8/11 groups showed significant variation in population size with shade cover and 5/11 showed a seasonal effect.

I found that arthropod communities in cocoa farms were dominated by Hymenoptera, which matches findings from similar tropical habitats (Dial et al., 2006). Hymenoptera is one of the largest insect orders, encompassing sawflies, bees, ants, and wasps, with a wide range of life-history strategies including eusocial living, parasitism, predation and herbivory (Goulet & Huber, 1993). Some Hymenoptera species in the Afrotropics are considered keystone species, for instance *Dorylus* ants that swarm the forest floor and surrounding vegetation, generating resources for a range of vertebrate and invertebrate species (Peters et al., 2011). In agroforestry, ants predate on pest insects (Bisseleua et al., 2013, 2017), as well as play a role as potential pollinators (Toledo-Hernández et al., 2021). Many parasitic wasps are natural enemies of pests (Bisseleua et al., 2013; Sperber et al., 2004). However, there is also some evidence showing that certain ant groups can damage cocoa crops by acting as mechanical vectors of disease (Bisseleua et al., 2017). I found no effect of shade cover on Hymenoptera abundance, possibly because the order is so diverse that different groups react differently to shade cover (e.g., Peters et al., 2011), resulting in an overall net-zero effect. I found a significant seasonal effect on Hymenoptera populations, with higher abundances in the dry season. This seasonal trend may be driven by flying Hymenoptera, that can show a preference for dryer conditions in the Afrotropics (Hopkins et al., 2019).

Hemiptera were the second most common order in cocoa farms. Though most Hemiptera are herbivorous, the degree of damage they cause crops is extremely variable (Yede et al., 2012). Mealybugs (Hemiptera: *Pscuedococcidae*), for instance, can occur at high abundances in cocoa farms and are responsible for spreading cocoa swollen shoot virus (CSSV) in the Afrotropics (Bagny Beilhe, Babin, et al., 2018). Overall, I found that there were ~6 times more non-pest hemipterans than pests. These may feed on other vegetation in cocoa farms such as shade trees or understorey vegetation. I found a negative trend of Hemipterans with increasing shade, indicating that sunnier farms would have higher burdens of hemipteran pests. This finding agrees with Ahenkorah et al. (1974, 1987), who report that sunny farms in the Afrotropics have shorter productive life-spans due to increasing pest burdens. Additionally, I found that Hemipterans were more abundant in the dry season. This may be due to climatic conditions, or it may be a result of population growth during the main fruiting season of cocoa (fruiting Sept-Dec, dry season Nov-Feb; Akesse-Ransford et al., 2021; Yede et al., 2012).

I investigated populations of brown capsids (a Hemipteran) at the species level, as this species is considered the primary pest of cocoa in Africa. I 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). Additionally, I found a significant decrease in capsid abundance with increasing shade cover, in accordance with Babin et al. (2010) and Bagny et al.

(2018). This trend indicates the risks incurred in the current push towards more intensified cocoa production in Africa (Armengot et al., 2016).

Similar to Hemiptera, I found an increase in Coleoptera abundance with decreasing shade cover. This order consists of mostly herbivorous species, though many species also feed on debris or predate other invertebrates (Santos-Heredia et al., 2018). In Indonesia, herbivorous coleoptera showed a preference for sunny open habitats, possibly due to lower predation rates (Klein et al., 2002). Similar to Hemiptera, I found ~5 times more non-pest Coleopterans compared to pests. In general, this group is not considered a major pest of cocoa in Africa, but in the Neotropics and Asia, weevils (Coleoptera: *Curculionidae*) and Ambrosia beetles of the genus *Xyleborus* cause damage to cocoa (Bagny et al., 2018). Lepidoptera, in contrast, showed no change in abundance with shade cover. This may be because Lepidoptera covers wide-ranging life-histories, from herbivorous caterpillars that are main cocoa pests in Indonesia (e.g., *Conopomorpha cramerella*; Maas et 2013) to nectarivorous adult butterflies and nocturnal moths (Schroth et al., 2004). Whilst caterpillars may benefit from lower predation in sunny farms (similar to Coleoptera), adult butterflies may show a preference for increased vegetation (and hence flower) diversity in shadier farms (Cassano et al., 2009; Schroth et al., 2004).

My results showed that Diptera, Blattodea and Araneae increased in abundance with increasing shade cover. Both Diptera and Blattodea prefer dark, damp habitats, which are likely more common in shady low-intensity farms (Sonwa et al., 2019; Toledo-Hernández et al., 2021). Diptera also showed a strong seasonal trend, with higher abundances in the rainy season. This phenomenon is well known in the tropics; for instance, mosquitoes carrying malaria tend to peak in the rainy season (Ngowo et al., 2017). 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 play a role in pollination as well (Toledo-Hernández et al., 2021). Most information on pollinators in cocoa is based on assessing flower visitors, and whilst some taxa that visit cocoa flowers are likely to pollinate, others may not. The true identity of cocoa pollinators is therefore widely unknown. My findings indicate that, if Dipterans indeed play a role in cocoa pollination in Africa, then shadier farms would have higher availability of pollinators. However, to definitively test this we would need further knowledge on the identity of pollinators (rather than flower visitors) in African cocoa.

Araneae may also be attracted to the dark and damp microhabitats offered by shady farms (Bisseleua et al., 2013; Sonwa et al., 2019), or their preference could be related to the availability of prey. Araneae may well prey on Diptera, which occur more commonly in shady farms, as well as on Hemiptera and other pest groups (Bisseleua et al., 2013); the lower abundances of pests in shaded farms could in part be due to higher predation pressures (Ferreira et al., n.d.).

Integrating data from the different survey types in this study allowed us to correct for the detection biases of each method and achieve precise population size estimates for a broad range of arthropod groups. My approach provides several advantages: first, estimating population size of key groups, such as pests, opens opportunities for quantification of services and dis-services to crops, which cannot be estimated with proxies of abundance (Deutsch et al., 2018). Second, my estimates of population size are comparable across taxa, allowing future studies to investigate community dynamics, and thus make long-term predictions about the influence of management on arthropod communities (Janssen & Rijn, 2021). Finally, my estimates of the effect of shade cover on abundance are likely more precise because of the increased sample sizes created by pooling data across survey methods (Kindsvater et al., 2018; Matthiopoulos et al., 2022).

The main limitation to my 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 my 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. Additional limitations include the level of taxonomic aggregation; whilst grouping species to order level facilitates model estimation, it may also obscure intra-order variability in effects of management.

In conclusion, I found that lower intensity cocoa agroforestry in the Afro-tropics benefits from lower pest burdens, and higher abundance of potential pollinators and natural enemies. This shift in community composition with management may lead to rapidly declining yields in intensive cocoa farms, an important issue when considering the general trend towards intensification of cocoa agriculture in Africa (Ordway et al., 2017; Tscharntke et al., 2011). My 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. Assessing the community dynamics of arthropods will provide a mechanistically-explicit holistic view of the effects of management on the provision of ecosystem services and dis-services. I encourage future in-depth studies of each of these arthropod groups and their associated services and dis-services. My results suggest that 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; Tscharntke et al., 2011).

Chapter 5 | States of communities in a complex agricultural setting: implications for conservation and productivity

ABSTRACT

Human populations and demand for commodity crops in tropical regions will continue to increase steeply in the following decades, putting increasing pressure on the natural resources of some of the world’s biodiversity hotspots. In these areas, we need solutions that allow increased food production without demolishing habitats for biodiversity. Agroforestry systems may offer this opportunity, providing habitat for rainforest fauna whilst producing high and sustainable agricultural yields. Ideally, agroforestry could be managed to achieve a desirable combination of biodiversity conservation and productivity; however, the influence of management on biodiversity and its implications for agricultural productivity are poorly understood. The main issue with understanding the relationship between biodiversity and productivity is the complexity of the system; in agroforestry, animal taxa provide both services (e.g., pollination) and dis-services (e.g., crop consumption by pests), interact with each other (e.g., birds predate pests) and may respond differently to management. Therefore, a specific management strategy may result in unpredictable cascading effects on the community, with consequences for the diversity and potential productivity of the system. Here, I developed a mechanistic community model of an agroforestry animal community that allowed us to investigate community dynamics and estimate community equilibrium states. I tested the model under simulation and found that it was able to retrieve community states, species interaction and growth parameters with high accuracy and precision. I then fit the model to data on birds and arthropods collected in African cocoa agroforestry to demonstrate how community states changed with shade cover (a proxy for management intensity). Communities in shady (low intensity) farms tended towards states with higher diversity of arthropods, higher biomass of potential pollinators and lower biomass of pests. Sunny (intensively managed) farms had a higher biomass of pests and higher total biomass of birds (driven by abundant habitat generalists). Additionally, I found that equilibrium biomasses of taxa were strongly dependent on both agroforestry shade cover and the other taxa in the community, emphasising the importance of direct and indirect effects in community dynamics. My results suggest that animal

communities in shady farms may be beneficial both for diversity and productivity. Although such apparent win-win management strategies may not apply everywhere, and may not hold if crop yields are explicitly examined, my work nevertheless provides a novel, holistic framework with which to assess community dynamics in complex habitats and understand the outcomes in terms of biodiversity conservation and productivity.

INTRODUCTION

Low intensity small-holder agriculture is the main agricultural practice in the tropics, which constitute some of the world's economically-poorest but biodiversity-richest regions (Tscharntke et al., 2012). In these areas, farmers commonly live on <£1/day, surrounded by some of the highest levels of wildlife diversity on Earth (Tscharntke et al., 2012). Agroforestry, the practice of growing crops under a canopy of shade trees, is a key example of low-intensity agriculture that offers opportunities for both agricultural productivity and biodiversity conservation (Clough et al., 2011; Tscharntke et al., 2011). However, it is yet unclear how to manage these small-holder systems to achieve viable combinations of agricultural yields and biodiversity conservation.

Wildlife-friendly agriculture is more important now than ever, given the current push towards intensifying cultivation (Tscharntke et al., 2012). The growing demand for commodity crops is pressurising policymakers into encouraging agricultural expansion and intensification (Ordway et al., 2017). Intensification of agroforestry means the removal of shade trees which exchanges floristically diverse agroforestry systems for monocultures (Clough et al., 2009; Tscharntke et al., 2011). This intensification results in community changes, loss of biodiversity and abundance declines (Cassano et al., 2009; De Beenhouwer et al., 2013; Jarrett, Smith, et al., 2021). Changes in wildlife communities could also lead to unexpected loss of agricultural productivity, for instance due to reductions in animal groups that provide ecosystem services, such as pollination and pest control (Ferreira et al., n.d.; Maas et al., 2013, 2016).

Understanding the trade-offs and synergies between biodiversity and productivity is a complex matter, and one that has rarely been approached from a community-wide perspective (but see Karp & Daily, 2014; Kean et al., 2003; Kross et al., 2011). Animal communities in agroforestry are diverse and contain species that influence productivity and biodiversity conservation outputs in different ways, both direct and indirect (Bagny et al., 2018; Maas et al., 2013; Toledo-Hernández et al., 2021). Therefore, different community compositions result in different outcomes for productivity and biodiversity conservation in agroforestry. For instance, a community dominated by pest insects with low numbers of predators would likely result in low productivity (and possibly low conservation value as well), whilst communities with high densities of rare species would result in high conservation value. Ideally, agroforestry would be managed to optimise a combination of desirable outcomes. However, because each taxon can respond differently to habitat management, creating a potential cascade of direct and indirect effects of management on the whole food-web, these responses of communities to agroforestry management are hard to predict.

Previous research into the effect of agroforestry management on biodiversity or productivity has mostly focussed on establishing correlations between the observed abundance of different groups and management covariates (Blaser et al., 2018; Clough et al., 2011). This approach has several important limitations: first, it assumes that the communities observed are at equilibrium, and consequently that observed changes in abundance with management reflect instantaneous changes in community composition. In reality, we are observing a transient state of the system, which may be very different from the equilibrium state (Hastings et al., 2018). Linked to this, these correlative analyses commonly assume that species respond to management independently from each other. In other words, a correlation is established between the observed density of a species and management covariates, without accounting for the fact that the densities of other species present may be as important, or even more important, in determining community states (Gotelli & Ellison, 2006; Janssen & Rijn, 2021; Kawatsu et al., 2021; Tylianakis et al., 2007).

One consequence of considering species independently is that we do not gain any information on the mechanisms driving their (trophic, competitive etc.) relationships (Gotelli & Ellison, 2006). Whilst we may observe a change in a species’ density with management, we cannot determine whether this change is due to a direct effect of management on the species’ carrying capacity (e.g., limitation in breeding sites) or due to an indirect effect such as an increase in predator densities (Barbosa et al., 2017; Gotelli & Ellison, 2006; Kawatsu et al., 2021; Vial et al., 2011). Our limited understanding of mechanisms could hinder the potential for manipulating a system to achieve a desired state. For instance, if we knew that the factor limiting a certain ecosystem service provider is nesting sites, then we could provide additional nesting sites to boost populations (García et al., 2021).

The common issue with mechanistic community models is that they involve many parameters, and are consequently hard to fit to short-term field study data (Burt et al., 2018; Curtsdotter et al., 2019; Kawatsu et al., 2021). Community models are typically believed to require long time-series of data on ecological communities in order to distinguish the noise (demographic stochasticity) from the parameters governing the composition of communities (Ellner et al., 2002; Yodzis, 1998). However, all forms of dynamical models (i.e., both difference and differential equation models) focus on rates of change, not absolute abundances. Information on rates of change does not necessarily require long time-series, just paired (successive) observations (Ives et al., 2003). Here, I wanted to investigate the potential of fitting complex mechanistic community models to short time-series by exploiting a space for time substitution; I considered paired observations from a range of sites with shared parameters, so that community composition at time t depended only on community composition at time t-1. This experimental design is a lot more common in ecological studies, making my modelling framework applicable to many field datasets.

I tackle the issue of understanding complex community dynamics by building a modelling framework, based on concepts from traditional community ecology, formulated as a series of GLMs, and thus directly fitted using Bayesian methods to imperfect community data collected from agroforestry sites. My model incorporates data and priors on species' abundances, their diets, and considers rates of change in the density of each species as a function of environmental covariates (including management strategies). Therefore, my models considered global-system dynamics, taking into account direct and indirect effects of management and species on each other. I focussed on the insectivore-insect food-web in agroforestry for several reasons: first, insectivores, especially avian insectivores, are common in agroforestry (Jarrett, Smith, et al., 2021; Jarrett et al., 2022) and can play an important role in pest control (Maas et al., 2016). Second, insectivores are vulnerable to habitat degradation and consequently should be a priority for conservation in these landscapes (Jarrett, Smith, et al., 2021; Powell et al., 2015). Insects are a widespread group in agroforestry, and can be beneficial (pollination, pest control) but also, extremely damaging to crops, causing crop losses of up to 40% (Akesse-Ransford et al., 2021; Bisseleua et al., 2013; Wessel & Quist-Wessel, 2015). The insectivore-insect food-web is therefore central to agroforestry, and a good exemplar of the broader research area into productivity-conservation relationships.

I fit my community model first to simulated data and then to data collected in African cocoa agroforestry. With the simulation, I aimed to assess whether the model could retrieve relevant parameters and predict current and future community compositions accurately. With the field data, I aimed to a) estimate community states from field data, b) investigate the effects of management on equilibrium densities of each taxon and c) evaluate the different management-induced states in terms of their productivity/biodiversity outputs.

METHODS

Conceptual background

I assumed that communities of species fluctuate around a given (potentially unobserved) equilibrium state (Fig. 16). I use the term ‘species’ to describe taxonomic groups, which may be species but could also be functional groups, families, etc. I define state as the vector of the abundances of all species at a given point in time $\boldsymbol{N}_t = \{N_{t1}, \dots, N_{ti}, \dots, N_{tI}\}$, where *I* is the total number of species, including those that happen to have a zero density in any particular system. Community state-space has as many dimensions as the number of species in the community, and in this *I*-dimensional state-space, any particular community composition (a given state) is represented by a single point. While equilibria cannot be assumed to be observed in the data (Fig. 16), they are latent states towards which a system will tend, so they are the objective of my estimation.

My framework considers community states as a function of species’ intrinsic growth, environmental conditions and interactions between species. Community dynamics occur in continuous time, but were observed in discrete time, with ‘snapshots’ taken at given timepoints (Fig. 16). Observations of the community captured a state of transience around the equilibrium (Fig. 16). Given replicated observations of different transient states, we should be able to differentiate the noise (demographic stochasticity), from the true parameters governing the equilibrium states. Commonly these replicated observations take the form of time-series data (Ellner et al., 2002). However, long time-series data on ecological communities are hard to acquire. More commonly, field studies are carried out over short time periods across replicated sites. I wanted to test whether I could successfully fit a community model to data collected following this common type of experimental design. Therefore, my model was designed to fit a set of paired time-points (time *t* and *t*+1), and these pairs could come from different locations characterised by different environmental and management regimes, but were assumed to be governed by shared parameters.

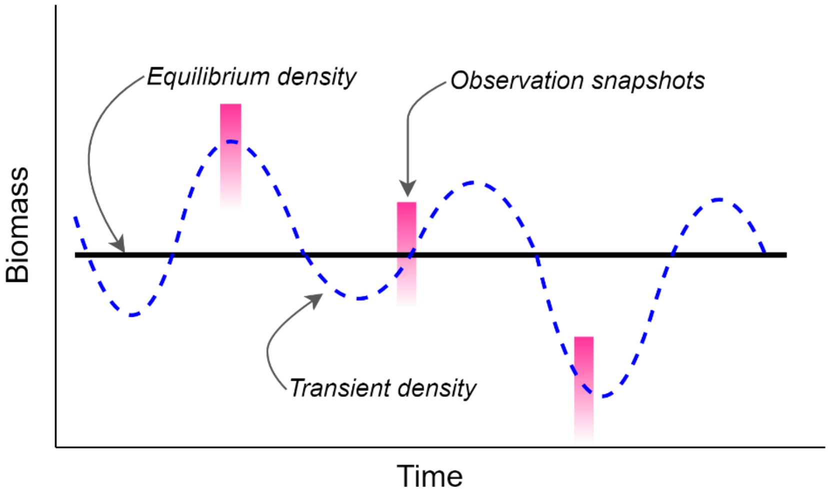


Figure 16. Theoretical background to my community model: I assume that the biomass of each species fluctuates around an equilibrium (solid black line), and this equilibrium density is determined by species' intrinsic growth rates (which are a function of environmental covariates) and inter and intraspecific interactions. When we observe species abundances, we see a snapshot of these transient densities (dashed blue line), but observation is inevitably made with error (represented by pink strips).

General model structure

My model was based on a discrete-time Lotka-Volterra community model with *I* potentially interacting species. I modelled biomass of each species (a continuous variable) but sought to keep the properties of a typical loglinear model (appropriate for abundances), so I used a Normal approximation of the Poisson, in which the variance was equal to the mean (in Equation 5.1, $\sigma_{ti} = \sqrt{\lambda_{ti}}$). The mean was written a function of biomass at the previous time-step and the exponential of a linear predictor L_{ti}, representing per-capita rate of change for each species at a given time.

$$N_{t+1i} \sim \text{Normal}(\lambda_{ti,}\ \sigma_{ti}) \qquad \textbf{(5.1)}$$

$$\lambda_{ti} = N_{ti} \exp(L_{ti}) \qquad \textbf{(5.2)}$$

The per-capita rate of change L_{ti} was written as a linear predictor, with an intercept b_i interpreted as the log of the species-specific intrinsic growth rate (i.e., rate of change in the absence of all other species, whether predators or prey), and the sum of the effects of all interactions between species.

$$L_{ti} = b_i + (\sum_{j=1}^{J} a_{ij} N_{tj}) \qquad \textbf{(5.3)}$$

The coefficients a_{ij} quantified the effect of the abundance of species *j* on the per-capita population growth rate of species *i*. Intraspecific effects (e.g., density dependence) were captured by a_{ii}. I assumed a Holling Type I functional response between predators and prey. Commonly used extensions of linear predictors in regressions (e.g., quadratic terms) could be used here, to represent non-linear functional responses or prey switching (Asseburg et al., 2006) and Allee effects (Lindmark et al., 2019), but this was not done here, keeping the model to its more parsimonious form.

In these coupled equations, the equilibrium state was given when $\exp(L_{ti}) = 1$ for all *i*, and therefore $b_i + \sum_{j=1}^{J} a_{ij} N_{tj} = 0$ for all *i*. The equilibrium state could be found by multiplying the inverse of the **A** matrix (containing a_{ij} elements) by the vector of growth rates **b** (containing b_i elements; Appendix 8).

$$\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{b} \quad \textbf{(5.4)}$$

Environmental covariates

I considered that the intrinsic growth rate (b_i) of species *i* could be influenced by environmental covariates.

$$b_i = \sum_{q=0}^{Q} \nu_{iq} X_q \qquad \textbf{(5.5)}$$

The linear predictor comprised Q covariates, X_q, affecting growth rate, and their respective regression coefficients ν_{iq}, where q refers to the qth covariate (the intercept ν_{i0} was included by setting $X_0 = 1$).

Including the effect of environmental covariates on b_i resulted in a $\mathbf{b}$ vector whose elements were functions of these covariates. Consequently, equilibrium densities as calculated in Equation 5.4 changed linearly with environmental covariates.

Simulation study

Data generation

My simulated study system consisted of 30 sites with varying environmental conditions. In these sites I simulated communities of 18 species in two trophic levels: predators (6 species) and prey (12 species). The dynamics of these communities were driven by an interaction matrix (**A**) which was shared across sites, and species-specific growth rates (**b**) that varied according to spatial and temporal environmental covariates. The parameters contained within **b** and **A** determined the equilibrium state of each community, which could differ between sites according to their respective covariates.

I started by assigning equilibrium biomasses for each species corresponding to a baseline of environmental covariates. The values of these equilibrium biomasses were not central to this exercise, but nevertheless I based them on my biological intuition of the system. I assigned baseline intrinsic growth rates ν_{i0} by assuming positive growth rates for prey and negative for predators (Table 6). In the absence of all other species the exponential of negative growth rates would result in a per-capita rate of change of $\exp(L_{ti}) < 1$, whilst a positive growth rate would result in $\exp(L_{ti}) > 1$. I considered intrinsic growth rates as a function of two covariates: one site-level covariate and one temporally varying covariate (Table 6), so that intrinsic growth rate of species *i* at each site *f* and timepoint *t* was modelled as:

$$b_{ift} = \nu_{i0} + \nu_{i1}X_{1f} + \nu_{i2}X_{2t} \quad \textbf{(5.6)}$$

I modelled regression coefficients as normally distributed (Table 6).

