CACAO POD YIELD AS A FUNCTION OF POLLINATION, PLANTATION MANAGEMENT AND LANDSCAPE CONTEXT IN WESTERN GHANA

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Thesis submitted to the University of Oxford in the fulfilment of the requirements for the degree of Doctor of Philosophy

Hilary 2023

I dedicate this thesis to my dear friend, Dr Deborah Rose (Nana Abena Nyansema I), who never ceases to inspire me, my beloved mum and rock, Victoria Addai (Yaa Osaa), my dad and oldest friend, Yaw Atta-Boateng who passed a year before completion of this work and for his incessant prayers, and my kind hearted siblings, Nana Ama Boateng, Afia Acheampomaa Atta-Boateng, Afia Pokua Atta-Boateng, Kwaku Addo Atta-Boateng and Kwadwo Asamoah Atta-Boateng.

ABSTRACT

Theobroma cacao (cacao) is an important commodity that supports the livelihood of Ghanaian smallholder farmers and makes a major contribution to the gross domestic product of Ghana. Unfortunately, cacao production impacts the environment through unsustainable expansion of farmlands into forest land with potential consequences for biodiversity conservation. The underlying motivation for expanding farmland is to increase cacao production. This thesis argues that increasing on-farm productivity by narrowing the existing cacao yield gap can reduce the environmental impact of cacao production in Ghana. The thesis supports this claim in three papers. Paper one identifies an existing yield gap in cacao and explores the potential avenues to effectively narrow the yield gap. The biotic, abiotic and management factors that impact cacao yield are identified, and it is suggested that the current yield gap is more related to tree physiology and pollination limitation. The second paper of the thesis expands on paper one to test whether physiological factors or pollination limitation has the greater impact on cacao yield in the study area. Using empirical data from eight plantations, paper two shows evidence of pollination limitation in the study area. Open pollination is estimated to achieve 43% yield, indicating a 56% pollination limited yield gap at peak growing season in the study area. The paper also identifies the abiotic and landscape factors that drive pollination limitation in the study area. To better understand the pollination biology of cacao, with the goal to address open pollination deficit, paper three evaluates the diversity and abundance of cacao flower

visitors. Twelve taxonomic groups of flower visitors are identified. The factors that affect the biodiversity of flower visitors are assessed, and the functional relationships between the flower visiting arthropods are analysed. Thrips and Dipterans are identified as the most abundant cacao flower visitors, most functionally implicated in the arthropod trophic network. The mechanism of cacao pollination by thrips is described for the first time. The thesis concludes by addressing the implication of the study with recommendations to sustain the future of the cocoa sector of Ghana, and the global value-chain.

ACKNOWLEDGEMENTS

I thank my supervisors, Prof Yadvinder Malhi, Dr Tonya Lander and Prof Thomas Wanger for their dedication, incredible patience in mentoring and support over the years.

I thank Green Templeton College administration for providing me with the learning environment and academic support. I thank Dr Stephen Harris for his invaluable support and helping to set me up for arthropod morphotyping at Herbarium in the Biology Department. I thank Dr Ricardo Pérez-de la Fuente, an insect and arachnid paleobiologist at the Oxford Museum of Natural History for his selfless support with microscopy and insect identification. I am also grateful to Dr James Hogan, Collections Manager, Hymenoptera and Lepidoptera at the Oxford Museum of Natural History, for his support with insect identification. I also grateful to Mr Moro Seidu, Director at Cacao360 who helped me to access cacao plantations in the Western Region of Ghana as well as helping me to find dedicated field assistants without whom this work would not be possible. I thank Kwadwo Asamoah Atta-Boateng, who devoted an incredible amount to time to establish field plots manage data collection team and led the field team during covid when I could not be in the field in-person and for all his intellectual inputs during field research campaigns. Lastly, I thank Papa Kwadwo Botsio and Josephine Agyeman-Duah, my college buddies who supported me throughout my work during many ups and downs as well as Huanyuan Zhang-Zheng and Carlota Segura Garcia, my lab colleagues for their friendship throughout my studies at Oxford.