I then parametrised the **A** matrix as follows: first, all interspecific interaction terms other than those relating to predator prey relationships were assumed to be 0; second, the terms describing the effect of prey on predator were generated assuming a Holling type I functional response, where a_{ij} was modelled as gamma distributed (Table 6). To reflect natural variation in trophic connectivity between species, I randomly set some interaction terms to 0, by multiplying each a_{ij} term by a Bernoulli trial with probability $p = 0.6$, so that 29 out of 72 (12 prey x 6 predators) possible prey-predator interactions were 0. Third, the terms describing the effect of predator on prey, were calculated as $a_{ji} = -a_{ij}/\varepsilon_i$, where ε_i was a trophic efficiency term (I set $\varepsilon_i = 0.5$; Table 6). Consequently, the effect of predator on prey was larger than the effect of prey on predator. Finally, I calculated the diagonals of the **A** matrix (a_{ii} terms) by solving Equation 5.3 for the system equilibrium point (Table 6), so that

$$a_{ii} = -(\nu_{i0} + \textstyle\sum_{j \neq i} a_{ij} N_j^*)/N_i^* \qquad \textbf{(5.7)}$$

With this parametrisation, I generated data for biomass N_{ti} over the 30 sites and 4 timepoints using Equations 5.1 – 5.3.

Table 6. Description of parameters used in simulation, including distribution or formula used to generate data and prior given to model. For gamma distributions, the parameters presented are shape and rate, for normal distributions they are mean and SD.

Parameter	**Description**	**Simulated from**	**Prior**
ν_{prey0}	Intercept of linear predictor of intrinsic growth rate for prey groups	$\Gamma(9,6)$	$\Gamma(44,22)$
$\nu_{predator0}$	Intercept of linear predictor of intrinsic growth rate for predator groups	$-\Gamma(25,8)$	$-\Gamma(25,17)$
ν_{i1}	Effect of site-level covariate on intrinsic growth rate	N(0,0.1)	N(0,0.5)
ν_{i2}	Effect of visit-level covariate on intrinsic growth rate	N(0,0.2)	N(0,0.5)
$a_{predator,prey}$	Interaction coefficient for prey on predator	$-a_{prey,predator}\ \varepsilon$	$\Gamma(0.25,25)$
$a_{prey,predator}$	Interaction coefficient for predator on prey	$-\Gamma(1,100)$	$-a_{predator,prey}/\varepsilon$
$a_{i,i}$	Density dependence coefficient	Equation 5.7	$\Gamma(0.25,25)$
ε	Energy efficiency of predators	0.5	$\Gamma(100,200)$

Model fitting

I fit the model to these generated data by running 3 chains for 500,000 iterations (50,000 sample x 10 thinning rate), with an adaptation period of 2,000 iterations and a burn-in of 20,000. The model took 3.3 hrs to run using 3 cores for each of the parallel chains. I assessed model convergence by visually inspecting chains and with the Gelman-Rubin R-hat diagnostic, with convergence presumed when R-hat < 1.1. Once the model finished running, I sampled the parameters by taking 1,000 random draws from their posteriors. These parameter draws were used to calculate **N*** (Equation 5.4), and I then compared estimated parameters and **N*** with true simulation values. I used the mean and 95% credible intervals (CIs) of these draws to assess model accuracy and precision.

Application to cocoa agroforestry

Data collection

I applied my model to field data collected in 28 Cameroonian cocoa farms during Jan-Feb and Aug-Sept 2019-2020 (Fig. 2). The farms were on a gradient of shade cover, ranging from 19% to 100% (Fig. 3). Each farm was visited 2-4 times, and on each occasion, we surveyed birds and arthropods. Based on our field data, I determined the main groups that formed the bird-arthropod food-web in these cocoa farms (Fig. 17). For birds, 60% of all insectivorous individuals captured belonged to one of 5 genera, or belonged to a guild of forest specialists (Jarrett, Smith, et al., 2021). The genera *Camaroptera*, *Hylia*, *Platysteira* (Wattle-eyes) and *Terpsiphone* (Paradise flycatchers) are small passerine birds, some species of which are sensitive to habitat degradation (Appendix 2 & 9; Jarrett, Smith, et al., 2021). *Ispidina* is a genus of small insectivorous kingfishers, considered habitat generalists (Jarrett, Smith, et al., 2021; Naidoo, 2004). I classified arthropods as either ‘pests’ or ‘non-pests’ and then grouped them by order, except for brown capsid (*Sahlbergella singularis*), the primary pest of cocoa in Africa (Bagny et al., 2018), which was included at species level. I aggregated species into the groups described to limit the number of parameters estimated by the model; this clustering may generate more noise in the results, but it is a practical course of action for complex field datasets like the one described here.

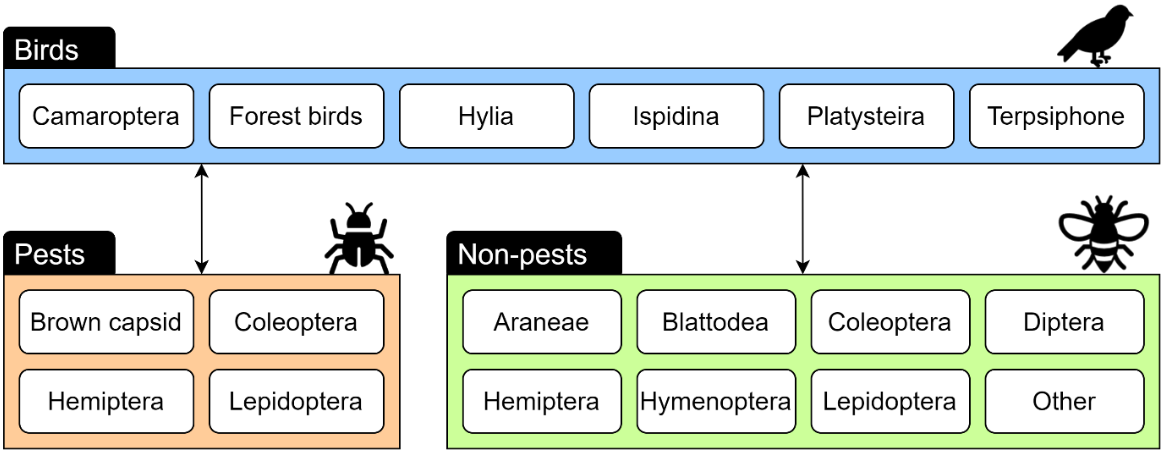


Figure 17. Structure of cocoa farm bird-arthropod food-web: two trophic levels representing insectivorous birds (predators) and arthropods (prey).

Birds: The bird dataset used for the model was identical to that of Chapter 3 and Jarrett et al. (2022), and consisted in bird mist-net captures and simultaneously collected acoustic recordings from Cameroonian cocoa farms from Jan-Feb and Aug-Sept 2019 – 2020. All birds caught and recorded were identified to species level and weighed, to allow conversion to biomass.

Arthropods: The arthropod dataset used for the model was identical to that of Chapter 4. It included count data for arthropods collected using three common survey methods: sweep-netting, malaise traps and visual surveys. Arthropods were identified to order level, except for brown capsid (*Sahlbergella singularis*), the primary pest of cocoa in Africa which was identified to species level.

Covariate data: the 28 cocoa farms sampled were on a gradient of shade cover. The method for quantifying shade is described in Jarrett, Smith, et al. (2021). Shade cover was measured as a percentage.

Observation models

Birds: I modelled bird population size by integrating mist-net captures and acoustic recordings into a joint likelihood, as in Chapter 3 and Jarrett et al. (2022). This model assumes that there was an underlying population of birds at each site, which was sampled by both methods. Therefore, the mark-recapture model for mist-net data and the acoustic model were both conditional on the latent population size.

I made the following modifications to the Jarrett et al. (2022) model: 1) The grouping of species was different, as I wanted finer taxonomic resolution on population size estimates. In this study, I was interested in the following bird groups: *Camaroptera, Hylia, Ispidina, Platysteira, Terpsiphone* and forest birds (Fig. 17). For the observation model, I used the whole dataset in order to maximise sample sizes for shared parameter estimation. Consequently, I ran the observation model with the entire dataset but then distinguished the subset of groups targeted in the process model. I assumed an equal mist-net capture rate for *Camaroptera, Hylia, Ispidina, Platysteira* and *Terpsiphone* as they all consist in small, morphologically similar genera. I allowed for distinct vocalisation rates between these genera. 2) The process model was distinct, as explained below.

<u>Arthropods:</u> I modelled arthropod population sizes by integrating data from three common survey techniques, as in Chapter 4. The observation model used here was identical to the one presented in Chapter 4, but the process model was distinct (see below).

I ran both the observation models with 3 chains for 20,000 iterations (plus 10,000 burn-in). I then calculated the mean of the MCMC chains for each model state (bird or arthropod population size at farm *f* and timepoint *t*). I converted population size to biomass by correcting for body mass and effective area sampled. For birds, I calculated average body mass for each taxon from field data. For arthropods, I assumed a mean body mass of 0.01 g across taxa (Byrne et al., 1988; Hancock & Legg, 2012). These biomass data were then provided as data to the process model.

Process model parametrisation

I modelled community dynamics of birds and arthropods in cocoa as described in equations 5.1 – 5.5. The number of interacting taxa (*I*) was 18 (Fig. 17).

I modelled growth rate of each taxon *i* as a function of shade cover at each farm *f* and the season during which timepoint *t* fell (Equation 5.8; categorical variable: $season_t = 0$ for dry season and $season_t = 1$ for wet season). I constrained growth rates of arthropods to be positive numbers and growth rates of birds to be negative (Table 7). Parameters describing the effects of covariates on growth rates were given normally distributed priors centred around 0 (Table 7).

$$b_{ift} = \nu_{i0} + \nu_{i1} canopy_f + \nu_{i2} season_t \qquad \textbf{(5.8)}$$

For the inter-specific interaction parameters, I assumed no direct competition, so that all within-trophic-level parameters were set to 0. That left 72 potential predator-prey interaction parameters (12 prey x 6 predators); of these, I set 12 to 0 based on evidence from diet metabarcoding data from birds, that indicated no trophic links between certain bird genera and insect orders (Powell et al., 2022 unpublished data; Appendix 10: Figure S1). I modelled the remaining consumption parameters $a_{predator,prey}$ as Gamma variates, assuming the effect of prey on predator growth rate was positive. I forced $a_{prey,predator}$ to be negative and scaled with an energy efficiency coefficient (Table 7), to represent the negative effect of predators on the growth rate of prey, and the process of energy exchange from prey to predator.

Modelling community dynamics in discrete time can be complicated by the lack of instantaneous feedback loops and instabilities caused by the implicit time-lags in the discrete time formulation (Caswell & Neubert, 2006). This can cause explosive model behaviour and consequently, difficulty with fitting the model to data. Whilst our data were collected approximately every six months (Jan-Feb and Aug-Sept), I fit the model to monthly time-steps to avoid such difficulties. Although it is possible for state-space models to impute multiple intermediate states between two endpoints (Dunn et al., 2022), in a system with multiple species, this becomes computationally prohibitive. Therefore, I imputed monthly time-steps from each pair of six-monthly data points using linear interpolations. My treatment of missing data was just one possible solution, but more suitable options could be available with sufficient computational power.

Table 7. Description of parameters estimated by field data model, including model priors and the justification for prior distribution

Parameter	Description	Prior	Justification of prior
ν_{prey0}	Intercept of linear predictor of intrinsic growth rate for prey groups	$\Gamma(25,16.6)$	Doubling time of arthropod population 10 - 30 days[1]
$\nu_{predator0}$	Intercept of linear predictor of intrinsic growth rate for predator groups	$-\Gamma(17.2,4.2)$	Half-time for bird population ranging 2 - 10 days[2]
ν_{i1}	Effect of canopy on intrinsic growth rate	$N(0,0.5)$	
ν_{i2}	Effect of season on intrinsic growth rate	$N(0,0.5)$	
$a_{predator,prey}$	Interaction coefficient for prey on predator	$\Gamma(1,20)$	Bird energy requirements ~4.2kJ/g, insect energy content ~6.75 kJ/g wet matter, insect water content 0.7, bird energy efficiency 0.75, approximate number of insect groups consumed = 7, $a_{prey,predator}$ = consumption / N^*_{prey}, $a_{predator,prey} = a_{prey,predator}$*energy efficiency[3]
$a_{prey,predator}$	Interaction coefficient for predator on prey	$-a_{prey,predator}/\varepsilon$	
$a_{i,i}$	Density dependence coefficient	$\Gamma(1,20)$	
ε	Energy efficiency of predators	$\Gamma(36,120)$	Bird energy efficiency 0.75[4]

[1] ν_{prey0} = log(2)/(doubling time [days] / 30)

[2] $\nu_{predator0}$ = log(0.5)/(half-time [days] / 30)

[3] (Gibb, 1957; Nyffeler et al., 2018)

Implications for diversity and productivity

To assess the conservation value of different community states, I considered total biomass and Shannon diversity of arthropods (excluding pests) and birds. I excluded pests from this calculation to avoid ‘rewarding’ community states containing diverse pest communities. The Shannon index measures the uncertainty associated with predicting the taxon-identity of a single individual in a sampling process; it therefore considers both richness and evenness of taxa. The Shannon index is expressed as:

$$H_{Shannon} = \sum_{j=1}^{I} p_i \log p_i \qquad \textbf{(5.9)}$$

Where p_i is the relative biomass of the ith taxon in a population of S taxa.

To assess the potential value of community states for productivity, I considered total biomass of pests and potential pollinators (Dipterans; Mortimer et al., 2017).

RESULTS

Simulation study

The model estimated all relevant parameters with high accuracy and precision (Fig. 18).

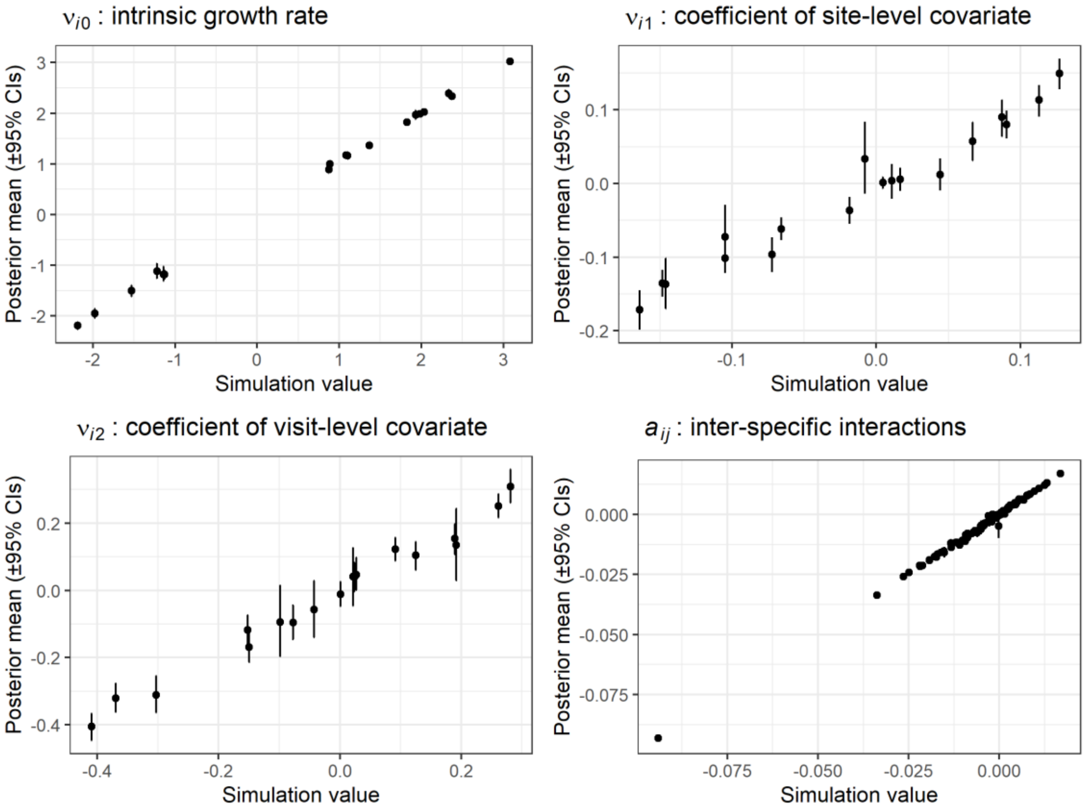


Figure 18. Correlation between parameter value used in simulation and parameter estimates from model. Parameter posteriors are represented using the median and 95% CIs of 1000 random draws from MCMC chains.

When I used parameter posteriors to estimate equilibrium biomasses of species, the retrieved biomasses were an accurate representation of the simulation biomasses (Fig. 19). In 17 out of 18 groups the effect of the site-level covariate on equilibrium biomasses was predicted accurately (exception was ‘Prey 9’; Fig. 19), and in 17 out of 18 groups the effect of the visit-level covariate was predicted correctly (exception was ‘Predator 4’; Fig. 19).

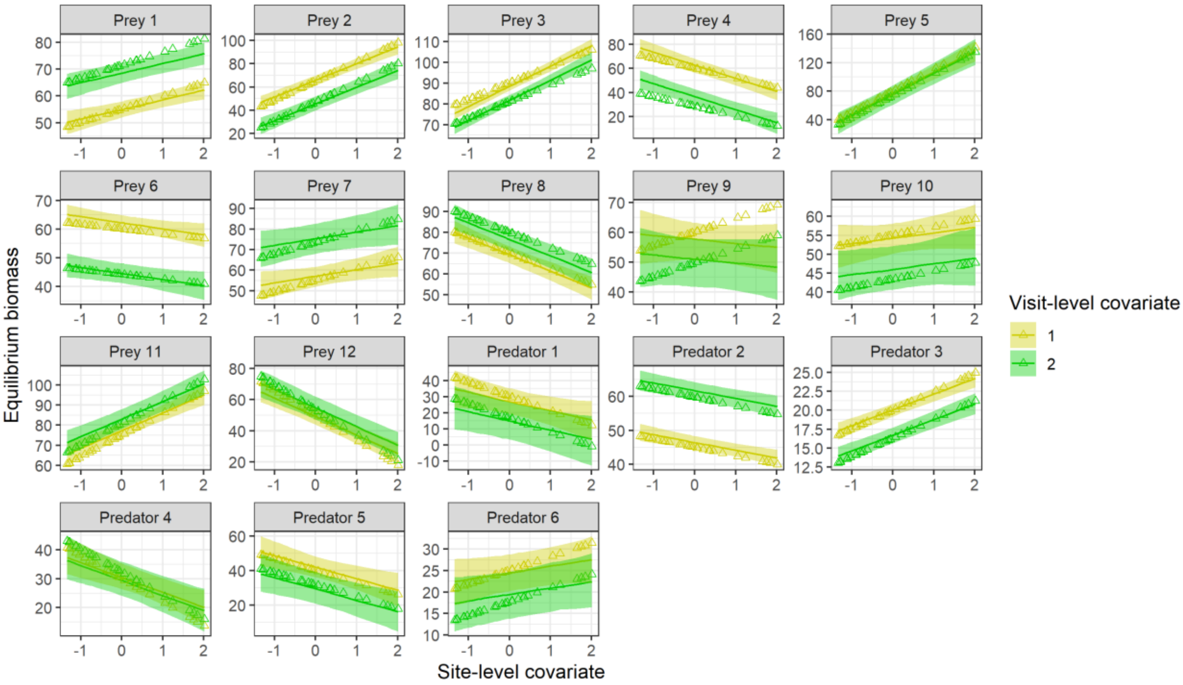


Figure 19. Effect of site-level covariate and visit-level covariate on true equilibrium biomasses (triangles) and equilibrium biomasses estimated from model predictions (lines and error shading). Equilibrium biomasses were calculated from 1000 random draws from parameter posteriors, and summarised using the mean and 95% CIs.

Application to cocoa agroforestry

Parameter estimates

Parameters relating to groups’ growth rates and interactions are presented in Figure 20. Intrinsic growth rates of arthropod groups ranged from 0.36 in Hymenopterans to 1.37 in Coleopteran pests, which is equivalent to a population doubling time in the range of 15 to

55 days. The intrinsic growth rates of birds ranged from -0.43 for forest birds to -0.14 for *Ispidina*, which is equivalent to a population half-life of 50 to 140 days.

The effect of season and shade cover on growth rates varied between taxa (Fig. 20). Forest birds showed a positive trend between growth rate and shade cover, whilst brown capsid, Hemiptera, Lepidoptera, *Camaroptera*, *Hylia* and *Ispidina* showed a negative trend. For season, forest birds had higher growth rates in the wet season, whilst Hymenoptera and Lepidoptera had higher growth rates in the dry season.

Interaction parameters ranged from -0.32 to 0.27, with the highest values associated to the interaction between bird taxa and pest arthropods, as well as density dependence parameters in certain arthropod taxa (Fig. 20). The a_{ij} parameters represent consumption scaled by density; for consumption per se see Appendix 10 (Figure S2).

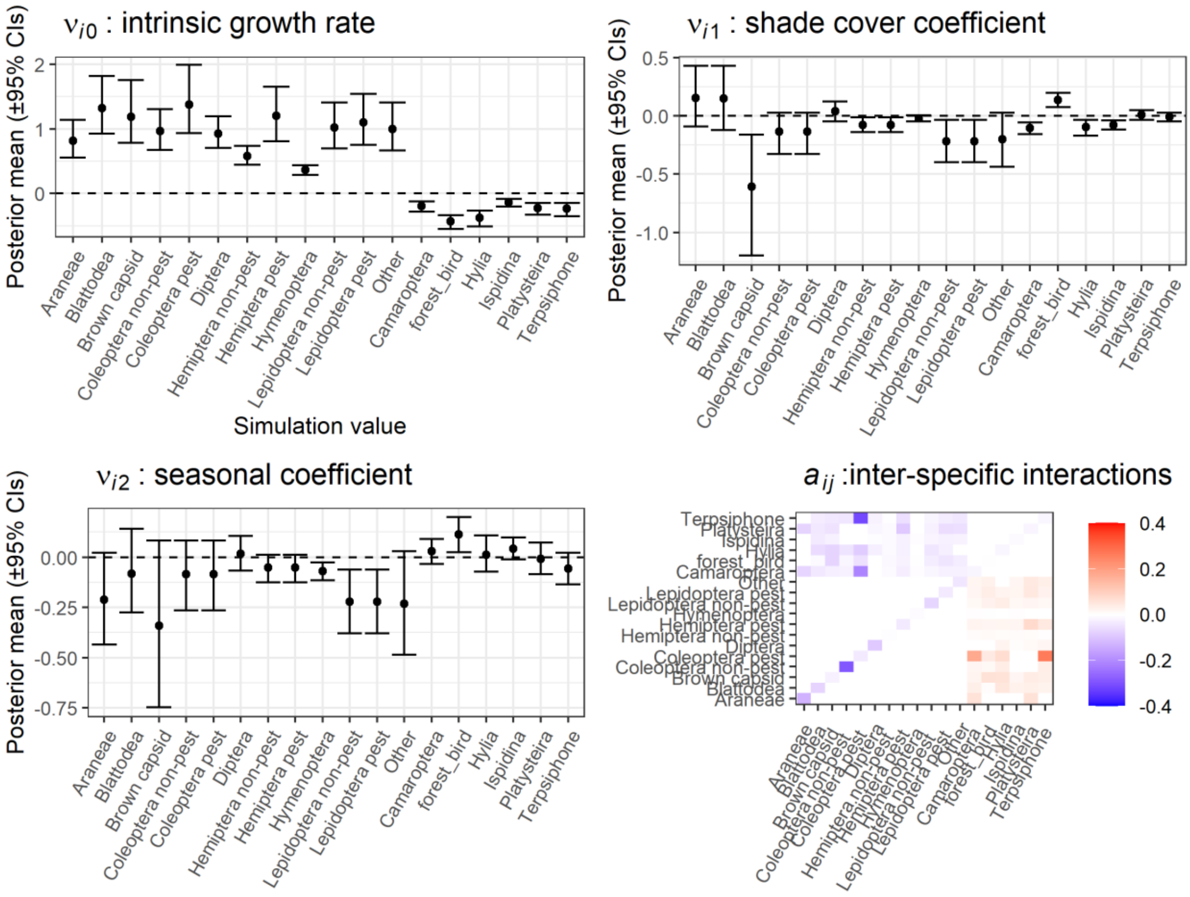


Figure 20. Growth rate and interaction parameters estimated by model. Parameter posteriors were summarised using the mean and 95% CIs of 1000 random draws from MCMC chains.

Estimating equilibrium states

I estimated equilibrium biomass for each taxon at each site and season using Equation 5.4 (Fig. 21). The groups that occurred at highest equilibrium biomass were Hemipterans, Hymenopterans and the bird genus *Ispidina*, and those with lowest biomass were Lepidopteran pests, Coleopteran pests and *Terpsiphone*. The trend in biomass with shade cover and season varied between groups (Fig. 21): Araneae, Blattodea, Coleopteran pest, Diptera, Hemipteran pest, *Platysteira* and *Terpsiphone* had higher equilibrium biomass in shadier farms, whilst the opposite was true for the remaining groups.

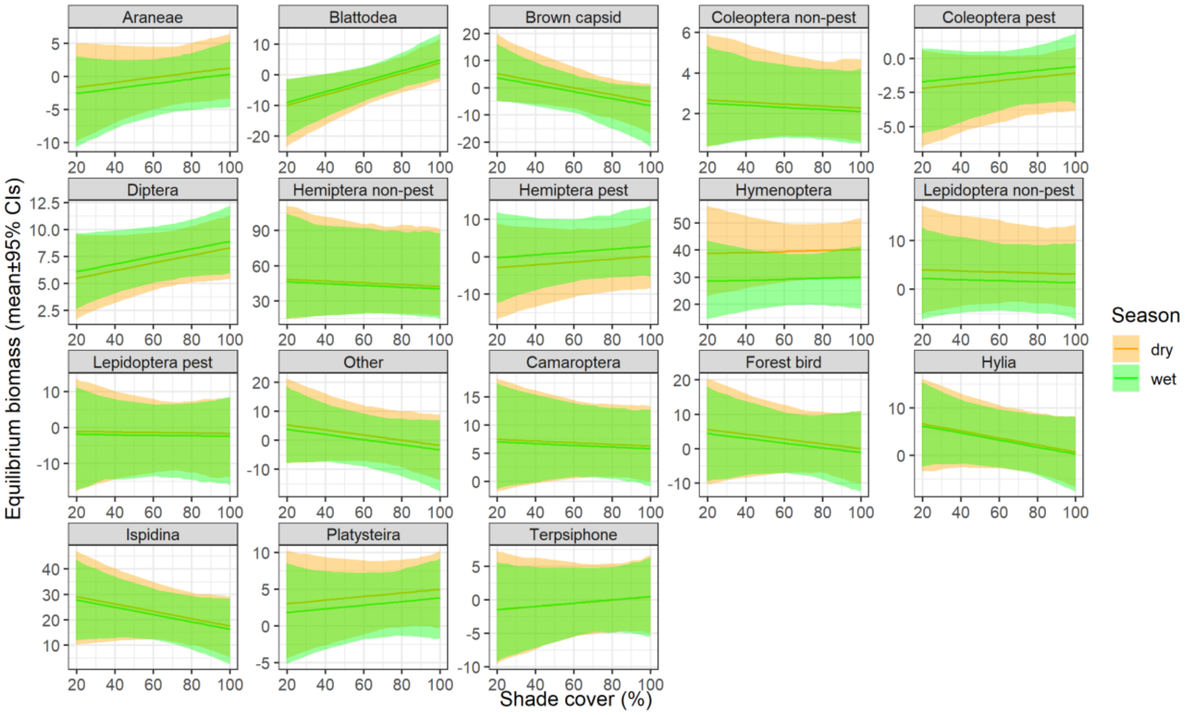


Figure 21. Effect of shade cover and season on equilibrium biomass of each group estimated from model parameters.

Implications for conservation and productivity

I evaluated the different community states estimated from model parameters in terms of their diversity and potential effect on productivity. I found that the total biomass of arthropods was not affected by shade cover, whilst the biomass of birds decreased with increasing shade cover from 52 kg/km^2 to 33kg/km^2 (Fig. 22). Shannon diversity of arthropods showed an increase at shade cover values above 60%, whilst Shannon diversity of birds was largely unaffected by shade cover (Fig. 22).

The biomass of pest groups was highest (7.5 kg/km^2) in sunny farms, and lowest (2.5 kg/km^2) at 85% shade cover, whilst the biomass of potential pollinators showed a linear increase with increasing shade cover (Fig. 23).

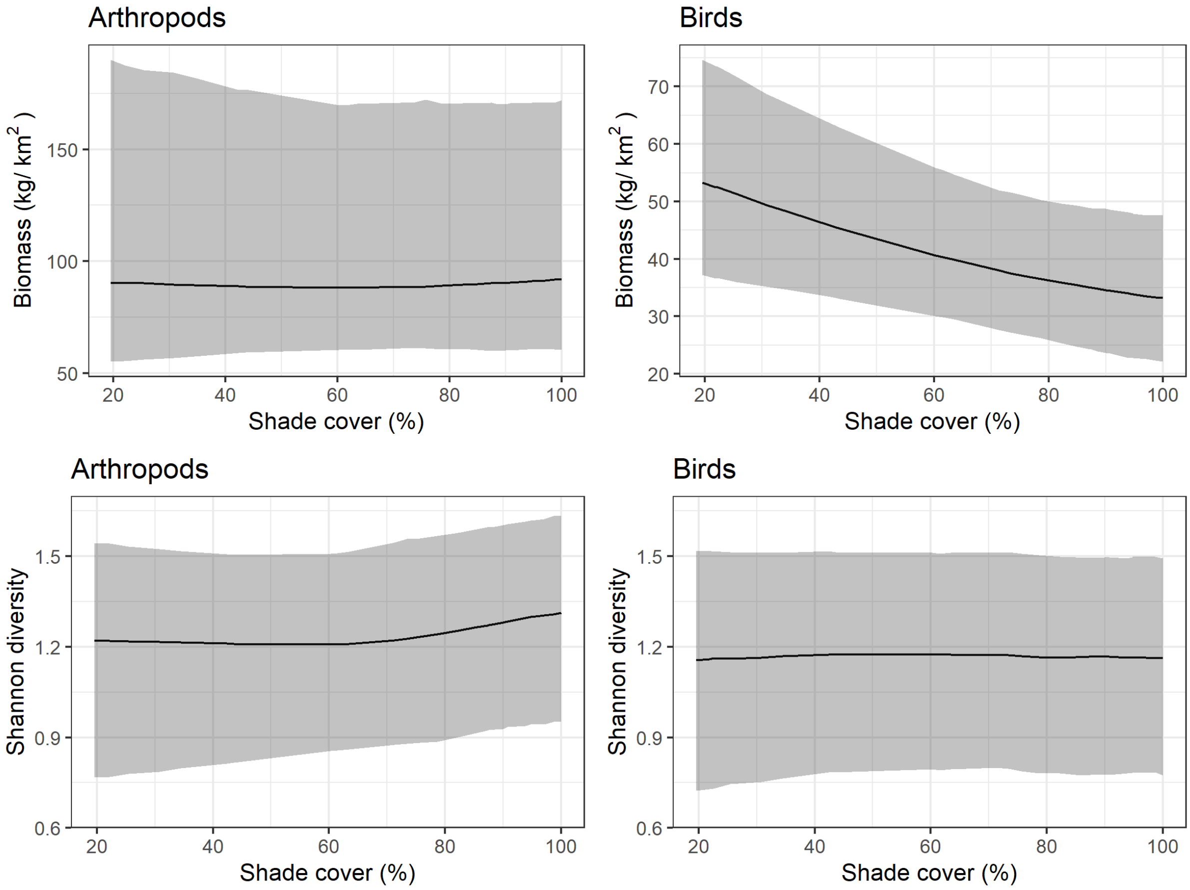


Figure 22. Effect of shade cover on equilibrium biomass and Shannon diversity of arthropods (excluding pests) and birds.

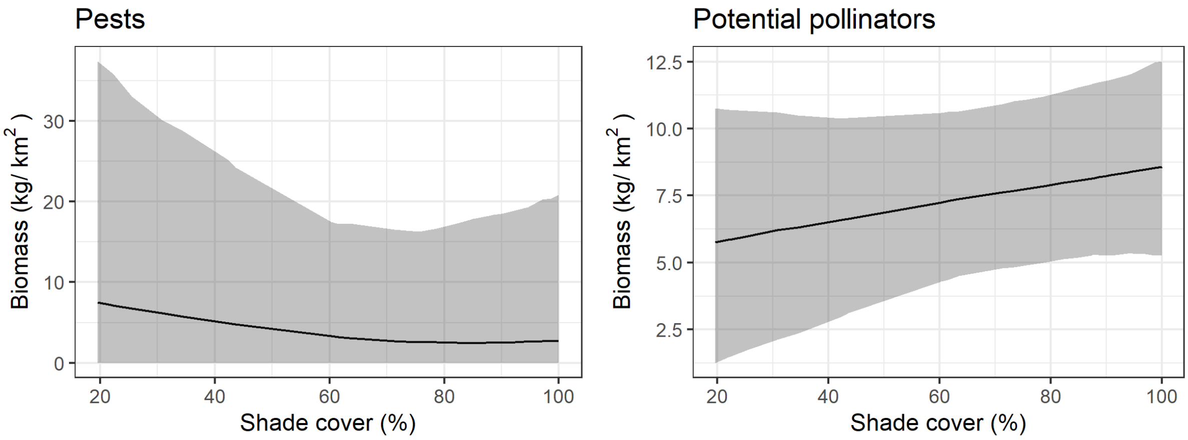


Figure 23. Effect of shade cover on equilibrium biomass of pests and potential pollinators.

DISCUSSION

I developed a modelling framework to investigate the dynamics of complex communities. Under simulation, my model was able to retrieve the underlying parameters with high accuracy and precision, and to estimate resulting community equilibrium states. When fit to field data from African cocoa agroforestry, the model showed important changes in community states with management, revealing that shady farms may favour arthropod diversity and pollinator abundance, whilst reducing pest biomass.

Simulation study

The accurate estimation of equilibrium densities is a complicated task because it requires accurate estimation of all parameters in the **b** vector and the **A** matrix (Equation 5.4). Then, there is an additional complication because equilibrium densities of species are estimated not directly from the parameters in the **A** matrix but the inverse of these. Each parameter in $\mathbf{A}^{-1}$ is a function of all the elements in the **A** matrix, not just the a_{ij} term. Consequently, small inaccuracies in estimated parameters in the **A** matrix could result in large changes in the inverse, and thus large differences in equilibrium densities estimated (Bender et al., 1984).

This difficulty was partly illustrated in my simulation results, where the estimated equilibrium densities of ‘Prey 9’ showed an opposite trend with shade cover to the simulation values. In the simulation, Prey 9 had a negative coefficient for the effect of shade cover on growth rate, yet its equilibrium densities increased with shade, indicating that the effect of interactions with other species outweighed the effect of shade on growth rate. The model estimated the direction of the effect of shade on growth rate correctly (negative), but then estimated equilibrium densities to decrease with shade cover, indicating a weaker influence of species interactions on equilibrium density. This is just one example of how small inaccuracies in parameter estimates can change results significantly.

The overall high accuracy of the model estimates under simulation was probably helped by two factors: first, the data were generated using the same process model the parameters were estimated with, therefore assuming that I had perfect knowledge of the food-web and specified it correctly (e.g., which species interact with each other). Second, the simulation assumed that I observed species densities perfectly. These two aspects of the simulation model are a simplification of reality, but are useful for testing the model under ideal conditions. Another simplifying assumption made in the simulation is that the effect of covariates on growth rates is a deterministic process with no noise, whilst it is likely that there are other factors plus stochasticity influencing these growth rates.

Application to cocoa agroforestry

When fit to field data, estimated parameters in general matched my biological expectations. Arthropod growth rates indicated population doubling times of 15-55 days, which is within the ranges documented by previous studies (Babin, 2009). The effect of shade cover on growth rates was negative for groups such as Hemiptera and Lepidoptera, matching previous findings (Ahenkorah et al., 1974, 1987). Bird groups had significantly higher growth rates than expected; a population half-life of 50 – 140 days seems unlikely for small predators with rapid metabolism. However, the effect of shade cover on bird groups matched biological intuition: growth rates were higher in shady farms for forest birds, whilst the opposite was true *Camaroptera*, *Hylia* and *Ispidina*, which contain habitat generalist species (Jarrett, Smith, et al., 2021; Naidoo, 2004).

Importantly, the direction of the effect of shade on growth rates did not always match the trend in equilibrium densities with shade cover. For instance, forest birds had a positive coefficient for the effect of shade on growth rate, but their equilibrium densities decreased with increasing shade cover. In contrast, Hemiptera pests had a negative coefficient for the effect of shade on growth rates, yet their equilibrium densities increased with increasing shade. These apparent discrepancies can be explained by effects of other species in the community (Duchardt et al., 2021; Kawatsu et al., 2021; Strauss, 1991): whilst forest birds may have higher growth rates in shady farms, there may not be enough prey to support them, and consequently the population equilibrium is lower. This process could indicate an ecological trap, whereby forest birds are attracted to shady farms due to the apparently favourable habitat, but then do not encounter sufficient prey for populations to persist (Robertson & Hutto, 2006). These findings reflect the power of my modelling framework: they demonstrate using modest amounts of field data that species' equilibrium densities depend both on the effect of habitat on the species itself but also on the populations of other species in the community, and that the relative influence of these two processes may vary between species.

Equally importantly, my results show that a) raw data from the field may not accurately represent transient densities unless corrected for detectability, and b) trends between transient densities and management may not reflect trends in equilibrium densities with management (Fig. 16). The first became clear when examining the differences between raw bird and arthropod counts and estimated densities (Chapt. 3, Chapt. 4). The second could be seen when comparing the trends in estimated densities with management (Chapt. 3, Chapt. 4) and the trends in equilibrium densities with management. These discrepancies likely occur because the estimated transient states are fluctuating around an unobserved equilibrium point, but estimating that equilibrium point requires considering the community as a whole. For instance, the transient densities of forest birds estimated showed a positive trend with shade cover (Jarrett, Smith, et al., 2021), whilst equilibrium densities showed the opposite trend. Presumably, high densities of forest birds observed in shady farms in the field reflect peaks in large fluctuations around an overall lower equilibrium point. My results indicate that directly interpreting correlations between field counts and management may be misleading: first, correcting for detection processes is important, and second, trends between transient densities and management may not reflect similar trends in equilibrium densities.

I assessed the diversity of communities in our farms and their potential value for agricultural productivity. My results indicate that increased shade cover may benefit arthropod diversity but result in lower bird biomass. The higher diversity of arthropods in shady farms may be associated to the microclimatic conditions created by shade trees, including increased humidity and reduced temperature fluctuations (Outhwaite et al., 2022; Tscharntke et al., 2011). The more diverse plant community found in shady farms may also offer improved resources, both in terms of food and microhabitats for arthropods (Outhwaite et al., 2022; Tscharntke et al., 2011). In contrast, the diversity of birds was not affected by shade cover, perhaps because the small insectivores considered in this study are largely generalist taxa (Jarrett, Smith, et al., 2021; Naidoo, 2004). The higher biomass of birds in sunny farms was mostly driven by the most abundant genus, *Ispidina*, which favours open habitat instead of closed-canopy forest (Naidoo, 2004). In terms of potential contribution to productivity, my results indicate that shady farms may be preferable as they contain higher biomass of potential pollinators (Dipterans) and lower biomass of pests. Higher biomass of Dipterans in shady farms may be due to their preference for humid environments for breeding (Bos & Sporn, 2012; Toledo-Hernández et al., 2021). In contrast, the increase in pest abundance with management intensity may be a result of reduced competition or predation from other arthropods (Akesse-Ransford et al., 2021; Rice & Greenberg, 2000).

My model did not explicitly examine agricultural yield, but rather, used pest and potential pollinator population densities as an indication of productivity outcomes. This means that, whilst I can discuss the potential contribution of wildlife community states to productivity, I cannot fully evaluate productivity. To do this, I would need to explicitly include agricultural crops into the model, and account for their own intrinsic changes with management. For instance, it could be that whilst brown capsids are more abundant in sunny farms, the intrinsic growth rate of crops is also higher, therefore still achieving higher yields than in the shade (Phalan et al., 2011). Adding crops into my community model is the next natural step in fully evaluating the implications of community states.

Other extensions to this model would be to include more types of species interactions (e.g., pollination, or predation between arthropod groups), as well as additional predators (e.g., insectivorous bats). Structural features such as non-linear functional responses, prey switching and Allee effects could be explored using common extensions of linear predictors (Asseburg et al., 2006; Lindmark et al., 2019). My intention was to test this model on a simplified scenario to minimise the number of parameters required, and therefore I clustered most species into higher taxonomic groups. More exploration is needed to investigate how data sufficiency compares with level of taxonomic aggregation. The less data there are, the more aggregated a model may need to be and the more noise the results will contain. Hierarchical modelling (where particular parameter values can be assumed to be shared to different degrees between species) might be a useful way to automate this without a-priori decisions about clumping. Whether our existing dataset would support a more complex food-web remains to be tested.

Here, I presented a novel method for investigating population dynamics of complex communities. My method revealed that several commonly made assumptions may not hold in these complex multispecies communities: first, it is essential to account for varying detectability in densities of species observed in the field. Second, trends in species densities with environmental covariates may not correspond to trends in equilibrium densities. And third, equilibrium densities of a species are significantly influenced by other species in the community; in some cases, the influence of other species may ‘flip’ the effect of environmental covariates. Applying my method to data from wildlife communities in agroforestry revealed that wildlife communities in shadier farms are important both for biodiversity conservation and for productivity. This win-win in low-intensity agroforestry is promising for a land-sharing scenario, and sheds light on the dangers of pursuing intensified agriculture in an era of biodiversity crisis.

Chapter 6 | Tropical agroforestry: a natural lab for studying community ecology?

Throughout this thesis, my aim has been to better understand animal communities in tropical agroforestry, including how they interact with management. I have addressed this issue using several methodologies, and as a result I have learned both about the ecology of these complex systems but also about the limitations and potential of different methods in studying community ecology. Here, I will discuss my main findings, both ecological and methodological, and consider their implications for the future of agroforestry research.

Agroforestry contains animal communities important for both conservation and agricultural productivity

Agroforestry systems are discrete habitat patches in which agricultural crops are planted beneath a canopy of shade trees (Tscharntke et al., 2011). The spatial scale of these systems makes them relevant to organisms such as birds, mammals and insects, and they are commonly maintained throughout time in relatively stable conditions (Perfecto & Vandermeer, 2008; Schroth & Harvey, 2007; Tscharntke et al., 2011). The ubiquity of agroforestry systems in the tropics (covering 12 million hectares worldwide; FAOSTAT, 2020) make them of interest for biodiversity conservation; in tropical regions, where human populations continue to expand, we need solutions that will allow food production whilst simultaneously providing habitat for wildlife (Bennett et al., 2021; Tscharntke et al., 2012). However, certain wildlife groups, such as Mirid bugs (Hemiptera: *Miridae*), some moth larvae (cocoa pod borer *Conopomorpha cramerella*, cocoa fruit borer *Carmenta theobromae*), and mealybugs (Hemiptera: *Pseudococcidae*), can cause severe damage to crops in agroforestry (Bagny Beilhe, Babin, et al., 2018; Wessel & Quist-Wessel, 2015). Therefore, the dynamics of the species contained in tropical agroforestry are highly relevant both for biodiversity conservation and agricultural productivity (Clough et al., 2011).

Animal communities in agroforestry have been widely studied, both from a conservation perspective and to better understand provision of ecosystem services and dis-services (Bennett et al., 2021; Bisseleua et al., 2013; Toledo-Hernández et al., 2021). The focus of these studies is often on how to manage these systems in order to benefit certain animal groups, such as rainforest birds (Bennett et al., 2021), ants (Delabie et al., 2007) or bats (Faria et al., 2006). However, the majority of these studies focus on agroforestry systems in the Neotropics and south-east Asia, with the Afrotropics being poorly represented (Bennett et al., 2021; De Beenhouwer et al., 2013). I aimed to contribute to correcting this geographical bias in Chapter 2 and the resulting publication (Jarrett, Smith, et al., 2021), where I assessed the effect of conversion to agroforestry and agroforestry management on bird communities in African cocoa farms. I found that the composition and diversity of bird communities in primary forest were different from those in cocoa farms. The implications of this finding are that, however much agroforestry is managed to favour biodiversity, it will still not act as a substitute for primary forest, and thus, it is necessary to conserve areas of forest to protect the most vulnerable forest-dependent groups (Stratford & Stouffer, 2013).