1 CONTENTS

1 GENERAL INTRODUCTION

1.1 Background

Several concerns have been raised regarding the sustainability and opportunity costs of the growth of the cocoa production sector. These include forest cover loss, child labour, the food security threat and economic ramifications of an agricultural economy based on a single commodity versus diverse staple foods essential for local consumption. Of these challenges, how to sustain cocoa production without environmental cost remains the major global priority (Niether et al., 2020a).

First, the environmental cost of cocoa production arises from farmer's need to increase profits. Ghana does not employ conventional free-market principles in cocoa trading; prices are fixed by the government. As a result, farmers can only increase their income by increasing production, mainly by converting forests or natural landscapes to farmlands. This is partly because the cocoa production sector has one of the lowest technology-adoption rates with respect to innovations that improve yield, compared to crops such as wheat or corn. The second challenge of cocoa production regards the fundamental constraints on yield: biotic (biological agencies), abiotic (physical conditions: light availability, water availability, temperature, soil nutrients), and management.

Biotic constraints to production constitute all biological processes and or interactions that affect *Theobroma cacao* productivity such as pollination service, pests, diseases, and competition

for edaphic resources. Biotic factors can broadly be framed as economic (mutualism and parasitism) or non-economic (commensalism) symbiotic relationships between cacao and other biological entities in the cacao-ecosystem. Several interventions exist to curb some of the common biotic constraints. For instance, cacao farmers regularly apply agrochemical to control pests, weeds, or diseases during the growing season. Nonetheless, all things been equal, commercially grown cocoa still does not reach its potential yield, suggesting there exists a yield gap.

Other biotic constraints that do not involve the interaction of *T. cacao* with biotic components are intraspecific, such as tree physiological processes that limit yield outcomes. *T. cacao* is cauliflorous, which means the reproductive parts grow directly from the stems. In most flowering plants, flowers and seeds grow from the axial peripheral region (shoot apical meristem). Such biological architecture may require specialized vascular phenomena and allocation strategy. Furthermore, *T. cacao* exhibits perennial flowering, the case whereby the tree flowers continuously throughout the year, when the growth conditions are conducive. It has been suggested that perennial flowering may be a strategy to increase the chances of successful pollination. However, despite the massive flower output, successful pollination occurs only in a small fraction of flowers within 48 hours anthesis. Furthermore, fertilization and fruit set after pollination depends on a selective genetic process termed self-incompatibility. Then of the successfully pollinated flowers that set fruit, nearly 95% of are aborted by a condition called cherelle loss (Melnick, 2016). These phases of selective pathway towards successful fruit production suggests that physiological constraints are a key yield limiting factor for *T. cacao* yield (Melnick, 2016).

Arguably, economic yield is the end goal of agriculture. However, agroecology, a discipline that integrates agricultural and ecological principles offers a path that can promote

sustainable food systems. In the case of cocoa production systems, Agroforestry is the agroecology solution commonly advocated and practiced. Agroforestry can be described as a land-use form that integrates and implement both forestry and agricultural principles and outcomes. In cacao agroforestry systems, trees or tree crops are often used to moderate abiotic factors such as light intensity to manage a biotic factor such as pollination service. However, to address cacao yield gap, there is need to understand the existing factors that limits yield, the extent to which the factors impact yield, what the practically addressable yield constraints are, which factors should be prioritized to attain maximum yield. Lastly, which knowledge gaps if prioritized, will narrow yield gaps the most.

1.2 Thesis aims and outline

In this thesis, I conducted repeated hand pollination experiments across the wet and dry seasons in Ghana. I also surveyed flower visiting arthropods across both wet and dry seasons and classified them by taxonomic groups. Lastly, I conducted a farmer survey on management cacao practices. Put together, the field data enabled me to investigate cacao yield, determine the current yield gaps, identify potential yield-limiting factors, and explore the biotic drivers of cacao yield.