Most noticeably, ant-followers (insectivores that forage on the forest floor following ant swarms) and forest specialists that combined constituted >40% of the bird community in primary forest, in shaded cocoa constituted ~7% of the community, and in sunny farms just ~1%. These findings indicate that intensification of cocoa agriculture and conversion to monocultures are damaging to rainforest bird populations (Maas et al., 2009; Sanderson et al., 2022; Şekercioglu et al., 2019; Waltert et al., 2005). From a conservation perspective, my results suggest that incentivising shady agroforestry (perhaps through appropriate subsidization) so that farmers who maintain shade in their farms and consequently contribute to rainforest bird conservation, could receive higher returns for their crops (Bisseleua et al., 2009).

Surveying animals in agroforestry is complex

Whilst Chapter 2 provided insights into the effect of management on bird communities in cocoa agroforestry, I could only assess relative community composition using mist-net captures as a proxy for abundance, because the dataset was compiled from many different projects and was not collected following a standardised methodology. Mist-nets, whilst one of the most common tools for surveying birds, tend to have varying capture probability depending on the characteristics of the surrounding habitat, and therefore data on captures may be biased by habitat characteristics (Rodrigues & Prado, 2018). In agroforestry especially, where vegetation structure is extremely variable (Tscharntke et al., 2011), we would expect differing capture rates from mist-nets. Indeed, this range of habitat characteristics common to agroforestry, coupled with the high diversity of species present, poses a general challenge when surveying animals in these habitats. For birds and bats, mist-nets may be influenced by vegetation density (Rodrigues & Prado, 2018), for arthropods, the varying ecology of species makes surveying the whole community complicated (Montgomery et al., 2021), and for terrestrial mammals, detection by camera traps may be biased by vegetation structure (Banks-Leite et al., 2014). This general challenge of assessing community composition in complex habitats led me to consider methods of statistical adjustments that would allow unbiased estimation of population size.

Data integration as a solution to estimating population size in complex habitats

In Chapter 3, I aimed to assess the effect of agricultural management on bird communities, but this time estimating bird population size. For this, I developed a model that combined mark-recapture and acoustic count data, correcting for vegetation-structure-driven biases in mist-net data. Estimating population size allowed me to establish that, for instance, ant-followers (vulnerable rainforest taxa) occurred at population sizes of ~1 individual per cocoa farm, meaning that if the whole landscape was converted to agriculture these groups would be at risk of local extinction. The integrated model estimated with more precision the effect of shade cover on bird guilds compared with a mark-recapture only model, because shade cover influenced both population size and detectability. Also, of five guilds that I considered in both Chapter 2 and 3, only two showed a trend with shade cover in Chapter 2, but by using the more sensitive methods of Chapter 3 this number rose to four. These findings demonstrate the potential of data integration to improve estimates of abundance, and emphasise the importance of accounting for detectability when considering communities in complex habitats (Banks-Leite et al., 2014; Rodrigues & Prado, 2018).

In Chapter 4, data integration permitted me to investigate the effect of management on arthropod communities. Arthropods are important in agroforestry because they play roles in providing ecosystem services to the crops, causing damage to crops, and serving as food to the bird community (Bagny Beilhe, Babin, et al., 2018; Maas et al., 2016; Toledo-Hernández et al., 2021). However, they are notoriously hard to sample due to their diverse life-histories and morphologies (Montgomery et al., 2021). In this chapter I integrated data from different methods to achieve precise estimates of population size of different arthropod taxa. I found that shady farms had lower population densities of pests, including brown capsid, the primary pest of cocoa in Africa, and higher densities of natural enemies & potential pollinators.

Chapter 4, as well as its preceding chapter, confirmed that data integration is an effective solution to improve precision of population size estimates from field data, and also to correct for sampling biases (Miller et al., 2019; Zipkin et al., 2019). Data integration for population size estimation is becoming more wide-spread, and yet the majority of studies on animal communities still tend to consider different data sources separately, hence losing precision due to smaller sample sizes, and missing an opportunity for correcting sampling biases (Kindsvater et al., 2018). The findings from my thesis show that estimating population size from modest field datasets is not only feasible, but also provides opportunities for types of analyses not possible with abundance proxies.

Transient population densities can reveal the mechanisms driving community dynamics

My main motivation to develop these methods to estimate population size was to make progress towards a predator-prey type community model of animal communities in cocoa agroforests. A model of this type would allow me to investigate dynamics of complex communities in agroforests, considering effects of environmental covariates as well as the trophic, competitive and indirect interactions between species. Importantly, these models distinguish transient community states from equilibrium states: when we observe communities, we see them at some (transient) point in state-space, but this may only be a temporary position from which communities will move (Pimm, 1982). A globally stable equilibrium state of a community is the region of state-space towards which it travels unless otherwise perturbed (Pimm, 1982). This type of community model, though extensively described and explored theoretically (Pimm, 1982), has rarely been parameterized from field data (and never from tropical agroforest data), due to the assumed requirement of a long time-series of data on populations (Ellner et al., 2002; Yodzis, 1998). In the fifth chapter of this thesis, I exploited the existing rich theoretical knowledge of community dynamics and coupled it with more modern approaches to field data, such as data integration and observation modelling. Ultimately, my aim was to understand the underlying states of communities in agroforestry, and how these related to biodiversity conservation and agricultural productivity.

The method I developed allowed me to accurately estimate parameters for growth rates and species interactions, and from these estimate equilibrium states of communities under different environmental conditions. The power of this approach was that it revealed the mechanisms driving the community dynamics in our farms. My findings demonstrate how both environmental covariates and interspecific interactions can be important drivers of community dynamics, and that the relative influence of these two forces may vary according to the species or environment. My results also showed that transient densities surveyed in the field may show different trends with environmental covariates compared with equilibrium densities. This finding shed light on the issues with assuming equilibrium when sampling animal communities.

Methodological advances help apply traditional community ecology to complex systems

Mechanistic community models, such as the one I developed in Chapter 5, are rarely parameterized from field data because of the requirement for large amounts of data that allow the estimation of many parameters (Yodzis, 1998). However, several recent methodological advances may make this task increasingly feasible. First, as mentioned previously, data integration provides the opportunity to exploit the available data to its full potential (Kindsvater et al., 2018; Miller et al., 2019). Second, the increasingly widespread use of hierarchical modelling facilitates estimation of population size by explicitly considering factors influencing detectability (Kéry & Royle, 2020). In terms of model parametrisation, the task may be greatly facilitated by increasingly common molecular techniques of diet analyses, which can reveal with high accuracy the prey species consumed by predators, thus giving detailed information on linkages between species (Hoenig et al., 2022). All these tools may result in a resurgence of community models as practical tools to assess the dynamics of complex communities, such as those in agroforestry. The work presented in my final chapter constitutes a first step towards this application, providing proof-of-concept and considerations for further developments.

Estimating community states is useful to assess implications of management in agro-ecosystems

In my fifth chapter, I found that community states in African cocoa farms varied with shade cover; in shady farms, communities contained higher diversity of arthropods, higher biomass of dipterans (potential pollinators), and lower biomass of pests, compared with sunny farms. These findings indicate that animal communities in shady farms are diverse and have the potential to contribute to agricultural productivity through increased pollination and reduced pest burdens. Importantly, whilst I recognise non-equilibrium dynamics in my data, I have based my management investigation around equilibria. This makes my results relating to management both more accurate (because they are not biased by the equilibrium assumption) and more cost-effective (because they allow the natural inertia of systems to be exploited).

The challenges of studying community ecology in agroforestry

Despite the promising potential of community models to unravel the dynamics of species in agroforestry, this system is challenging due to its complexity and our limited understanding of its functioning, especially in the Afrotropics. First, the composition of animal communities is still poorly understood: for instance, during our work we encountered issues with arthropod identification (many tropical African arthropods are still undescribed; Goulet & Huber, 1993) and even bird identification (several disputed species e.g., *Terpsiphone sp*; Fabre et al., 2012). Then, information on interactions between species in tropical agroforestry is extremely limited; for instance, whilst the diets of temperate species such as *Parus* sp. are described in detail by many sources (Jarrett et al., 2020), the diets of Afrotropical birds are mostly unknown in the academic literature. Finally, the provision of ecosystem services and dis-services, and their influence of agricultural productivity in African agroforestry is poorly understood (De Beenhouwer et al., 2013).

In general, an easier trajectory could have been to develop my community model on a simpler better-known system, where parameters, food-web structure, and other assumptions could have been much better informed. An example of this could be Mediterranean vineyards or apple orchards (Charbonnier et al., 2021; García et al., 2021). In these systems, the species present are well studied, pests are monitored, and predator diets are known. Developing the model in this habitat would be a simpler task and still serve as proof-of-concept, and once this was accomplished, the framework could be extended to systems with more unknowns.

The process of developing the analyses methods presented in this thesis has taught me several lessons about the ideal design of data collection for community ecology research. Most noticeably, the issue of estimating densities of species from field counts was a challenging one, and one that could have perhaps been simplified with different field methods. If I was to repeat this type of study, I would choose my field protocols in order to optimise the precision of density estimates; for birds for instance, this would probably involve a more rigorous mark-recapture study design, coupled with acoustic recording. For arthropods, I would probably carry out more extensive visual surveys, perhaps with some calibration exercises in a lab environment. I would additionally attempt finer taxonomic resolution of counts, and importantly, species-level identification of pest insects. An increased precision in the density estimates would result in increased precision also in the parameters and states estimated by the community model.

Critically, the analyses of this project would have been facilitated by field data collected at smaller intervals, for instance monthly. Arguably, one year of monthly sampling would have been better suited than several years of 6-monthly sampling. Of course, time and budget limitations often end up dictating these decisions.

Overall, our understanding of communities in agroforestry could be greatly improved by collecting data that: a) encompasses entire communities and rather than single species (or specific taxa), b) allows population size estimation, c) investigates connections between species (trophic interactions, competition, parasitism), d) quantifies environmental covariates that are likely to influence species. Ideally, these data collection protocols should be conducted year-round and at regular intervals. If long-term data collection is not possible, then relevant spatial replication may be a useful alternative.

Conclusion

Despite some limitations, this thesis provides an in-depth study of animal communities in agroforestry, with important advances both in our ecological understanding of the system, but also in the tools available to study it. My findings shed light on the many benefits of shaded agroforestry, including higher abundances of pollinators and natural enemies, and lower abundances of pests. Importantly, my investigations consider the equilibria of communities; this is a novel contribution and one with the potential to provide accurate and cost-effective management recommendations to combine high biodiversity and productivity in agro-ecosystems. I provide tools to correct for sampling bias in these complex habitats, as well as to estimate density of species and investigate the dynamics of communities. Future agroforestry research could benefit from a community ecology approach to fully understand the potential of agroforestry as a land-sharing solution.

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Appendices

Appendix 1: Chapter 2 sampling sites

Table S1. List of sampling sites for birds in cocoa and mature forest.

Site ID	Habitat	Captures	Latitude	Longitude	No. Sampling Days*	Sampling Years	Region
1	cocoa	290	3.47207	11.26735	3	2019-2020	South
2	cocoa	262	2.73968	11.23124	9	2006	South
3	cocoa	48	4.83992	9.45138	2	2017-2018	West
4	cocoa	91	4.83352	9.45303	2	2017-2018	West
5	cocoa	45	4.56451	11.16261	2	2017-2018	Ecotone
6	cocoa	143	5.56455	14.09011	6	1990, 1995	Ecotone
7	cocoa	84	3.00444	12.34778	3	2005	South
8	cocoa	93	4.97334	9.46334	2	2017-2018	West
9	cocoa	81	4.76749	9.47407	2	2017-2018	West
10	cocoa	56	4.76727	9.48378	2	2017-2018	West
11	cocoa	116	4.79418	9.48258	2	2017-2018	West
12	cocoa	140	3.90672	12.51043	5	2017-2020	South
13	cocoa	30	3.91195	12.50733	4	2017-2019	South
14	cocoa	100	4.04347	12.70014	4	2017-2019	South
15	cocoa	87	3.57199	11.33040	3	2019-2020	South
16	cocoa	44	4.08369	12.68218	4	2017-2019	South
17	cocoa	94	3.89624	11.71760	3	2019-2020	South
18	cocoa	156	3.90349	11.71650	3	2019-2020	South
19	cocoa	53	5.08295	9.41241	2	2017-2018	West
20	cocoa	64	5.07988	9.40237	2	2017-2018	West
21	cocoa	275	3.54058	12.84585	18	1999, 2009, 2014	South
22	cocoa	60	4.45000	11.55000	2	1997	Ecotone
23	cocoa	72	3.35773	12.73720	3	2019-2020	South
24	cocoa	42	2.35693	11.37630	2	2006	South
25	cocoa	45	2.35964	11.38080	2	2006	South
26	cocoa	54	2.57866	11.03326	2	2006	South
27	cocoa	78	2.58369	11.02485	2	2006	South
28	cocoa	58	3.26333	11.79228	2	2006	South
29	cocoa	60	3.27026	11.79395	2	2006	South
30	cocoa	57	4.76667	10.83333	3	1997	Ecotone
31	cocoa	132	3.86398	12.43288	5	2017-2020	South
32	cocoa	72	3.86365	12.42673	4	2017-2019	South
33	cocoa	44	3.59393	11.33310	2	2019	South
34	cocoa	66	3.58884	11.32920	3	2019-2020	South
35	cocoa	28	4.25548	11.24738	2	2006	Ecotone
36	cocoa	58	4.24970	11.23558	2	2006	Ecotone

37	cocoa	107	4.07666	11.55443	4	2006	South
38	cocoa	217	3.86694	13.31611	9	1990, 1993, 2005	South
39	cocoa	160	4.16678	11.55236	8	1997, 2010	Ecotone
40	cocoa	54	3.45469	11.25530	2	2019	South
41	cocoa	37	3.98575	12.43751	2	2019	South
42	cocoa	125	3.97200	12.45021	3	2019-2020	South
43	cocoa	134	3.38741	12.74300	3	2019-2020	South
44	cocoa	71	4.03817	10.57422	3	2000	South
45	cocoa	40	4.06842	10.56138	2	2000	West
46	cocoa	104	3.39001	12.74920	3	2019-2020	South
47	cocoa	71	3.38308	12.74530	3	2019-2020	South
48	cocoa	51	3.58430	11.32460	2	2019	South
49	cocoa	41	4.55887	11.09055	2	2017-2018	Ecotone
50	cocoa	64	2.97893	11.12102	1	2020	South
51	cocoa	44	2.79648	11.18457	1	2020	South
52	cocoa	37	2.82250	11.16628	1	2020	South
53	cocoa	54	2.88723	11.20725	1	2020	South
54	cocoa	57	3.01429	11.11771	1	2020	South
55	cocoa	43	2.98922	11.11367	1	2020	South
56	cocoa	64	2.83045	11.15124	1	2020	South
57	cocoa	28	2.77107	11.21139	1	2020	South
58	mature forest	113	3.42500	10.77675	6	2005, 2007	South
59	mature forest	7	3.47278	12.78396	1	2009	South
60	mature forest	239	2.65472	13.47111	10	1993, 2005	South
61	mature forest	197	3.19056	12.81167	23	1995-1996, 1999	South
62	mature forest	49	3.18853	12.80192	6	2017	South
63	mature forest	311	5.15745	9.33401	17	2016	West
64	mature forest	316	5.17541	9.34544	12	2016	West
65	mature forest	386	5.19040	9.34578	17	2016	West
66	mature forest	384	5.17543	9.45589	14	2016	West
67	mature forest	70	3.19444	12.81630	2	2019	South
68	mature forest	74	2.96972	11.37531	3	2005	South
69	mature forest	107	4.31900	10.33000	8	2013, 2015	West
70	mature forest	160	3.52778	12.82455	4	2010	South
71	mature forest	124	2.31043	15.75552	3	1993	South
72	mature forest	39	3.18352	12.81350	2	2019	South

73	mature forest	103	4.45639	9.00917	5	2005, 2007	West
74	mature forest	166	3.50058	10.03951	5	2005, 2007	South
75	mature forest	209	3.51756	10.00914	6	2006-2007	South
76	mature forest	112	2.33714	10.19378	7	2005, 2007	South
77	mature forest	77	2.98072	12.40264	3	2005	South
78	mature forest	56	3.19443	12.80950	2	2019	South
79	mature forest	106	2.62351	14.01054	4	2007	South
80	mature forest	826	1.61475	10.87810	27	2014, 2016-2017	South
81	mature forest	53	3.19138	12.82040	2	2019	South
82	mature forest	81	3.43250	13.59417	5	2005	South
83	mature forest	320	2.65861	13.39694	14	1990, 1993, 2005	South

* One sampling day represented 4-6 hrs of mist-netting, between dawn (~6:30) to 12.30-17:00.
At each site, we opened 12 - 20 mist-nets (12 m long x 3 m high, 30 mm mesh)

Appendix 2: Chapter 2 captures

Table S2. Species captured in Cameroonian and Equato-Guinean cocoa and mature forest sites, with characteristics used for analyses and the proportion of total captures they represented. The proportion of captures was calculated by dividing the number of captures for each species by the total captures in each habitat type (4778 in cocoa and 4788 in mature forest). Abbreviations: 'Y' = yes, 'N' = no, 'R' = rare, 'O' = occasional, 'F' = frequent, 'U' = unknown.

Species	Dietary guild	Endemic	IUCN Status	Mixed species flock *	Ant following +	Forest specialist	Proportion of captures in COCOA	Proportion of captures in FOREST
Accipiter castanilius	Carnivore	Y	LC	N	N	Y	0.0008	0.0000
Accipiter erythropus	Carnivore	N	LC	N	N	N	0.0006	0.0000
Accipiter toussenelii	Carnivore	N	LC	N	N	N	0.0010	0.0004
Acrocephalus rufescens	Insectivore	N	LC	N	N	N	0.0000	0.0002
Agelastes niger	Insectivore	Y	LC	N	N	Y	0.0000	0.0002
Alcedo quadribrachys	Piscivore	N	LC	N	N	N	0.0000	0.0021

Alethe castanea	Insectivore	Y	LC	O	F	Y	0.0111	0.0940
Anthreptes rectirostris	Insectivore	N	LC	F	N	N	0.0004	0.0000
Anthreptes seimundi	Nectarivore	N	LC	F	N	N	0.0015	0.0000
Apalis binotata	Insectivore	Y	LC	N	N	N	0.0002	0.0002
Apalis rufogularis	Insectivore	Y	LC	F	N	Y	0.0002	0.0000
Apaloderma aequatoriale	Insectivore	Y	LC	N	N	Y	0.0000	0.0006
Atimastillas flavicollis	Frugivore	N	LC	F	O	N	0.0008	0.0000
Atronanus fuliginosus	Insectivore	Y	LC	N	N	N	0.0002	0.0000
Baeopogon indicator	Frugivore	N	LC	O	O	Y	0.0010	0.0002
Bathmocercus rufus	Insectivore	Y	LC	N	O	N	0.0000	0.0008
Batis minima	Insectivore	Y	LC	U	U	N	0.0002	0.0000
Bleda notatus	Insectivore	Y	LC	F	F	Y	0.0048	0.0827
Bleda syndactylus	Insectivore	Y	LC	F	F	Y	0.0031	0.0286
Buccanodon duchaillui	Frugivore	N	LC	O	N	Y	0.0006	0.0013
Butorides striata	Piscivore	N	LC	N	N	N	0.0000	0.0002
Bycanistes albotibialis	Frugivore	Y	LC	N	N	Y	0.0013	0.0008
Bycanistes fistulator	Frugivore	N	LC	N	N	Y	0.0002	0.0002
Calyptocichla serina	Frugivore	N	LC	O	N	Y	0.0000	0.0038
Camaroptera brachyura	Insectivore	N	LC	N	N	N	0.0293	0.0008
Camaroptera chloronota	Insectivore	N	LC	O	O	N	0.0094	0.0019
Camaroptera superciliaris	Insectivore	N	LC	N	N	Y	0.0015	0.0004
Campethera cailliautii	Insectivore	N	LC	N	N	N	0.0002	0.0000
Campethera caroli	Insectivore	N	LC	F	N	Y	0.0040	0.0013
Campethera nivosa	Insectivore	N	LC	F	N	N	0.0004	0.0054
Centropus monachus	Insectivore	N	LC	N	N	N	0.0002	0.0000
Ceratogymna atrata	Frugivore	N	LC	N	N	Y	0.0002	0.0004
Ceuthmochares aereus	Insectivore	N	LC	N	N	Y	0.0002	0.0000
Chalcomitra rubescens	Nectarivore	Y	LC	N	N	N	0.0006	0.0000
Chamaetylas poliocephala	Insectivore	N	LC	F	F	Y	0.0000	0.0386
Chlorocichla falkensteini	Frugivore	Y	LC	O	N	N	0.0025	0.0000

Chlorocichla simplex	Frugivore	N	LC	O	N	N	0.0059	0.0000
Chloropicus fuscescens	Insectivore	N	LC	F	N	N	0.0004	0.0000
Chloropicus gabonensis	Insectivore	Y	LC	N	N	N	0.0000	0.0004
Chrysococcyx caprius	Insectivore	N	LC	N	N	N	0.0013	0.0000
Cinnyris batesi	Nectarivore	Y	LC	F	N	Y	0.0002	0.0002
Cinnyris chloropygius	Nectarivore	N	LC	N	N	N	0.0109	0.0010
Cinnyris coccinigastrus	Nectarivore	N	LC	N	N	N	0.0002	0.0000
Cinnyris johannae	Insectivore	N	LC	N	N	N	0.0002	0.0000
Cinnyris minullus	Nectarivore	N	LC	F	N	N	0.0077	0.0004
Cinnyris superbus	Nectarivore	N	LC	N	N	N	0.0021	0.0000
Cinnyris venustus	Nectarivore	N	LC	F	N	N	0.0004	0.0000
Cisticola erythrops	Insectivore	N	LC	N	N	N	0.0006	0.0000
Clytospiza monteiri	Granivore	Y	LC	N	N	N	0.0004	0.0000
Colius striatus	Frugivore	N	LC	N	N	N	0.0000	0.0002
Columba larvata	Granivore	N	LC	N	N	N	0.0000	0.0002
Columba unicincta	Granivore	N	LC	N	N	Y	0.0002	0.0000
Corythornis leucogaster	Piscivore	N	LC	N	N	Y	0.0021	0.0192
Cossypha cyanocampter	Insectivore	N	LC	N	N	Y	0.0000	0.0004
Cossypha natalensis	Insectivore	N	LC	N	N	Y	0.0008	0.0002
Cossypha niveicapilla	Insectivore	N	LC	N	N	N	0.0006	0.0000
Cossypha polioptera	Insectivore	N	LC	N	N	Y	0.0002	0.0000
Criniger barbatus	Insectivore	N	LC	F	O	Y	0.0002	0.0000
Criniger chloronotus	Insectivore	Y	LC	F	F	Y	0.0000	0.0092
Criniger sp	Insectivore	N	LC	F	O	Y	0.0042	0.0115
Cuculus gularis	Insectivore	N	LC	N	N	N	0.0002	0.0000
Cyanomitra cyanolaema	Nectarivore	N	LC	N	N	N	0.0019	0.0008
Cyanomitra olivacea	Nectarivore	N	LC	F	N	N	0.2131	0.1487
Cyanomitra verticalis	Nectarivore	N	LC	N	N	N	0.0036	0.0000
Deleornis fraseri	Nectarivore	N	LC	F	N	N	0.0019	0.0038
Dendropicos elliotii	Insectivore	Y	LC	F	N	Y	0.0000	0.0002

Dicrurus atripennis	Insectivore	N	LC	F	N	Y	0.0002	0.0025
Dicrurus modestus	Insectivore	N	LC	N	N	N	0.0004	0.0004
Dicrurus sharpei	Insectivore	N	LC	F	N	N	0.0002	0.0002
Dryoscopus sabini	Insectivore	N	LC	N	N	N	0.0002	0.0000
Dryoscopus senegalensis	Insectivore	Y	LC	N	N	N	0.0006	0.0000
Elminia albiventris	Insectivore	Y	LC	O	N	Y	0.0000	0.0002
Elminia longicauda	Insectivore	N	LC	N	N	N	0.0006	0.0000
Elminia nigromitrata	Insectivore	N	LC	O	N	Y	0.0006	0.0107
Eremomela badiceps	Insectivore	N	LC	N	N	N	0.0023	0.0000
Erythrocercus mccallii	Insectivore	N	LC	F	N	N	0.0008	0.0000
Estrilda astrild	Granivore	N	LC	N	N	N	0.0023	0.0000
Estrilda atricapilla	Granivore	Y	LC	N	N	N	0.0006	0.0000
Estrilda melpoda	Granivore	N	LC	N	N	N	0.0013	0.0004
Estrilda nonnula	Granivore	Y	LC	N	N	N	0.0013	0.0002
Euplectes hordeaceus	Granivore	N	LC	N	N	N	0.0008	0.0000
Eurillas ansorgei	Frugivore	N	LC	O	N	Y	0.0002	0.0004
Eurillas curvirostris	Frugivore	N	LC	F	N	N	0.0071	0.0025
Eurillas gracilis	Frugivore	N	LC	O	N	N	0.0048	0.0004
Eurillas latirostris	Frugivore	N	LC	R	N	N	0.1078	0.1855
Eurillas virens	Frugivore	N	LC	R	N	N	0.1762	0.0466
Fraseria caerulescens	Insectivore	N	LC	O	N	N	0.0002	0.0000
Fraseria cinerascens	Insectivore	N	LC	N	N	Y	0.0004	0.0010
Fraseria griseigularis	Insectivore	N	LC	F	N	N	0.0000	0.0004
Fraseria tessmanni	Insectivore	N	LC	N	N	N	0.0008	0.0000
Gelochelidon nilotica	Insectivore	N	LC	N	N	N	0.0000	0.0002
Geokichla camaronensis	Insectivore	Y	LC	N	N	Y	0.0000	0.0021
Geokichla princei	Insectivore	N	LC	O	O	Y	0.0000	0.0002
Glaucidium sjostedti	Insectivore	Y	LC	N	N	Y	0.0000	0.0010
Gymnobucco bonapartei	Frugivore	Y	LC	N	N	N	0.0080	0.0000

Gymnobucco calvus	Frugivore	N	LC	N	N	N	0.0002	0.0000
Gymnobucco peli	Frugivore	N	LC	N	N	N	0.0002	0.0000
Halcyon badia	Insectivore	N	LC	N	N	N	0.0004	0.0008
Halcyon leucocephala	Insectivore	N	LC	N	N	N	0.0004	0.0000
Halcyon malimbica	Insectivore	N	LC	N	N	N	0.0015	0.0006
Halcyon senegalensis	Insectivore	N	LC	N	N	N	0.0006	0.0002
Hedydipna collaris	Nectarivore	N	LC	F	N	N	0.0027	0.0008
Horizocerus albocristatus	Frugivore	N	LC	F	O	Y	0.0004	0.0000
Hylia prasina	Insectivore	N	LC	F	N	N	0.0186	0.0134
Illadopsis cleaveri	Insectivore	N	LC	F	N	N	0.0006	0.0123
Illadopsis fulvescens	Insectivore	N	LC	F	N	N	0.0008	0.0090
Illadopsis puveli	Insectivore	N	LC	F	N	N	0.0006	0.0000
Illadopsis rufipennis	Insectivore	N	LC	F	N	N	0.0008	0.0159
Indicator conirostris	Insectivore	N	LC	N	N	Y	0.0004	0.0002
Indicator exilis	Insectivore	N	LC	N	N	N	0.0033	0.0002
Indicator maculatus	Insectivore	N	LC	N	N	N	0.0004	0.0088
Indicator minor	Insectivore	N	LC	N	N	N	0.0000	0.0010
Indicator willcocksi	Insectivore	N	LC	R	N	N	0.0010	0.0000
Ispidina lecontei	Insectivore	N	LC	O	O	N	0.0048	0.0038
Ispidina picta	Insectivore	N	LC	N	O	N	0.0414	0.0021
Ixonotus guttatus	Frugivore	N	LC	N	N	N	0.0004	0.0000
Lanius mackinnoni	Insectivore	Y	LC	N	N	N	0.0004	0.0000
Lophoceros fasciatus	Frugivore	Y	LC	N	N	N	0.0002	0.0000
Macrosphenus concolor	Insectivore	N	LC	F	N	Y	0.0000	0.0002
Macrosphenus flavicans	Insectivore	Y	LC	F	N	Y	0.0002	0.0004
Malaconotus cruentus	Frugivore	N	LC	N	N	N	0.0002	0.0000
Malimbus malimbicus	Insectivore	N	LC	F	N	N	0.0002	0.0006
Malimbus nitens	Insectivore	N	LC	F	N	N	0.0006	0.0010
Malimbus racheliae	Insectivore	Y	LC	F	N	Y	0.0000	0.0002
Mandingoa nitidula	Granivore	N	LC	N	N	N	0.0096	0.0002

Megabyas flammulatus	Insectivore	N	LC	N	N	N	0.0004	0.0000
Melignomon zenkeri	Insectivore	N	LC	N	N	N	0.0002	0.0002
Melocichla mentalis	Insectivore	N	LC	N	N	N	0.0002	0.0000
Merops albicollis	Insectivore	N	LC	N	N	N	0.0002	0.0000
Merops mentalis	Insectivore	N	NT	N	N	N	0.0000	0.0004
Merops muelleri	Insectivore	Y	LC	N	N	N	0.0002	0.0004
Muscicapa comitata	Insectivore	N	LC	N	N	N	0.0013	0.0002
Muscicapa epulata	Insectivore	N	LC	N	N	N	0.0004	0.0000
Muscicapa sethsmithi	Insectivore	Y	LC	N	N	N	0.0015	0.0006
Neocossyphus poensis	Insectivore	N	LC	O	F	N	0.0025	0.0180
Neocossyphus rufus	Insectivore	N	LC	O	F	Y	0.0002	0.0031
Nicator chloris	Insectivore	N	LC	O	N	N	0.0021	0.0013
Nicator vireo	Insectivore	Y	LC	N	N	N	0.0017	0.0013
Nigrita bicolor	Granivore	N	LC	F	N	N	0.0013	0.0010
Nigrita canicapillus	Granivore	N	LC	F	N	N	0.0006	0.0002
Nigrita fusconotus	Insectivore	N	LC	F	N	N	0.0008	0.0000
Nigrita luteifrons	Frugivore	Y	LC	F	N	N	0.0004	0.0000
Oriolus nigripennis	Insectivore	N	LC	O	N	N	0.0002	0.0000
Parmoptila woodhousei	Insectivore	Y	LC	F	N	N	0.0031	0.0031
Passer griseus	Granivore	N	LC	N	N	N	0.0042	0.0008
Peliperdix lathami	Insectivore	N	LC	N	N	Y	0.0000	0.0006
Phyllastrephus albigularis	Insectivore	N	LC	F	N	Y	0.0038	0.0036
Phyllastrephus poensis	Insectivore	Y	LC	F	N	Y	0.0000	0.0010
Phyllastrephus scandens	Insectivore	N	LC	F	N	N	0.0002	0.0000
Phyllastrephus sp	Insectivore	N	LC	F	N	Y	0.0025	0.0439
Phylloscopus sibilatrix	Insectivore	N	LC	N	N	N	0.0031	0.0000
Phylloscopus trochilus	Insectivore	N	LC	N	N	N	0.0000	0.0002
Platysteira blissetti	Insectivore	N	LC	F	N	N	0.0015	0.0000
Platysteira castanea	Insectivore	Y	LC	F	N	N	0.0306	0.0086
Platysteira chalybea	Insectivore	Y	LC	O	N	Y	0.0015	0.0000

Platysteira concreta	Insectivore	N	LC	F	N	Y	0.0000	0.0079
Platysteira cyanea	Insectivore	N	LC	N	N	N	0.0059	0.0000
Platysteira tonsa	Insectivore	Y	LC	F	N	Y	0.0015	0.0000
Ploceus aurantius	Insectivore	N	LC	F	N	N	0.0002	0.0000
Ploceus bicolor	Insectivore	N	LC	F	N	N	0.0006	0.0000
Ploceus cucullatus	Granivore	N	LC	F	N	N	0.0071	0.0038
Ploceus luteolus	Insectivore	N	LC	F	N	N	0.0000	0.0002
Ploceus nigerrimus	Insectivore	Y	LC	F	N	N	0.0031	0.0006
Ploceus nigricollis	Insectivore	N	LC	F	N	N	0.0029	0.0000
Pogoniulus atroflavus	Frugivore	N	LC	N	N	N	0.0107	0.0006
Pogoniulus bilineatus	Frugivore	N	LC	O	N	N	0.0065	0.0006
Pogoniulus chrysoconus	Frugivore	N	LC	N	N	N	0.0002	0.0000
Pogoniulus scolopaceus	Frugivore	N	LC	R	N	N	0.0080	0.0006
Pogoniulus subsulphureus	Frugivore	N	LC	N	N	N	0.0023	0.0000
Prinia bairdii	Insectivore	Y	LC	N	N	N	0.0027	0.0006
Prinia subflava	Insectivore	N	LC	N	N	N	0.0004	0.0000
Prodotiscus insignis	Insectivore	N	LC	O	N	N	0.0002	0.0004
Psalidoprocne nitens	Insectivore	N	LC	N	N	N	0.0000	0.0002
Psalidoprocne pristoptera	Insectivore	N	LC	N	N	N	0.0006	0.0000
Pycnonotus barbatus	Frugivore	N	LC	N	N	N	0.0222	0.0004
Pyrenestes ostrinus	Granivore	N	LC	N	N	N	0.0015	0.0004
Sarothrura pulchra	Insectivore	N	LC	N	N	N	0.0002	0.0000
Schistolais leucopogon	Insectivore	Y	LC	N	N	N	0.0013	0.0000
Sheppardia bocagei	Insectivore	Y	LC	O	O	N	0.0000	0.0004
Sheppardia cyornithopsis	Insectivore	N	LC	O	O	N	0.0000	0.0113
Smithornis capensis	Insectivore	N	LC	O	N	N	0.0008	0.0000
Smithornis rufolateralis	Insectivore	N	LC	R	N	N	0.0006	0.0008
Smithornis sharpei	Insectivore	Y	LC	N	N	Y	0.0002	0.0000
Spermestes bicolor	Granivore	N	LC	N	N	N	0.0069	0.0002
Spermestes cucullata	Granivore	N	LC	N	N	N	0.0046	0.0000

Spermestes fringilloides	Granivore	N	LC	N	N	N	0.0019	0.0000
Spermophaga haematina	Granivore	N	LC	O	N	N	0.0163	0.0132
Stelgidillas gracilirostris	Frugivore	N	LC	O	N	N	0.0002	0.0113
Stiphrornis erythrothorax	Insectivore	N	LC	O	O	Y	0.0031	0.0391
Stizorhina fraseri	Insectivore	Y	LC	O	O	N	0.0025	0.0023
Strix woodfordii	Carnivore	N	LC	N	N	N	0.0002	0.0000
Sylvietta denti	Insectivore	N	LC	F	N	N	0.0002	0.0000
Sylvietta virens	Frugivore	N	LC	R	N	N	0.0044	0.0006
Tchagra australis	Insectivore	N	LC	F	N	N	0.0008	0.0000
Terpsiphone batesi	Insectivore	Y	LC	F	N	N	0.0015	0.0000
Terpsiphone rufiventer	Insectivore	N	LC	F	N	N	0.0061	0.0119
Terpsiphone sp	Insectivore	N	LC	F	N	N	0.0213	0.0021
Terpsiphone viridis	Insectivore	N	LC	F	N	N	0.0023	0.0000
Thescelocichla leucopleura	Frugivore	N	LC	R	O	N	0.0008	0.0002
Tockus erythrorhynchus	Frugivore	N	LC	N	N	N	0.0002	0.0000
Trachyphonus purpuratus	Frugivore	Y	LC	N	N	N	0.0002	0.0002
Tricholaema hirsuta	Frugivore	N	LC	O	N	Y	0.0004	0.0004
Trochocercus nitens	Insectivore	N	LC	F	O	N	0.0004	0.0044
Turdus pelios	Insectivore	N	LC	N	O	N	0.0021	0.0000
Turtur afer	Granivore	N	LC	N	N	N	0.0130	0.0002
Turtur brehmeri	Granivore	N	LC	N	N	N	0.0002	0.0044
Turtur tympanistra	Granivore	N	LC	N	N	N	0.0182	0.0006
Verreauxia africana	Insectivore	Y	LC	O	N	Y	0.0019	0.0025
Vidua macroura	Granivore	N	LC	N	N	N	0.0000	0.0002
Zosterops senegalensis	Insectivore	N	LC	F	N	N	0.0002	0.0000

* For analyses, I included species classed as 'frequent' and 'occasional' in the mixed-species flock category

† For analyses, I included species classed as 'frequent' and 'occasional' in the ant-follower category

Appendix 3: Diversity measures

For partitioning biodiversity, I used Rényi's generalized relative entropy (Rényi, 1961), an extension of Hill (1973), Jost (2007) and Leinster and Cobbold's (2012) notions of ecosystem diversity. Implemented in Reeve et al.'s (2016) framework, it measures components of alpha, beta and gamma diversity over a continuum of viewpoint parameters, q, with decreasing emphasis on rare species as q increases (Hill, 1973). The viewpoint parameter q focuses on rarity at a different scale for alpha, beta and gamma diversities: for alpha, the emphasis is on species that are locally rare in the subcommunity, for gamma, those that are globally rare in the metacommunity, and for beta diversity the species that are relatively rare at the subcommunity level compared to the metacommunity. Calculating diversity over a range of q values allows us to investigate evenness; for instance if a community shows high alpha diversity at q = 0 but then a steep decline as q increases, then it is uneven, likely dominated by a small number of abundant species alongside many rare species.

The Reeve et al. (2016) framework considers a metacommunity composed of multiple subcommunities, each containing a number of species. Power means (or generalized means) are used to calculate these diversity measures (and many others), and are indicated by the letter M with the order of the power mean $(1 - q)$ in subscript (Reeve et al., 2016). Power means can be weighted; a $1 - q$ order power mean of $u = u_1, \dots, u_n$ weighted by $w = w_1, \dots, w_n$ is written as $M_{1-q}(w, u)$. In the Reeve et al. (2016) framework, power means are weighted by the relative size of the subcommunity (for metacommunity metrics) or the relative abundance of species in a subcommunity (for subcommunity metrics). However, in my analyses I used a standardised number of captures for each site, and therefore the weighting by subcommunity size becomes obsolete.

In a given metacommunity, there are S species of relative abundance $p = (p_1, \dots, p_S)$, partitioned into N distinct subcommunities. P is the relative abundance of the S species in N subcommunities such that $\sum i \sum j \, P_{ij} = 1$ and P_{ij} is the relative abundance of species i in subcommunity j. For a given subcommunity j, $P_{\cdot j}$ is a matrix describing the relative abundance of each species. Considering all subcommunities yields $p = \sum_j P_{\cdot j}$, the relative abundance of species in the metacommunity as a whole.

From the Reeve et al. (2016) framework I calculated the following measures (Appendix S2):

a) Metacommunity gamma: effective number of species in a metacommunity, calculated as ${}^{q}G = \mathrm{M}_{1-q}\left({}^{q}\gamma_j\right)$, where ${}^{q}\gamma_j$ denotes gamma diversity of subcommunity j (see below).

b) Subcommunity gamma: contribution per subcommunity to metacommunity diversity, calculated as ${}^{q}\gamma_j = M_{1-q}\left(P_{\cdot j}, p^{-1}\right)$

c) Subcommunity alpha: effective number of species in subcommunity *j* in isolation, calculated as ${}^{q}\alpha_j = M_{1-q}\left(P_{\cdot j}, (P_{\cdot j})_i^{-1}\right)$, where $(P_{\cdot j})_i^{-1}$ is the relative abundance of each species in the subcommunity as a fraction of the metacommunity.

d) Representativeness (beta diversity): measure how representative, or typical, a subcommuity is of the metacommunity, calculated as ${}^{q}\rho_j = M_{1-q}\left(P_{\cdot j}, \frac{p_i}{(P_{\cdot j})_i}\right)$

Table S3. Diversity measures used to compare bird communities in cocoa and forest plots, from Reeve *et al.* (2016). For metacommunity-level metrics I present here the mean and 95% confidence intervals (CIs) derived from the 50 iterations of the analyses. For subcommunity-level metrics, I calculated the mean and CIs for each subcommunity across the 50 iterations, and present here the aggregated values for each habitat type.

					Results				
Metric	Level	Partitioning	Definition	Formula	q = 0	q = 1	q = 2	q = ∞	Habitat
Gamma diversity	Metacommunity	Separate metacommunity for cocoa and forest	Effective number of species in metacommunity	${}^qG = M_{1-q}({}^q\Upsilon_j)$ *	90.0 {83.6, 96.4}	27.4 {24.7, 30.0}	12.8 {11.1, 14.6}	1.0 {1.0, 1.0}	Cocoa
					71.0 {64.8, 77.2}	22.3 {20.2, 24.4}	11.5 {9.9, 13.1}	1.0 {1.0, 1.0}	Forest
Gamma diversity	Subcommunity	The metacommunity comprises all sites	Contribution per individual to metacommunity diversity	${}^q\Upsilon_j = M_{1-q}(P_{\cdot j}, p^{-1})$	136.7 {115.5, 157.8}	36.0 {28.5, 43.4}	13.2 {11.5, 15.0}	5.0 {4.9, 5.1}	Cocoa
					100.2 {83.6, 116.9}	30.4 {26.6, 34.2}	13.5 {12.3, 14.6}	4.9 {4.8, 5.0}	Forest
Alpha diversity	Subcommunity	The metacommunity comprises all sites	Effective number of species in subcommunity *j* in isolation	${}^q\alpha_j = M_{1-q}(P_{\cdot j},(P_{\cdot j})_i^{-1})$	12.4 {10.2, 14.5}	9.0 {7.1, 11.0}	6.8 {5.1, 8.6}	1.0 {1.0, 1.0}	Cocoa
					12.2 {10.7, 13.7}	9.3 {7.7, 10.8}	7.3 {6.0. 8.6}	1.0 {1.0, 1.0}	Forest
Beta diversity	Subcommunity	Separate metacommunity for cocoa and forest	Representativeness of subcommunity *j*	${}^q\rho_j = M_{1-q}(P_{\cdot j}, p_i/(P_{\cdot j})_i)$	0.61 {0.59, 0.63}	0.39 {0.36, 0.42}	0.23 {0.21, 0.25}	0.05 {0.04, 0.06}	Cocoa
					0.64 {0.62, 0.66}	0.45 {0.42, 0.48}	0.30 {0.27, 0.33}	0.09 {0.06, 0.11}	Forest

Weighted power means are used to calculate many diversity metrics: a 1-q order power mean of $u= u_{1,} \ldots, u_n$ weighted by $w= w_{1,} \ldots, w_n$ is written as $\mathrm{M}_{(1\text{-}q)}\ (w,u)$. The relative abundance of S species in a single population is given by the vector p = ($p1$,. .., pS), where p_i is the relative abundance of the ith species. P is the relative abundance of the S species in the N subcommunities such that $\sum i \sum jPij = 1$ and Pij is the relative abundance of species i in subcommunity j.

Appendix 4: Chapter 2 model output

Table S4. Output of minimum adequate models, after elimination of non-significant factors, investigating bird community composition in cocoa farms and mature forest, and effect of shade and forest cover on bird communities.