The aims of the study were:

a. To identify the key factors that limit cacao yield and evaluate the best avenues to narrow yield-gaps.
b. To evaluate the yield-limiting factors of cacao and estimate the yield gap in the study area.

c. To explore the biodiversity and ecological relations of the biotic drivers of cacao yield.

To address these aims, I set up experimental plots in eight plantations in cacao growing areas in Western Ghana. I applied statistical models, taxonomy, and network analysis to answer research questions as elaborated in the three papers of the thesis. The thesis is organized in the following order. The first chapter is background introduction to cacao production constraints. This is followed by a review of subject area, laboratory and analytical methods employed in the thesis.

In the next section of the thesis, I present the three papers.

Paper one, "Achieving a livelihoods-conservation win-win by reducing the yield gap in cocoa production", explores sustainable cacao production through the lens of optimality, in which increasing farm productivity by closing the yield gap in cacao production is argued to increase economic returns for farmers thereby alleviating the need to convert the forest to farmlands. The paper explores cacao yield gaps attributed by constraining factors related to biotic, abiotic and management, and examine potential interventions to bridge yield gap.

Paper two focuses on two competing factors that play critical roles in cacao productivity yet with unresolved interventions. The paper tests the pollination limitation hypothesis versus physiological limitation, statistically determine the most limiting in the study case, evaluates the factors that drive pollination limitation, and estimates natural pollination levels and the pollination yield-gap in the study plantations.

Paper three explores the biodiversity and abundance of cacao flower visitors, and the examine the landscape factors that affect their biodiversity. The paper further investigates the functional relationships between cacao flower visitors revealing previously unknown functional

network complexities implicated in pollination services.

In the final two chapters, I discuss the three papers in the context of the thesis aims, and the broader implications of the findings for sustainable cacao production with emphasis on cross-stakeholder role and thesis on future outlook.

2 LITERATURE REVIEW

This section reviews material and methods, methodological concepts, programs, and protocols applied to the achieving the goals of all the thesis papers. However, the methods section of each respective paper also describes the methods applied to answer the questions within each paper.

2.1 Cacao production

The term "cocoa" (pronounced – "*kow-kow*") is the commonly used trading name of *Theobroma cacao.* However, 'cocoa' also refers to the product derived from cacao bean used to make hot chocolate beverage drink. The species name, *'*cacao' (pronounced – *"ka-kau"*) is also commonly used to refer to the plant species, *T. cacao*. Cacao is cultivated mainly by smallholder farmers in low-income economies across the global tropics, mainly in Latin America, West Africa, and Southeast Asia (Franzen and Borgerhoff Mulder, 2007). Cacao production for confectionery, dairy, wine/distillery, perfumery/cosmetics, and pharmaceutical industries (Gavrilova, 2021), supports 40-50 million people of which 4-6 million are farmer household (Voora et al., 2019a; WCF, 2019). Income from cocoa production, estimated at USD100 billion per year (Potts et al., 2014) and additional value over USD 50 billion from the commodities market (Gavrilova, 2021), directly and indirectly supports critical social needs such as healthcare and children's education for some of the world's poorest farmers in producer countries (Frimpong et al., 2020) while addressing the United Nations Sustainable Development Goals 1(no poverty), 2 (zero hunger) and 3 (good health and wellbeing) (United Nations, 2015).

Although West Africa accounts for about 75% of global supply, cacao originated from Southern America. Cacao is cultivated mainly by smallholder farmers in mixed agroforests or in monocultures largely in the global South. In West Africa, Ivory Coast, Ghana, Cameroon, and Nigeria are the main producers. Prior to the invention of the chocolate recipe, *T. cacao* had been consumed for over 2000 years across many civilizations, making *T. cacao* the most important valued soft commodity in the history of humankind.