Response variable	Explanatory variable	Estimate	Std.Error	t value	p value
Insectivore abundance					
	Intercept	-1.34	0.07	-18.74	<2E-16
	Habitat[a]	0.58	0.1	5.75	1.02E-08
Frugivore abundance					
	Intercept	-1.02	0.09	-11.78	<2E-16
	Habitat	-0.49	0.1	-5.06	4.23E-07
	Season[b]	0.17	0.07	2.45	1.40E-02
Nectarivore abundance					
	Intercept	-1.6	0.08	-19	<2E-16
Ant-follower abundance					
	Intercept	-4.1	0.23	-18.1	<2E-16
	Habitat	2.81	0.3	9.46	<2E-16
Mixed-flock abundance					
	Intercept	-0.87	0.06	-13.12	<2E-16
	Habitat	0.48	0.07	6.55	5.76E-11
Forest specialist abundance					
	Intercept	-3.68	0.19	-19.73	<2E-16
	Habitat	2.41	0.24	9.85	<2E-16
	Season	0.28	0.11	2.5	1.00E-02
Endemic abundance					
	Intercept	-2.48	0.09	-27.69	<2E-16
	Habitat	0.94	0.14	6.61	3.98E-11
Insectivore species richness					
	Intercept	-0.82	0.05	-17.84	<2E-16
	Habitat	0.45	0.07	6.24	4.29E-10
Frugivore species richness					
	Intercept	-1.24	0.05	-23.19	<2E-16
	Habitat	-0.83	0.12	-7.14	8.86E-13
Nectarivore species richness					
	Intercept	-1.98	0.07	-27.19	<2E-16
	Habitat	-0.56	0.15	-3.81	0.0001
Ant-follower species richness					
	Intercept	-2.02	0.07	-27.26	<2E-16
	Habitat	0.97	0.1	9.61	<2E-16

Mixed-flock species richness					
	Intercept	-0.81	0.06	-12.51	<2E-16
	Habitat	0.57	0.11	5.17	2.34E-07
	Season	0.15	0.09	1.64	7.00E-02
	Habitat:Season	-0.26	0.14	-1.86	6.00E-02
Forest specialist species richness					
	Intercept	-2.5	0.23	-10.99	<2E-16
	Habitat	1.68	0.23	7.29	3.05E-13
	Season	0.46	0.2	2.29	2.00E-02
	Habitat:Season	-0.52	0.27	-1.95	5.00E-02
Endemic species richness					
	Intercept	-1.91	0.07	-27.03	<2E-16
	Habitat	0.48	0.11	4.51	6.43E-06

Insectivore abundance					
	Intercept	-1.54	0.21	-7.29	3.12E-13
Frugivore abundance					
	Intercept	-0.67	0.2	-3.32	9.00E-04
	Shade cover	-0.0045	0.002	-2.189	2.80E-02
Nectarivore abundance					
	Intercept	-1.32	0.1	-13.71	<2E-16
Ant-follower abundance					
	Intercept	-10.71	1.37	-7.82	5.44E-15
	Shade cover	0.07	0.01	5.36	8.31E-08
	Forest cover	0.04	0.01	3.03	2.00E-03
Mixed-flock abundance					
	Intercept	-1.18	0.15	-7.88	3.32E-15
	Shade cover	0.006	0.002	2.84	4.40E-03
Forest specialist abundance					
	Intercept	-7.42	0.74	-10.03	<2E-16
	Shade cover	0.04	0.008	5.48	4.18E-08
	Forest cover	0.02	0.008	2.75	6.00E-03
Insectivore species richness					
	Intercept	-1.15	0.07	-15.87	<2E-16
Frugivore species richness					
	Intercept	-1.16	0.07	-15.9	<2E-16
Nectarivore species richness					
	Intercept	-1.89	0.1	-19.21	<2E-16
Ant-follower species richness					
	Intercept	-3.05	0.29	-10.74	<2E-16
	Forest cover	0.02	0.006	3.43	5.90E-04

Mixed-flock species richness					
	Intercept	-0.82	0.062	-12.72	<2E-16
Forest specialist species richness					
	Intercept	-4.93	0.5	-10	<2E-16
	Forest cover	0.05	0.01	5.15	2.57E-07

[a] Reference level for habitat is cocoa.

[b] Reference level for season is dry.

Appendix 5: Chapter 3 simulation results

Table S5. Mean (95% Bayesian Credible Intervals) for population size estimations from mark-recapture model and integrated model, and true value used in simulation. Parameter names are formulated as N_{ijz}, corresponding to abundance of species *i* in farm *j* and visit *z*.

Parameter	**Simulation value**	**Mark-recapture**	**Integrated**
N[A,1,1]	301	302 (186, 440)	284 (192, 384)
N[A,2,1]	176	164 (97, 237)	162 (105, 221)
N[A,3,1]	212	198 (131, 270)	193 (130, 259)
N[A,4,1]	287	272 (170, 382)	259 (175, 350)
N[A,5,1]	214	206 (139, 282)	202 (134, 271)
N[A,6,1]	298	288 (176, 408)	272 (182, 366)
N[A,7,1]	202	180 (113, 252)	180 (121, 245)
N[A,8,1]	236	201 (131, 271)	200 (136, 267)
N[A,9,1]	348	328 (189, 483)	306 (208, 415)
N[A,10,1]	325	309 (191, 447)	288 (196, 390)
N[A,11,1]	335	336 (191, 498)	311 (213, 424)
N[A,12,1]	324	332 (190, 490)	308 (208, 418)
N[A,13,1]	203	178 (111, 250)	177 (117, 240)
N[A,14,1]	361	356 (191, 535)	328 (222, 445)
N[A,15,1]	188	145 (79, 222)	145 (93, 198)
N[A,16,1]	289	307 (183, 449)	286 (195, 391)
N[A,17,1]	167	165 (101, 240)	167 (110, 226)
N[A,18,1]	184	172 (106, 245)	171 (112, 233)
N[A,19,1]	291	295 (181, 420)	279 (191, 377)
N[A,20,1]	254	227 (152, 306)	219 (150, 296)
N[B,1,1]	54	67 (23, 120)	68 (28, 112)
N[B,2,1]	32	39 (15, 65)	39 (15, 65)
N[B,3,1]	21	43 (16, 73)	41 (16, 73)
N[B,4,1]	37	60 (22, 107)	60 (27, 104)
N[B,5,1]	28	45 (17, 78)	44 (16, 76)
N[B,6,1]	28	63 (22, 113)	58 (22, 102)
N[B,7,1]	39	39 (14, 68)	39 (13, 68)

N[B,8,1]	27	44 (18, 75)	42 (17, 74)
N[B,9,1]	47	76 (29, 137)	70 (30, 118)
N[B,10,1]	52	67 (23, 121)	65 (26, 110)
N[B,11,1]	49	76 (27, 138)	72 (31, 121)
N[B,12,1]	54	73 (27, 135)	67 (28, 117)
N[B,13,1]	27	39 (13, 66)	41 (16, 70)
N[B,14,1]	35	78 (25, 145)	73 (30, 124)
N[B,15,1]	18	30 (9, 55)	30 (11, 55)
N[B,16,1]	42	72 (27, 128)	69 (29, 115)
N[B,17,1]	15	36 (13, 62)	35 (14, 63)
N[B,18,1]	26	41 (17, 69)	39 (15, 68)
N[B,19,1]	34	64 (24, 117)	60 (23, 104)
N[B,20,1]	32	50 (21, 87)	52 (21, 87)
N[C,1,1]	166	369 (65, 830)	294 (77, 604)
N[C,2,1]	119	201 (51, 433)	177 (48, 355)
N[C,3,1]	121	233 (54, 504)	198 (52, 405)
N[C,4,1]	192	340 (65, 750)	277 (76, 560)
N[C,5,1]	153	255 (63, 549)	219 (63, 438)
N[C,6,1]	152	356 (67, 793)	284 (74, 580)
N[C,7,1]	117	220 (53, 474)	188 (48, 383)
N[C,8,1]	109	237 (59, 511)	203 (55, 410)
N[C,9,1]	203	403 (69, 906)	318 (89, 656)
N[C,10,1]	183	374 (62, 832)	295 (78, 606)
N[C,11,1]	215	417 (75, 933)	329 (90, 665)
N[C,12,1]	208	407 (64, 910)	319 (82, 652)
N[C,13,1]	123	214 (53, 463)	187 (52, 377)
N[C,14,1]	185	435 (69, 984)	337 (88, 689)
N[C,15,1]	89	171 (40, 372)	152 (41, 308)
N[C,16,1]	208	382 (70, 859)	305 (87, 624)
N[C,17,1]	101	198 (49, 425)	169 (41, 345)
N[C,18,1]	105	218 (52, 461)	188 (56, 383)
N[C,19,1]	201	360 (61, 804)	292 (77, 591)
N[C,20,1]	147	276 (64, 605)	231 (65, 469)
N[A,1,2]	369	334 (202, 478)	314 (213, 427)
N[A,2,2]	195	189 (119, 272)	190 (126, 255)
N[A,3,2]	253	220 (149, 301)	219 (151, 294)
N[A,4,2]	302	307 (197, 427)	294 (202, 396)
N[A,5,2]	271	231 (155, 312)	227 (152, 304)
N[A,6,2]	336	323 (204, 456)	308 (213, 416)
N[A,7,2]	207	197 (126, 277)	196 (131, 267)
N[A,8,2]	226	223 (150, 305)	220 (150, 294)
N[A,9,2]	380	365 (213, 537)	341 (231, 461)
N[A,10,2]	323	335 (201, 481)	313 (211, 425)
N[A,11,2]	399	370 (216, 553)	349 (236, 473)
N[A,12,2]	360	362 (207, 534)	338 (227, 460)
N[A,13,2]	217	200 (127, 280)	197 (130, 264)
N[A,14,2]	417	393 (217, 596)	363 (241, 491)

N[A,15,2]	186	161 (89, 247)	160 (104, 220)
N[A,16,2]	390	352 (214, 505)	332 (227, 446)
N[A,17,2]	204	183 (109, 263)	183 (125, 251)
N[A,18,2]	244	208 (137, 290)	209 (143, 277)
N[A,19,2]	291	326 (204, 465)	307 (205, 413)
N[A,20,2]	284	258 (175, 344)	249 (173, 335)
N[B,1,2]	55	75 (26, 135)	74 (32, 125)
N[B,2,2]	26	38 (13, 68)	37 (12, 67)
N[B,3,2]	28	50 (21, 84)	51 (21, 86)
N[B,4,2]	51	67 (25, 120)	66 (27, 113)
N[B,5,2]	43	53 (23, 90)	54 (22, 90)
N[B,6,2]	36	73 (28, 130)	69 (27, 117)
N[B,7,2]	32	46 (18, 78)	45 (18, 78)
N[B,8,2]	43	48 (19, 82)	47 (19, 82)
N[B,9,2]	51	84 (30, 150)	82 (35, 135)
N[B,10,2]	48	76 (28, 137)	72 (29, 122)
N[B,11,2]	54	82 (27, 152)	73 (26, 126)
N[B,12,2]	53	81 (27, 150)	79 (36, 136)
N[B,13,2]	34	44 (17, 75)	46 (18, 78)
N[B,14,2]	60	91 (32, 166)	86 (39, 145)
N[B,15,2]	26	36 (12, 63)	36 (14, 63)
N[B,16,2]	66	78 (29, 141)	76 (32, 127)
N[B,17,2]	35	39 (12, 67)	39 (14, 69)
N[B,18,2]	25	47 (19, 77)	47 (21, 80)
N[B,19,2]	50	72 (25, 129)	66 (25, 115)
N[B,20,2]	29	56 (23, 96)	54 (21, 93)
N[C,1,2]	232	420 (81, 940)	339 (95, 689)
N[C,2,2]	130	225 (58, 486)	193 (53, 395)
N[C,3,2]	164	260 (61, 566)	222 (58, 456)
N[C,4,2]	191	381 (73, 842)	309 (87, 634)
N[C,5,2]	157	282 (70, 611)	238 (68, 489)
N[C,6,2]	205	400 (79, 889)	324 (86, 658)
N[C,7,2]	137	245 (61, 533)	210 (54, 430)
N[C,8,2]	149	266 (68, 576)	225 (63, 460)
N[C,9,2]	207	451 (74, 1015)	356 (101, 736)
N[C,10,2]	208	421 (81, 945)	336 (93, 687)
N[C,11,2]	201	460 (80, 1039)	365 (100, 746)
N[C,12,2]	219	455 (84, 1029)	358 (98, 734)
N[C,13,2]	149	242 (62, 520)	209 (62, 429)
N[C,14,2]	265	488 (79, 1105)	377 (98, 774)
N[C,15,2]	109	188 (39, 408)	163 (38, 339)
N[C,16,2]	247	434 (82, 962)	344 (97, 702)
N[C,17,2]	118	221 (55, 477)	190 (50, 390)
N[C,18,2]	147	240 (59, 517)	207 (59, 425)
N[C,19,2]	206	408 (76, 900)	329 (94, 669)
N[C,20,2]	161	310 (70, 674)	259 (72, 527)

Appendix 6: Chapter 3 real data parameters

Table S6. Parameters in model of population size of birds in Cameroonian cocoa farms and forest. For each parameter: prior (standard deviation) and mean (95% Bayesian Credible Intervals) of parameter estimates from model with only mark-recapture data and integrated model. The distribution of the priors was normal, in every case. See Equations 3.1-3.12 for further details.

Parameter	**Description**	**Prior (SD)**	**Mark-recapture**	**Integrated**
$v_{insectivore0}$	Intercept of linear predictor of population size for insectivores	6.00 (0.82)	4.44 (4.17, 4.72)	4.36 (4.11, 4.62)
$v_{frugivore0}$	Intercept of linear predictor of population size for frugivores	6.00 (0.82)	5.25 (4.91, 5.59)	5.22 (4.91, 5.52)
$v_{nectarivore0}$	Intercept of linear predictor of population size for nectarivores	6.00 (0.82)	4.94 (4.62, 5.28)	4.92 (4.6, 5.24)
$v_{granivore0}$	Intercept of linear predictor of population size for granivores	6.00 (0.82)	4.64 (3.83, 5.48)	3.24 (2.83, 3.67)
$v_{ant\text{-}follower0}$	Intercept of linear predictor of population size for ant-followers	6.00 (0.82)	3 (2.17, 3.89)	2.08 (1.78, 2.38)
v_{other0}	Intercept of linear predictor of population size for others	6.00 (0.82)	5.28 (3.98, 6.54)	4.35 (2.55, 5.84)
$v_{insectivore1}$	Effect of canopy on population size of insectivores	0.00 (0.10)	-0.26 (-0.36, -0.17)	-0.15 (-0.2, -0.09)
$v_{frugivore1}$	Effect of canopy on population size of frugivores	0.00 (0.10)	-0.23 (-0.32, -0.14)	-0.12 (-0.17, -0.06)
$v_{nectarivore1}$	Effect of canopy on population size of nectarivores	0.00 (0.10)	0 (-0.1, 0.09)	0.02 (-0.04, 0.09)
$v_{granivore1}$	Effect of canopy on population size of granivores	0.00 (0.10)	-0.48 (-0.6, -0.35)	-0.24 (-0.32, -0.16)
$v_{ant\text{-}follower1}$	Effect of canopy on population size of ant-followers	0.00 (0.10)	0.66 (0.51, 0.82)	0.48 (0.35, 0.61)
v_{other1}	Effect of canopy on population size of others	0.00 (0.10)	0.03 (-0.16, 0.22)	0.07 (-0.1, 0.24)
v_2	Effect of season on population size	0.00 (0.20)	-0.17 (-0.25, -0.1)	-0.23 (-0.29, -0.17)
$\rho_{insectivore0}$	Intercept of linear predictor of capture rate for insectivores	0.00 (3.16)	-4.3 (-4.58, -4.03)	-4.18 (-4.44, -3.94)
$\rho_{frugivore0}$	Intercept of linear predictor of capture rate for frugivores	0.00 (3.16)	-4.73 (-5.07, -4.39)	-4.66 (-4.96, -4.36)
$\rho_{nectarivore0}$	Intercept of linear predictor of capture rate for nectarivores	0.00 (3.16)	-4.57 (-4.9, -4.23)	-4.53 (-4.85, -4.22)
$\rho_{granivore0}$	Intercept of linear predictor of capture rate for granivores	0.00 (3.16)	-5.88 (-6.68, -5.03)	-4.42 (-4.84, -4.02)
$\rho_{ant\text{-}follower0}$	Intercept of linear predictor of capture rate for ant-followers	0.00 (3.16)	-4.35 (-5.3, -3.53)	-3.32 (-3.64, -3.01)
ρ_{other0}	Intercept of linear predictor of capture rate for others	0.00 (3.16)	-9.68 (-11.16, -8.16)	-8.74 (-10.44, -6.84)
ρ_1	Effect of canopy cover on capture rate	0.00 (0.10)	-0.17 (-0.25, -0.08)	-0.25 (-0.3, -0.2)

$\Psi_{insectivore0}$	Intercept of linear predictor of vocalisation rate for insectivores	-5.00 (2.00)		-4.42 (-4.7, -4.16)
$\Psi_{frugivore0}$	Intercept of linear predictor of vocalisation rate for frugivores	-5.00 (2.00)		-4.97 (-5.28, -4.67)
$\Psi_{nectarivore0}$	Intercept of linear predictor of vocalisation rate for nectarivores	-5.00 (2.00)		-5.9 (-6.23, -5.57)
$\Psi_{granivore0}$	Intercept of linear predictor of vocalisation rate for granivores	-5.00 (2.00)		-3.79 (-4.25, -3.37)
$\Psi_{ant\text{-}follower0}$	Intercept of linear predictor of vocalisation rate for ant-followers	-5.00 (2.00)		-3.96 (-4.28, -3.64)
$\Psi_{others0}$	Intercept of linear predictor of vocalisation rate for others	-5.00 (2.00)		-8.23 (-9.83, -6.48)

Appendix 7: Arthropod observation model simulation

METHODS

I generated data corresponding to an insect community made up of 7 groups, 3 of which contained pest and non-pest species. The community was sampled during 20 visits using sweep-netting, malaise traps and visual surveys. I assumed that visual surveys had a capture rate across taxa, whilst the capture rate of sweep-netting and malaise traps was higher for some taxa than others (for parameter details see Table S7). Using equations 4.1 – 4.10, I generated count data from Poisson-Gamma distributions for each of the methods (Table S7). I then fit the model to these data and evaluated accuracy and precision by comparing the mean and Bayesian Credible Intervals (BCIs) from each parameter posterior with the simulation value (Table S7).

RESULTS

Model estimates of population size and capture rate parameters are presented in Table S7. For every parameter, 95% BCIs of posterior overlapped the true value used in simulation. Precision of parameter estimates was high; for instance, in 6 out of 7 groups BCIs for parameter γ_{j1} (effect of shade cover on population size) did not overlap 0, thus giving an informative representation of this coefficient.

Table S7. Parameters used in model, with value assigned in simulation, prior and model estimate (summarised with mean and 95% BCIs of posterior).

Parameter	**Description**	**Simulation value**	**Prior**	**Model estimate (mean ± 95% BCIs)**
γ_{10}	Intercept of linear predictor for population size of non-pest taxa 1	4.4	N(5, 3.2)	4.3 (4.1, 4.5)
γ_{20}	Intercept of linear predictor for population size of non-pest taxa 2	4.8	N(5, 3.2)	4.6 (4.4, 4.8)
γ_{30}	Intercept of linear predictor for population size of non-pest taxa 3	4.1	N(5, 3.2)	3.9 (3.7, 4.2)
γ_{40}	Intercept of linear predictor for population size of non-pest taxa 4	2.9	N(5, 3.2)	2.9 (2.7, 3.1)
γ_{50}	Intercept of linear predictor for population size of non-pest taxa 5	3.8	N(5, 3.2)	3.8 (3.4, 4.2)
γ_{60}	Intercept of linear predictor for population size of non-pest taxa 6	3.6	N(5, 3.2)	3.6 (3.4, 3.8)
γ_{70}	Intercept of linear predictor for population size of non-pest taxa 7	1.4	N(5, 3.2)	1.6 (1.3, 1.8)
γ_{80}	Intercept of linear predictor for population size of pest taxa 1	2.0	N(5, 3.2)	2.1 (1.9, 2.4)
γ_{90}	Intercept of linear predictor for population size of pest taxa 2	3.4	N(5, 3.2)	3.4 (3.2, 3.6)
γ_{100}	Intercept of linear predictor for population size of pest taxa 3	3.6	N(5, 3.2)	3.6 (3.4, 3.8)
γ_{11}	Coefficient for effect of shade cover on population size of non-pest taxa 1	0.1	N(0, 0.2)	0.1 (0.1, 0.2)
γ_{21}	Coefficient for effect of shade cover on population size of non-pest taxa 2	-0.2	N(0, 0.2)	-0.2 (-0.3, -0.2)
γ_{31}	Coefficient for effect of shade cover on population size of non-pest taxa 3	-0.2	N(0, 0.2)	-0.2 (-0.3, -0.2)
γ_{41}	Coefficient for effect of shade cover on population size of non-pest taxa 4	0.1	N(0, 0.2)	0.1 (0.1, 0.2)
γ_{51}	Coefficient for effect of shade cover on population size of non-pest taxa 5	-0.3	N(0, 0.2)	-0.3 (-0.3, -0.2)
γ_{61}	Coefficient for effect of shade cover on population size of non-pest taxa 6	0.2	N(0, 0.2)	0.2 (0.1, 0.3)
γ_{71}	Coefficient for effect of shade cover on population size of non-pest taxa 7	0.1	N(0, 0.2)	0.1 (-0.1, 0.2)
γ_{81}	Coefficient for effect of shade cover on population size of pest taxa 1	0.0	N(0, 0.2)	-0.1 (-0.2, 0.1)
γ_{91}	Coefficient for effect of shade cover on population size of pest taxa 2	-0.2	N(0, 0.2)	-0.2 (-0.3, -0.2)
γ_{101}	Coefficient for effect of shade cover on population size of pest taxa 3	-0.3	N(0, 0.2)	-0.3 (-0.3, -0.2)
γ_{12}	Coefficient for effect of season on population size of non-pest taxa 1	0.1	N(0, 0.2)	0 (-0.1, 0.1)
γ_{22}	Coefficient for effect of season on population size of non-pest taxa 2	-0.4	N(0, 0.2)	-0.3 (-0.4, -0.2)
γ_{32}	Coefficient for effect of season on population size of non-pest taxa 3	-0.2	N(0, 0.2)	-0.1 (-0.2, 0)
γ_{42}	Coefficient for effect of season on population size of non-pest taxa 4	0.1	N(0, 0.2)	0.1 (0, 0.2)

γ_{52}	Coefficient for effect of season on population size of non-pest taxa 5	0.2	N(0, 0.2)	0.2 (0.1, 0.3)
γ_{62}	Coefficient for effect of season on population size of non-pest taxa 6	0.0	N(0, 0.2)	0 (-0.2, 0.2)
γ_{72}	Coefficient for effect of season on population size of non-pest taxa 7	0.3	N(0, 0.2)	0.1 (-0.1, 0.3)
γ_{82}	Coefficient for effect of season on population size of pest taxa 1	0.2	N(0, 0.2)	0 (-0.2, 0.2)
γ_{92}	Coefficient for effect of season on population size of pest taxa 2	-0.2	N(0, 0.2)	-0.1 (-0.2, 0)
γ_{102}	Coefficient for effect of season on population size of pest taxa 3	0.2	N(0, 0.2)	0.2 (0.1, 0.3)
β_{11}	Capture rate of survey method 1 on taxa 1	-1.6	N(-1, 2)	-1.4 (-1.6, -1.2)
β_{12}	Capture rate of survey method 1 on taxa 2	-1.0	N(-1, 2)	-0.9 (-1.1, -0.7)
β_{13}	Capture rate of survey method 1 on taxa 3	-0.2	N(-1, 2)	-0.2 (-0.4, -0.1)
β_{14}	Capture rate of survey method 1 on taxa 4	-1.9	N(-2, 2)	-1.9 (-2.2, -1.7)
β_{15}	Capture rate of survey method 1 on taxa 5	-1.4	N(-1, 2)	-1.3 (-1.5, -1.1)
β_{16}	Capture rate of survey method 1 on taxa 6	-1.5	N(-2, 2)	-1.4 (-1.6, -1.2)
β_{17}	Capture rate of survey method 1 on taxa 7	-2.8	N(-1, 2)	-2.8 (-3.3, -2.4)
β_{21}	Capture rate of survey method 2 on taxa 1	-1.5	N(-1, 2)	-1.4 (-1.5, -1.2)
β_{22}	Capture rate of survey method 2 on taxa 2	-1.0	N(-1, 2)	-0.9 (-1.1, -0.7)
β_{23}	Capture rate of survey method 2 on taxa 3	-0.8	N(-1, 2)	-0.9 (-1.1, -0.7)
β_{24}	Capture rate of survey method 2 on taxa 4	0.9	N(1.2, 2)	0.9 (0.7, 1.1)
β_{25}	Capture rate of survey method 2 on taxa 5	-1.6	N(-1, 2)	-1.7 (-1.9, -1.5)
β_{26}	Capture rate of survey method 2 on taxa 6	-1.0	N(-2, 2)	-0.9 (-1.1, -0.8)
β_{27}	Capture rate of survey method 2 on taxa 7	1.2	N(1.2, 2)	1.2 (1.0, 1.4)
β_{31}	Capture rate of survey method 3 on taxa 1	-0.3	N(-0.2, 0.1)	-0.2 (-0.4, 0)
β_{32}	Capture rate of survey method 3 on taxa 2	-0.3	N(-0.2, 0.1)	-0.2 (-0.4, 0)
β_{33}	Capture rate of survey method 3 on taxa 3	-0.1	N(-0.2, 0.1)	-0.2 (-0.4, 0)
β_{34}	Capture rate of survey method 3 on taxa 4	-0.2	N(-0.2, 0.1)	-0.2 (-0.3, 0)
β_{35}	Capture rate of survey method 3 on taxa 5	-0.2	N(-0.2, 0.1)	-0.2 (-0.4, 0)
β_{36}	Capture rate of survey method 3 on taxa 6	-0.3	N(-0.2, 0.1)	-0.2 (-0.4, -0.1)
β_{37}	Capture rate of survey method 3 on taxa 7	-0.2	N(-0.2, 0.1)	-0.2 (-0.3, 0)

Appendix 8: Equilibrium point calculation

Equations 5.1 – 5.3 can be re-written as

$$N_{t+1i} = N_{ti}\exp(b_i + (\sum_{j=1}^{J} a_{ij}N_{tj}))$$

For the system to be at equilibrium, $\exp(b_i + (\sum_{j=1}^{J} a_{ij}N_{tj}) = 1$ for all i, and therefore $b_i + (\sum_{j=1}^{J} a_{ij}N_{tj}) = 0$ for all i. Therefore, the internal equilibrium point is given by

$$\mathbf{b} = -\mathbf{A}\mathbf{N}^*$$

$$\mathbf{N}^* = -\mathbf{A}^{-1}\mathbf{b}$$

Appendix 9: Taxonomic grouping for community model

Table S8. Total number of captures of each species considered in community model, and grouping applied to species.

Group	Species	Captures
Forest specialist	*Alethe castanea*	34
Forest specialist	*Bleda notatus*	43
Forest specialist	*Bleda syndactylus*	12
Forest specialist	*Campethera caroli*	10
Forest specialist	*Chamaetylas poliocephala*	3
Forest specialist	*Criniger calurus*	2
Forest specialist	*Criniger sp*	13
Forest specialist	*Neocossyphus poensis*	9
Forest specialist	*Neocossyphus rufus*	1
Forest specialist	*Phyllastrephus albigularis*	2
Forest specialist	*Phyllastrephus sp*	7
Forest specialist	*Stiphrornis erythrothorax*	17
Forest specialist	*Stizorhina fraseri*	5
Forest specialist	*Trochocercus nitens*	1
Forest specialist	*Verreauxia africana*	3
Camaroptera	*Camaroptera brachyura*	95
Camaroptera	*Camaroptera chloronota*	14
Camaroptera	*Camaroptera superciliaris*	1
Hylia	*Hylia prasina*	42
Ispidina	*Ispidina lecontei*	4
Ispidina	*Ispidina picta*	155
Platysteira	*Dyaphorophyia castanea*	49
Platysteira	*Dyaphorophyia tonsa*	1
Platysteira	*Platysteira cyanea*	7

Terpsiphone	*Terpsiphone batesi*	8
Terpsiphone	*Terpsiphone rufiventer*	23
Terpsiphone	*Terpsiphone sp*	13
Terpsiphone	*Terpsiphone viridis*	13

Appendix 10: Trophic connections

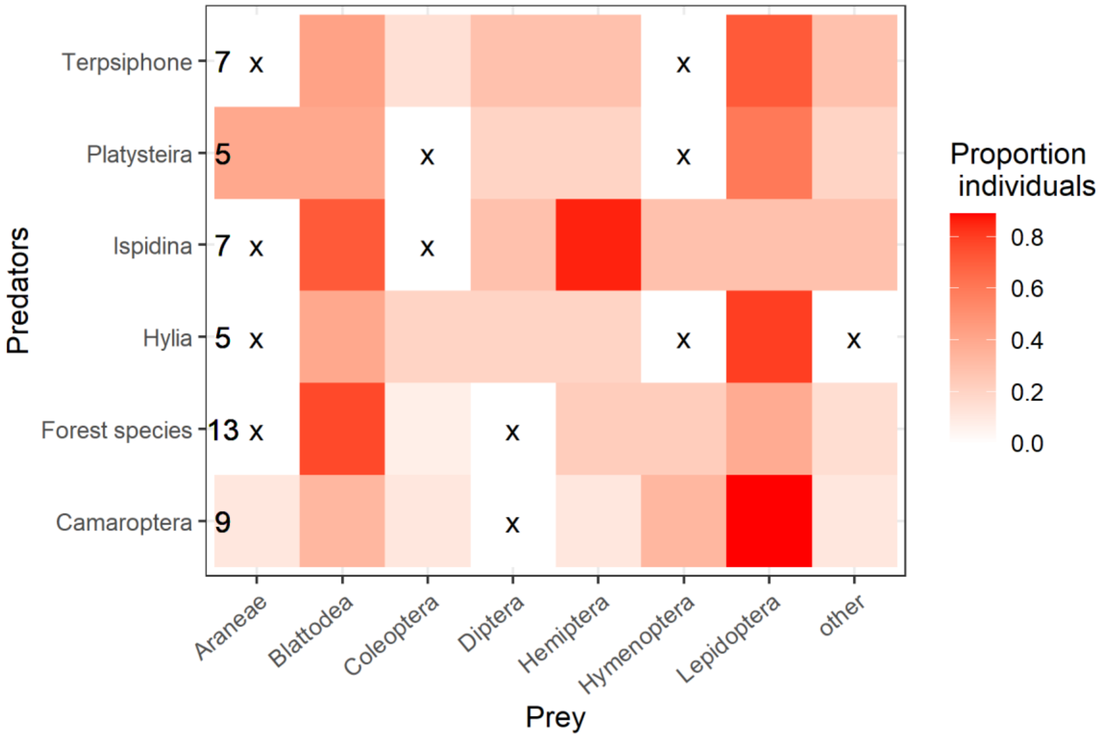

Figure S1. Data on bird diets from faecal diet metabarcoding (Powell et al., unpublished data). Numbers on y-axis indicate sample size (number of faecal samples from distinct individuals analysed). Colour intensity indicates the proportion of individuals whose faecal sample contained a given prey taxa. An ‘X’ indicates that no individuals contained that prey taxa in their diets.

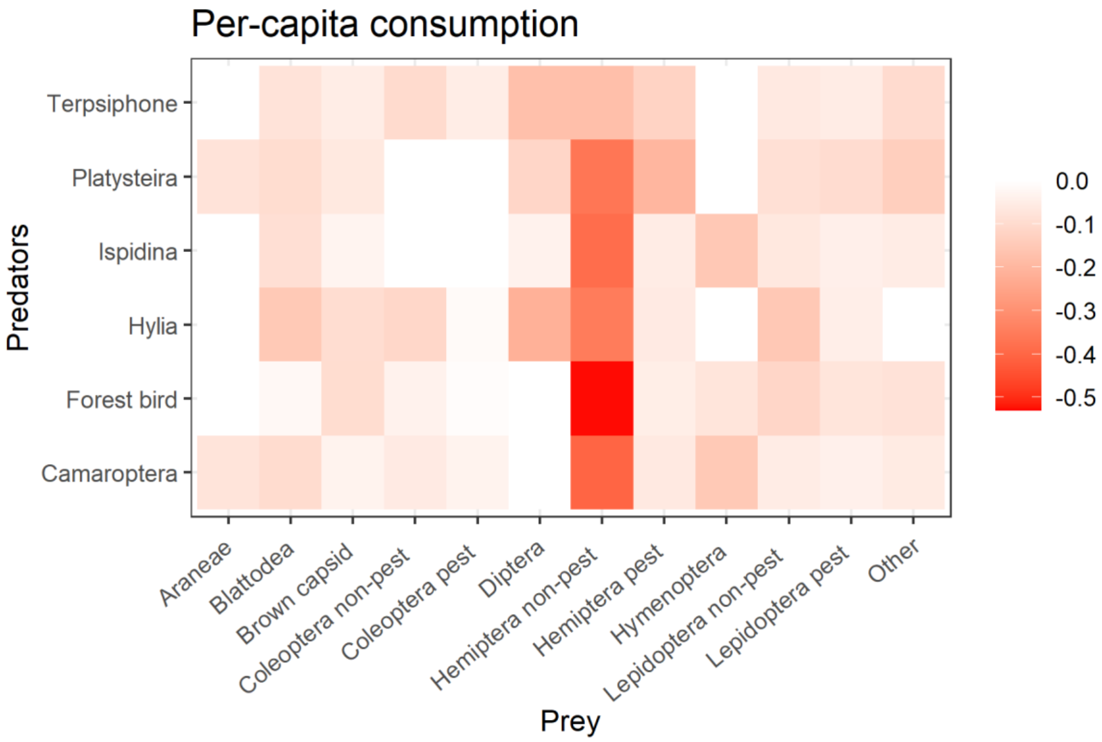

Figure S2. Per-capita consumption (kg/km^2/month) by predators of prey taxa. estimated by model. Per-capita consumption was calculated by multiplying the $a_{prey,predator}$ terms estimated by model by the mean equilibrium biomasses of species.

Appendix 11: Publication of Chapter 2

Published manuscript presenting work from Chapter 2 of this thesis.

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RESEARCH ARTICLE

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Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores

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Abstract

1. Forests are being converted to agriculture throughout the Afrotropics, driving declines in sensitive rainforest taxa such as understorey birds. The ongoing expansion of cocoa agriculture, a common small-scale farming commodity, has contributed to the loss of 80% rainforest cover in some African countries. African cocoa farms may provide habitat for biodiversity, yet little is known about their suitability for vertebrate fauna, or the effect of farm management on animal communities.
2. Here, we report the first in-depth investigation into avian diversity and community composition in African cocoa, by assembling a dataset of 9,566 individual birds caught across 83 sites over 30 years in Southern Cameroon. We compared bird diversity in mature forest and cocoa using measures of alpha, beta and gamma diversity, and we investigated the effect of cocoa farm shade and forest cover on bird communities.
3. Gamma diversity was higher in cocoa than forest, though alpha diversity was similar, indicating a higher dissimilarity (beta diversity) between cocoa farms. Cocoa farms differed from forest in community composition, with a distinctive decrease in relative abundance of insectivores, forest specialists and ant-followers and an increase in frugivores.
4. Within cocoa farms, we found that farms with high shade cover in forested landscapes resulted in higher relative abundance and richness of sensitive forest species; shady farms contained up to five times the proportion of forest specialists than sunny farms.
5. *Synthesis and applications*. Sunny African cocoa farms were less able to support sensitive bird guilds compared with shaded farms in forested landscapes. Our

findings support the notion that certain ecological and dietary guilds, such as ant-followers and forest specialists are disproportionately affected by land-use change. In light of the current push to increase cocoa production in sub-Saharan Africa, our results provide policymakers opportunities for more wildlife-friendly cocoa schemes that maximize avian diversity.

KEYWORDS

African bird, agroforestry, cocoa, farm management, forest cover, forest specialist, insectivore

1 | INTRODUCTION

Agricultural expansion is the main cause of terrestrial biodiversity loss worldwide (Newbold et al., 2015). The tropics, particularly sub-Saharan Africa, have the highest risk of biodiversity loss due to limited coverage of protected areas, low conservation spending and high agricultural growth (Kehoe et al., 2017). With agricultural demands projected to double in the next decades (Tscharntke et al., 2012), there is an urgent need for strategies that will combine agricultural production and biodiversity conservation. Trade-offs exist between agricultural production and biodiversity conservation, yet these aims need not be mutually exclusive: high-yield food production and high biodiversity are able to coexist in tropical smallholder agroforestry systems, in which agricultural crops are grown among shade trees (Clough et al., 2011; Perfecto & Vandermeer, 2010; Priess et al., 2007).

Cocoa is the fastest expanding export-oriented crop in the Afrotropics (Ordway et al., 2017), driven by a booming market in Europe (Squicciarini & Swinnen, 2016). Cocoa cultivation has caused mass deforestation in countries such as Ivory Coast, where it is now grown industrially in full-sun monocultures because of lack of forest land (Maclean, 2017). In other countries such as Cameroon, the 5th top exporter of cocoa worldwide, it is grown in a less intensive manner, usually under a thick forest canopy (Rice & Greenberg, 2000). Though short-term yields may be higher in full-sun plantations, shaded cocoa farms have a longer productive life span and suffer lower pest burdens, making long-term yields comparable (Tscharntke et al., 2011). However, the Government of Cameroon aims to triple cocoa production by 2035 (Ordway et al., 2017), which may lead to clearing of forested land for monocultures and conversion of shade-grown cocoa to sun monocultures (Andres et al., 2016; Schroth & Harvey, 2007).

Cocoa agroforestry systems often maintain a high diversity of rainforest shade trees that may resemble the rainforest they replaced (Bisseleua et al., 2013; Sonwa et al., 2007). Partly due to this, several studies have suggested that cocoa agroforestry systems contain considerably higher biodiversity than intensive cocoa plantations (Bhagwat et al., 2008; Bisseleua et al., 2009; Tscharntke et al., 2011; Vergara & Badano, 2009). However, most studies on cocoa are from the Neotropics and South-East Asia. In their meta-analysis, De Beenhouwer et al. (2013) highlight a lack of research on the capacity of African cocoa agroecosystems to maintain biodiversity. Specifically, we know little regarding vertebrate communities, and how they are affected by farm management practices (Schroth & Harvey, 2007; Sekercioglu, 2012). The notable exceptions are Waltert et al. (2005) and Kupsch et al. (2019), who surveyed birds across a gradient of land-use intensification which included some cocoa plots, and found that although species richness did not decrease with increasing habitat modification, community composition was significantly affected, with a decrease in abundance of large-bodied frugivores and terrestrial insectivores.

Factors affecting animal diversity in cocoa agroforestry systems occur at two spatial scales: farm level (0.25–5 Ha) and landscape level. Within the farm, management actions such as shade tree removal and pruning will affect an animal community. In the Neotropics, farms with dense, structurally diverse vegetation have been shown to support a higher diversity of birds (Cassano et al., 2009), ants (Philpott et al., 2006) and amphibians (Deheuvels et al., 2014). At a landscape scale, animals are affected by habitat connectivity as has been shown in Brazil where farms in forested areas support higher diversity of birds, bats and frogs than farms in disturbed non-forested landscapes (Cassano et al., 2009; Faria et al., 2006).

Birds are good indicators of habitat quality (Kupsch et al., 2019), with groups such as insectivores showing high sensitivity to habitat degradation (Karp et al., 2011; Powell et al., 2015; Stratford & Stouffer, 2013; Tchoumbou et al., 2020; Wolfe et al., 2015). In the tropics, many bird species depend strictly on microhabitats often only present in pristine forest (forest specialists; Stratford & Stouffer, 2013). Here we focus attention on two additional sensitive guilds of birds: ant-followers and mixed-flock species. Ant-followers are birds that pursue army ants, consuming the invertebrates flushed by the swarm (Peters & Okalo, 2009). Ant-followers are vulnerable to habitat degradation, and they are often the first guild to disappear with habitat conversion (Peters et al., 2008; Peters & Okalo, 2009). Also sensitive to habitat disturbance are mixed-species flocks, assemblages of birds of different species that move through the forest together foraging (Cordeiro et al., 2015).

In this study, we investigated the diversity of ecological bird guilds in African cocoa farms using a dataset collected over 30 years of bird mist-net captures across Southern Cameroon and Equatorial Guinea. We contrasted avian diversity and community composition patterns between forest and cocoa across varying shade and forest cover. Specifically, we asked the following questions: (a) Are bird communities in cocoa farms less diverse than in the forest? (b) Is bird community composition different between forest and cocoa? (c) How do shade and forest cover influence bird communities in cocoa farms?

2 | MATERIALS AND METHODS

2.1 | Bird mist-net captures

We considered bird mist-net captures from Cameroonian cocoa farms and mature forest, and from one mature forest site in Equatorial Guinea, between 1990 and 2020 (see Appendix S1). These data were collected for a range of projects, and therefore did not have a standardized methodology or sampling effort. However, the similarities in the overall approach made the data comparable: at each site, we set up 12 to 20 12 × 3 m mist-nets (30-mm mesh) for 6–11 hr per day (~6:30 to 12.30–17:30; Jarrett et al., 2021; Smith et al., 2005). Nets were set up either in a straight transect or in two smaller transects. The number of sampling days per site varied (Appendix S1). We used two methods to account for this unstandardized sampling effort: (a) For diversity analyses, we sampled a standardized number of captures and sites (n = 25 sites per habitat type, n = 30 captures per site) and (b) for community composition analyses, we considered only relative abundance and species richness of foraging guilds, calculated for each sampling unit by dividing the number of captures or species of each foraging guild by total captures or species.

We excluded individual birds that were not identified to species level, except for the commonly caught genera *Criniger*, *Phyllastrephus* and *Terpsiphone*. The resulting database consisted of 9,566 birds captured across 83 sites (26 forest and 57 cocoa; Figure 1; Appendix S1). We used the Handbook of the Birds of the World (del Hoyo et al., 2019) to classify each species according to its primary food type, its foraging guild and whether it was a forest specialist. Species could belong to more than one category (e.g. insectivorous and forest specialist; Appendix S2). Additionally, we determined the conservation status of each species (IUCN, 2020) and whether they were geographically restricted to the Congo Basin area (Appendix S2).

We considered sampling sites independent if they were separated by at least 500 m, those separated by less were pooled. The mature forest sites were at least 1 km from forest edge, had a closed canopy and were considered largely undisturbed by logging activity. Sites were classified into three regions: south, ecotone and west, corresponding to distinct ecoregions in Cameroon (Tamungang et al., 2014). We assigned each sampling visit to a season, either wet or dry, according to rainfall patterns of the corresponding region (Molua, 2006).

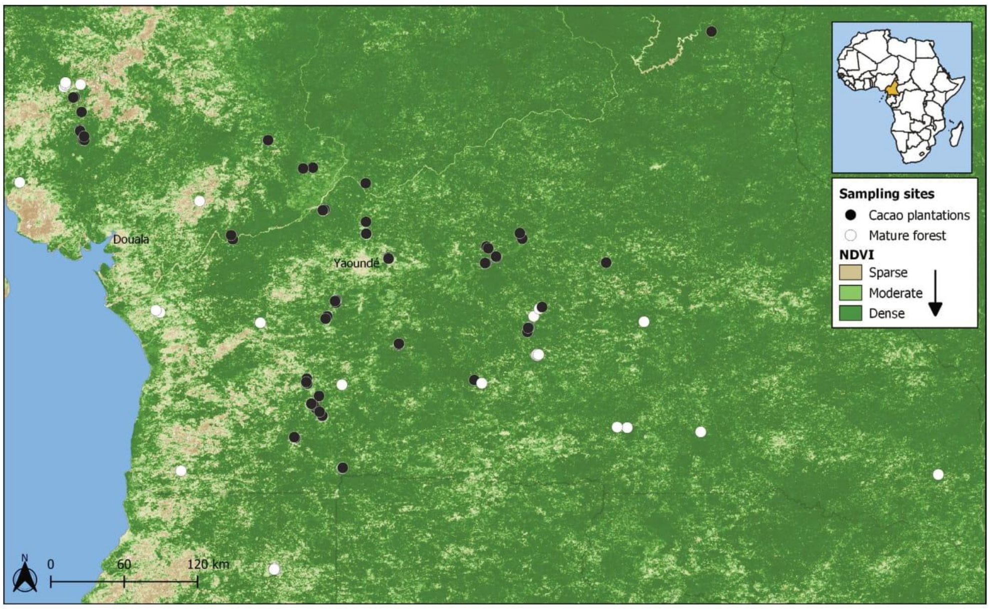

FIGURE 1 Map of all mature forest (white) and cocoa (black) sample sites across Southern Cameroon and Northern Equatorial Guinea. The base map shows eMODIS Normalized Difference Vegetation Index (NDVI; October 2018), as an indicator of vegetative land cover (accessed from https://earlywarning.usgs.gov/)

2.2 | Quantifying diversity

We quantified diversity using Reeve et al.'s (2016) framework implemented in the package RDIVERSITY (Mitchell et al., 2020), which measures components of alpha, beta and gamma diversity over a continuum of viewpoint parameters, *q* (for details see Allen et al., 2019; Kirkpatrick et al., 2018; Kumar Sarker et al., 2019). The value of *q* determines the relative importance attributed to species of differing rarity, giving less importance to rare species as *q* increases (Appendix S3). Here, we used $q = 0, 1, 2$ and ∞ as they align with commonly used diversity metrics (species richness, Shannon entropy, Simpson diversity and Berger Parker diversity). The framework considers a metacommunity composed of multiple subcommunities, each containing a number of species (Appendix S3). From the framework we calculated, metacommunity gamma diversity, subcommunity gamma diversity, subcommunity alpha diversity and representativeness of subcommunities within the metacommunity (a type of beta diversity; Appendix S4). Representativeness takes a value between 0 and 1; it is smallest when species present in each subcommunity are not present elsewhere in the metacommunity, and largest when all species in the metacommunity are present in the subcommunity (Appendix S3; Reeve et al., 2016).

We standardized number of sites ($n = 25$ per habitat type) and number of captures ($n = 30$ per site) for beta and gamma diversity measures. For alpha diversity, we standardized number of captures per site ($n = 30$) but included all sites, as this measure was calculated for each site in isolation and therefore was not affected by the number of sites. We then repeated each analysis 50 times. We excluded any sites below the capture threshold. We chose this number of individuals as it allowed us to maximize the number of captures while preserving the greatest number of sites. Diversity measures displayed in our results section are an average across the iterations. To improve robustness of our results for subcommunity alpha, we interpolated to 30 captures and extrapolated to 200 captures using the package INEXT (Hsieh et al., 2016; Appendix S3). We conducted all analyses in R version 3.6.3 (R Core Team, 2020).

2.3 | Shade and forest cover measurements

We investigated the effects of forest cover on birds in a subset of cocoa farmssek ($n = 28$) for which we had canopy measurements. We considered the following spatial scales of forest cover: cover of the farm itself (~1.5 Ha; henceforth shade cover) and mean forest cover in a 1.4, 2.5 and 4 km radius surrounding the farm (henceforth forest cover; Appendix S3). Shade cover was an indication of how intensely the farm was managed; traditional or shade farms preserved a mostly intact forest canopy, while in intensive or full-sun farms, shade trees were cut exposing cocoa trees to sunlight. Forest cover was a measure of how degraded the landscape was surrounding the farm.

To measure shade cover, we took photographs at 10 locations in each farm, spaced out by 24 m and at minimum 50 m from farm edge. We took photographs using a camera with a fish-eye lens on an extendable pole (12 m). Using the software ImageJ (Schneider et al., 2012), we converted the photographs to black and white, and then calculated the percentage of black (vegetation) in each photograph. The shade cover value used was a mean of the 10 pictures. To measure forest cover, we used the percent tree cover layer of the MODIS Vegetation Continuous Fields (MOD44B; Dimiceli et al., 2011), which is published yearly and has a resolution of 250 m. We downloaded the MOD44B layer corresponding to 2018 (birds were captured 2017–2020). In QGIS 2.18.23 (QGIS Development Team, 2018), we created a 1.4, 2.5 and 4 km radius buffer around each farm and extracted the mean percentage tree cover from the pixels within the buffer (Appendix S3). Shade cover measurements ranged from 19.6% in the most intensively managed farm to 98.7% in the least, and forest cover ranged from 9.0% in an urbanized area to 65.8% in a farm adjacent to a forest reserve.

2.4 | Data analysis

We used GLMMs with a binomial distribution to investigate the differences in bird community between forest and cocoa, and to investigate the effect of shade and forest cover on bird community composition in the subset of 28 farms for which we had canopy cover data. We grouped visits to a site in the same season and year into one sample unit. We used relative abundance and relative species richness as response variables to allow for varying sample size. For the comparison between cocoa and forest, full models contained an interaction term between season and habitat (forest or cocoa), a fixed effect for region and random factors for site and year. For the cocoa shade and forest cover analyses, full models contained fixed effects for shade cover, forest cover and season, and random effects for site and year. Here we present results for the largest buffer size (4 km radius), which was overall the best predictor of bird community composition (but see Appendix S3 for model selection and full results). We performed backwards model selection using likelihood ratio tests on fully nested models (LRTs, cut-off probability $p > 0.05$), until reaching a minimal adequate model.

We used minimal adequate models to estimate coefficients; we report estimates and 95% confidence intervals. All GLMMs were ran using the package GLMMTMB (Brooks et al., 2017) in R.

3 | RESULTS

3.1 | Bird diversity in cocoa plantations and mature forest

Metacommunity gamma diversity was higher in cocoa than in forest, though the difference became smaller at increasing values of *q* (Figure 2a). At $q = 0$, gamma diversity in cocoa was 90.0 and in

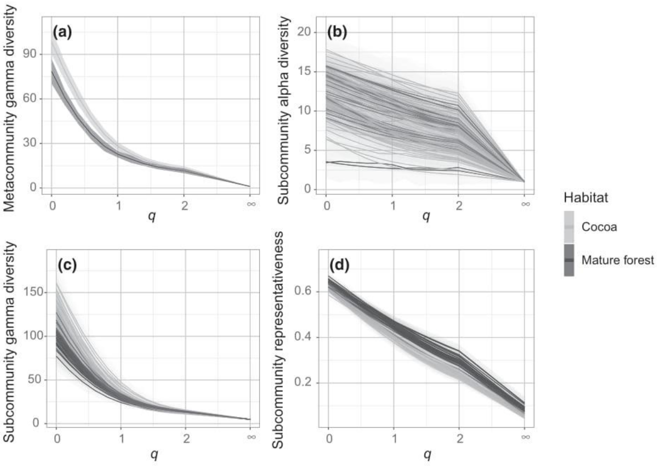

FIGURE 2 Measures of diversity in cocoa and mature forest sites across varying values of q: (a) Metacommunity gamma, (b) Subcommunity alpha, (c) Subcommunity gamma and (d) Subcommunity representativeness (a type of beta diversity; see Reeve et al., 2016). Measures of gamma and beta diversity were calculated over $n = 25$ sites per habitat type and $n = 30$ captures per site, and alpha diversity was calculated for $n = 30$ captures per site. Shaded areas represent 95% confidence intervals derived from the 50 iterations of the analyses

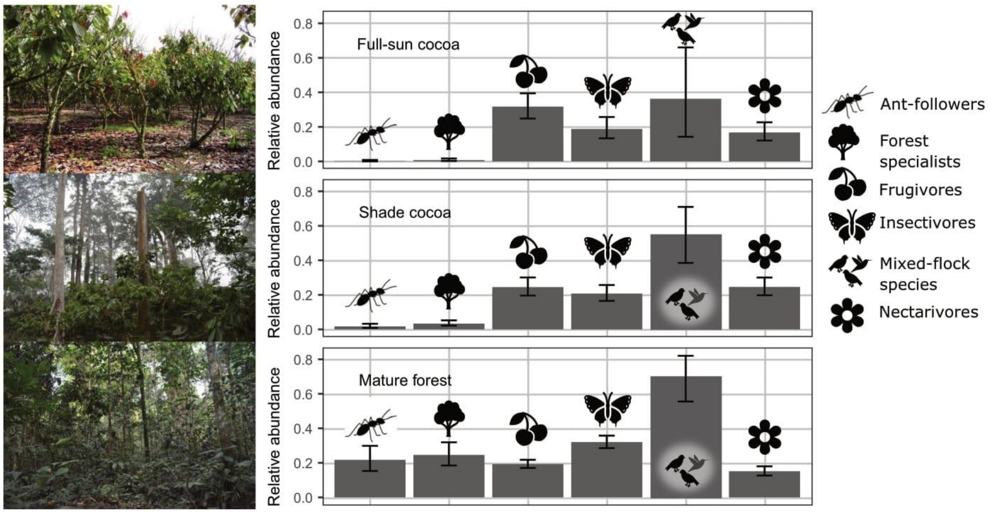

FIGURE 3 Relative abundance foraging guilds in full-sun cocoa (20% shade cover), shady cocoa (90% shade cover) and mature forest. Shaded bars and error bars represent the fitted values and 95% confidence intervals from the minimal adequate models. Top photograph: photo by Bea Maas—used with permission

forest 71.0, and at $q = 2$ it was 12.8 in cocoa and 11.5 in forest. Subcommunity alpha diversity was similar between cocoa and forest across all values of q; after 30 captures at $q = 0$ cocoa reached 12.4 species and forest reached 12.2 species (Figure 2b). Subcommunity gamma diversity was higher in cocoa than forest at low values of q, but became similar as q increased (Figure 2c). At $q = 0$, subcommunity gamma in cocoa was 136.7 and in forest 100.2. Subcommunity representativeness was consistently lower in cocoa than in forest over all values of q; at $q = 0$ representativeness in cocoa was 0.61 and in forest 0.64 (Figure 2d).

3.2 | Community composition in cocoa plantations and mature forest

Bird communities in cocoa and forest differed in their composition (Figure 3; Table 1; Appendix S5). Habitat was a significant variable in explaining the relative abundance of insectivores, forest specialists, ant-followers and mixed-flock species; these groups constituted a smaller proportion of all captures in cocoa farms than in forest. The largest effect size was for forest specialists that made up 25% of captures in forest and 3% in cocoa. Frugivores

TABLE 1 Relative abundance and species richness of feeding guilds in cocoa and mature forest as predicted by minimal adequate models

		Cocoa			Forest			Dry			Wet		
Type of analysis	**Response guild**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**
Abundance	Insectivores	0.2[a]	0.19	0.23	0.32	0.28	0.36						
	Forest specialists[b]	0.03	0.02	0.04	0.25	0.18	0.32	0.04	0.03	0.06	0.06	0.04	0.08
	Nectarivores[c]	0.18	0.16	0.21	0.15	0.13	0.18						
	Mixed-flock species	0.49	0.40	0.58	0.70	0.56	0.82						
	Frugivores	0.28	0.25	0.31	0.19	0.17	0.22	0.24	0.21	0.27	0.27	0.25	0.30
	Ant-followers	0.03	0.02	0.04	0.24	0.18	0.31						
Species richness	Insectivores	0.30	0.29	0.33	0.41	0.38	0.43						
	Nectarivores	0.18	0.16	0.21	0.15	0.13	0.18						
	Frugivores	0.22	0.20	0.24	0.11	0.09	0.13						
	Ant-followers	0.11	0.10	0.13	0.26	0.23	0.29						

		Cocoa						Forest					
		Dry			Wet			Dry			Wet		
Type of analysis	**Response guild**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**	**Estimate**	**Lower**	**Upper**
Species richness	Mixed-flock species[d]	0.31	0.28	0.34	0.34	0.32	0.37	0.44	0.40	0.49	0.41	0.38	0.45
	Forest specialists	0.08	0.05	0.11	0.11	0.08	0.16	0.31	0.24	0.39	0.29	0.24	0.35

[a] Values displayed are the fitted values and 95% CIs predicted by the minimal adequate models. Where only habitat had a significant effect, there are two fitted values.

[b] In cases where both habitat and season had a significant effect on relative abundance, there are four fitted values.

[c] Habitat was not significant in the model predicting relative abundance of nectarivores

[d] For mixed-flock and forest specialist species richness, the interaction between habitat and season was retained in the minimal adequate model.

constituted a larger proportion of total captures in cocoa farms than in forest, and occurred in higher relative abundance in the wet season.

Relative species richness of insectivores, ant-followers, mixed-flock species and forest specialists was significantly higher in forest than cocoa (Table 1; Appendix S5). Relative species richness of frugivores and nectarivores was higher in cocoa farms. For mixed-flock species and forest specialists, the effect of season on relative species richness depended on habitat; these groups made up a larger fraction of all captures in the wet season (compared with the dry season) in cocoa, but the opposite was true in the forest.

3.3 | Effect of farm shade and forest cover on bird communities

Effects of shade and forest cover on bird abundance varied between guilds (Figures 3 and 4; Appendix S5). The only guild that decreased in relative abundance with increasing shade cover was frugivores, from 32% in full-sun farms to 24% in the most shaded farms. Ant-followers increased in relative abundance with both shade and forest cover; they constituted 0.2% of captures in sunny farms and 2% in shady farms, and they increased from 0.1% to 6% with increasing forest cover. Forest specialists increased in relative abundance also with shade and forest cover; shady farms had five times the relative abundance of forest specialists than full-sun farms, and their relative abundance increased from 0.7% in farms with minimum forest cover to 7% in farms with high forest cover. Neither shade cover nor forest cover had significant effects on the relative abundance of insectivores, nectarivores or mixed-flock species.

Shade cover and forest cover had no effect on the relative species richness of frugivores, nectarivores, insectivores and mixed-flock species (Appendix S5). Relative species richness of ant-followers increased significantly with forest cover; from 5% in farms with low forest cover to 18% in farms with high forest cover. Forest cover had a significant effect on the relative richness of forest specialists, increasing from 1% at low forest cover to 19% at high forest cover.

4 | DISCUSSION

Our study is the first to specifically examine African cocoa farms as habitat for birds. We found that sensitive guilds such as forest specialists and ant-followers represented a larger proportion of the community in shady farms compared with full-sun farms, and that these groups occurred at higher relative abundance in farms with high forest cover. In the current climate of agricultural intensification, our findings highlight the potential for farmland to

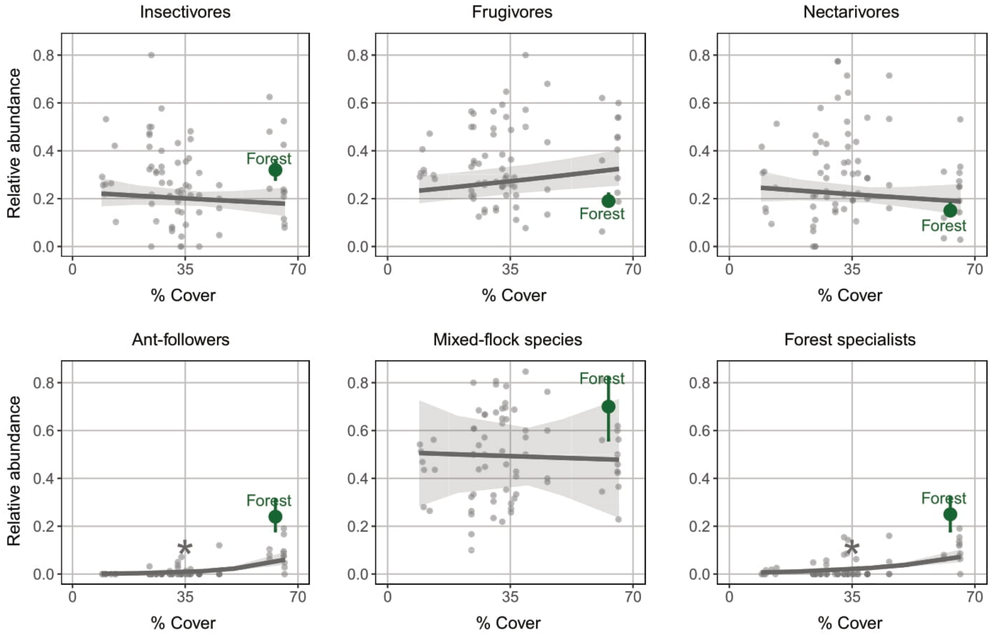

FIGURE 4 Effect of landscape forest cover on the relative abundance of foraging guilds. The line indicates the effect size predicted by the minimal adequate model and the shading corresponds to the 95% CIs. The asterisks indicate statistical significance. The point represents the relative abundance of the corresponding foraging guild in mature forest, with associated CIs. The dots correspond to the raw data

be managed in favour of avian communities, and we provide further evidence of the importance of maintaining forested areas in the landscape.

We found that the cocoa-farms bird assemblage comprised more species than the forest assemblage. This could possibly be due to the variability of habitat characteristics in cocoa farms, which can range from full-sun scrubby plantations to shaded farms that are structurally similar to the forest (Sonwa et al., 2007; Tscharntke et al., 2011). Indeed, the lower representativeness of cocoa farms indicates that they were more dissimilar between each other compared with forest sites. These findings support Solar et al. (2015), who report increased beta diversity between secondary forest sites than between undisturbed forest sites. The authors argue that the higher between-site beta diversity of disturbed forests may attenuate species loss at a larger scale. However, though cocoa farms may contain more species that are rare across the metacommunity, these are likely not forest- or range-restricted species (Appendix S2). Indeed, there is an overall trend towards increasing generalist species in disturbed forest landscapes (Rutt et al., 2019). Therefore, while cocoa farms may play a role in the conservation of certain bird guilds, we must also prioritize protection of undisturbed primary forests that provide habitat for specialized species that do not frequently occur in modified habitats (Stratford & Stouffer, 2013; Tscharntke et al., 2011).

Our results support Waltert et al. (2005), who found that species richness in Afrotropical forest did not differ between mature and agroforest. However, other studies showed different patterns. For example, Reitsma et al. (2001) found lower alpha and gamma diversity of birds in Costa Rican forest compared with managed cocoa, yet De Beenhouwer et al. (2013) found an 11% decrease in bird species richness from forest to agroforestry. Importantly, the diversity patterns we observed were affected by the q value. At higher values of q, gamma diversity became similar between forest and cocoa, indicating that both habitats contained a similar number of abundant species. Clear examples in forest were Fire-crested Alethe *Alethe castanea* and Yellow-lored Bristlebill *Bleda notatus*, two forest specialist species, that made up a considerable fraction of the community in almost all forest sites. Our results demonstrate how conclusions about diversity can change depending on the measurement parameters. We argue that using a range of metrics and q values gives more detailed and useful information about a community's diversity.

The broad differences in community composition that we found between cocoa farms and forest are consistent with literature from across the tropics. The shift from forest to cocoa results in a decrease in insectivores, forest specialists and ant-followers and an increase in frugivores and nectarivores in the Neotropics (Faria et al., 2006; Rice & Greenberg, 2000) and Asia (Maas et al., 2016; Marsden et al., 2006). Our findings contribute to a growing recognition that species loss in forested systems is linked to certain ecological guilds. Throughout tropical realms, distantly related species have evolutionarily converged on similar behaviours, such as ant-following and participating in mixed-species flocks, which reduce their resiliency to forest loss and habitat degradation (Powell et al., 2015).

We found that the community composition of birds in cocoa farms was significantly affected by shade and forest cover, with an increased relative abundance of forest specialists, ant-followers and mixed-flock species in shaded farms with high forest cover. Forest specialists are closely tied to vegetation structure (Powell et al., 2015; Stratford & Stouffer, 2013), especially with the understorey, which is entirely removed in intensive cocoa plantations (Kessler et al., 2005). Additionally, habitat amount (e.g. proportion of forest in landscape) is important in determining bird abundance and richness, and this effect may be more pronounced in understorey or forest specialist species (Carrara et al., 2015; De Camargo et al., 2018), explaining the increased relative abundance and diversity of these birds with forest cover. Given the current rate of land-use change, forest birds are under severe threat and will likely undergo rapid species loss (Maas et al., 2009; Powell et al., 2015; Sekercioglu, 2012).

Ant-follower abundance is driven by the abundance of swarm-raiding army ants (Peters et al., 2008; Peters & Okalo, 2009). Ants are affected by farm management: Bisseleua et al. (2009) found that ant species richness was significantly higher in structurally diverse, low-intensity cocoa systems compared with intensive systems. Additionally, ants are affected by landscape-level processes, as their sensitivity to temperature limits their ability to move between habitat patches (Rizali et al., 2013). Therefore, shaded farms in forested landscapes likely contain a community of ants like that in the forest, in turn supporting the ant-following bird population. Mixed-flocks have hardly been studied in the Afrotropics (but see Cordeiro et al., 2015; Péron & Crochet, 2009), but literature from other regions suggests that this guild is sensitive to disturbance (Goodale et al., 2015; Tien et al., 2005). Mixed-flock frequency and attendance seems to increase with vegetation density and structure, perhaps due to increased prey availability, reduced exposure to predators and protection from climatic conditions (Tien et al., 2005).

Contrary to expectations, we found no effect of shade or forest cover on relative abundance or richness of insectivorous birds. This could be driven by species such as the Chestnut Wattle-eye *Platysteira castanea* and the Paradise Flycatcher *Terpsiphone* sp., which occurred in relatively high abundances in most cocoa farms. Indeed, studies such as Waltert et al. (2005) and Sekercioglu (2012) suggest that small-bodied insectivores respond less to land-use change compared with large-bodied insectivores. From a human perspective, the presence of these small insectivores in cocoa farms could be beneficial due to their role in agricultural pest control (Karp et al., 2013; Maas et al., 2016).

In this study, we were able to see general trends in bird communities in forest and cocoa through mist-net capture data. However, given the variable sampling effort, we were only able to consider relative abundance, which may not be representative of absolute abundance. Additionally, the abundance of species' can be a misleading indicator of habitat quality as human-modified habitats can act as population sinks or ecological traps (Johnson, 2007; Robertson &

Hutto, 2006). Future studies in Afrotropical cocoa should consider demographic and morphological data to help establish the value of agroforestry systems as buffer habitat and wildlife corridors (Jarrett, Powell, et al., 2021; Schroth et al., 2004).

Our study provides strong evidence that African cocoa plantations can be of value for conserving avian diversity. However, plantations need appropriate management if habitat is to be provided for forest bird communities. Low-intensity shaded cocoa not only provides habitat for forest birds and other vulnerable taxa but can also produce high yields and farmer income, comparable to more intensive systems, thanks to lower pest burdens, longer productive life span of trees and lower input costs (Armengot et al., 2016; Clough et al., 2011; Tscharntke et al., 2011). This dual function of cocoa agroforestry systems aligns with a land-sharing perspective, in which agriculture is managed at low intensity and in favour of biodiversity. However, our results also demonstrate that even the shadiest cocoa farms are not equivalent to forest, and therefore we argue that within a land-sharing scenario there must be areas of forest preserved on the landscape. In conclusion, to prevent extreme deforestation and biodiversity loss in one of the world's diversity hotspots, policymakers should actively encourage ecologically sustainable agricultural practices such as shaded cocoa agroforestry that employs science-based management.

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AUTHORS' CONTRIBUTIONS

C.J., T.B.S. and L.L.P. conceived the ideas and designed the methodology; C.J., T.B.S., L.L.P., T.T.R.C., D.F.F., M.T., M.N.F.E., J.W. and K.B. collected the data; R.H. and A.J.W. contributed to fundraising and logistical support; C.J. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.13526318.v2 (Jarrett, Smith, et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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