2.1.1 Industry, conservation, economic challenges and opportunities

Over four million tons of cocoa is produced annually in the three most important producer countries (Ivory Coast, Ghana, and Ecuador) at 3% global annual market growth and a predicted 30% increased demand between 2017 and 2020 growth year (Beg et al., 2017). The export value of the cacao bean was valued at USD 8.6 billion in 2017, with the chocolate industry alone consuming 43% of cocoa at a USD 106 billion retail value of in 2017 and projected to reach USD 190 billion by 2026 (Voora et al., 2019a). Increasing demand for cacao has led to increase in high-yield production methods, mainly monocultures of new cacao varieties often with limited canopy shade cover, as well as plantation expansion into forest areas which leads to biodiversity loss and elevated carbon emissions (Ruf and Schroth, 2004).

The conservation challenge of the cacao sector is summed by the New York Times (20th December 2022 edition) entitled, “The forest in your chocolate”, with the open statement, “Global demand for chocolate, not least during the holiday season, has devoured tropical forests where cocoa trees grow. Now, lawmakers in the European Union, the world’s largest cocoa buyer, have vowed to import only what doesn’t destroy or degrade forests…” (New York Times, 2022). Given

the biodiversity conservation link to cocoa production, sustainability has been a critical center of production market in the past two decades and has resulted in the emergence of a sustainability standard compliance sector with key agencies including, UTZ certification, Fairtrade International, Rainforest Alliance, and Organic. (Voora et al., 2019a). Sustainably sourced cocoa accounted for 29% share of 2016 global production (Voora et al., 2019a). This indicates a significant sustainability commitment in the cocoa industry. Cocoa sourcing traders and grinders committed to 100% sustainability by 2025 includes Barry Callebaut, Cargill, Cemoi, Cocoanect, Ecom, Olam, Sucden and Touton (Voora et al., 2019a). As of the year 2020, the global chocolate manufacturing companies; Mondelez, Mars, Hershey, Ferrero were committed to 100% sustainability sourcing while Nestlé was committed to 53% sustainability sourcing (Voora et al., 2019a). About 75% of the USD 2 billion valued compliant production comes from West Africa (Voora et al., 2019a) and signals rapid adoption of sustainable production food systems in the region.

Despite the economic opportunities in the growing demand for cocoa, mainly in Western Europe and the rapidly developing Asian markets (Voora et al., 2019a), average yield remain low and forecasted at approximately 0.54 tons/ha by the year 2050 (see table 1 for summary of country specific estimates).

Table 1: Model forecast of cacao yield in 2050 in major producer countries. Data was compiled from (Kozicka et al., 2018). ARIMA is Autoregressive Repeated Integrated Moving Average for forecasting from past time series data. IMPACT is the International Model for Policy Analysis of Agricultural Commodities and Trade.

Producer country	ARIMA model (tons/ha)	IMPACT model (tons/ha)
Ivory coast	0.84	1
Ghana	0.38	0.51
Indonesia	0.43	1
Cameroon	0.55	0.41
Nigeria	0.32	0.62
Brazil	0.39	0.35
Ecuador	0.26	0.36
Peru	0.58	0.86
Dominican Republic	0.36	0.36
Colombia	0.46	0.79
Mean	0.457	0.626
Grand mean = 0.5415		

The projection does not indicate major increases from the global average of 0.4 tons/ha compared to many food-security crops like grains and expected to further decline in specific producer countries (Kozicka et al., 2018). To close the yield gap and meet the growing demand and future production under climate uncertainties, it is essential to understand the key constraints that limit cacao productivity both currently and constraints that might be critical under future scenarios. Challenges in the cocoa sector are multifaceted in nature. Besides ageing trees and high rising temperature in West Africa that impact yield, leading to land use shift and deforestation (Schroth et al., 2016), systemic poverty in producer regions and uncertainty of market price volatility together also poses significant challenge to farmers (Voora et al., 2019a). During the second quarter of 2024, commodity prices increased by four-fold (Nasdaq, 2024b) due to supply deficit from West Africa caused by El Niño climatic event. This shows that addressing challenges must go beyond biotic and abiotic interventions but also recognize market related problems as well as the socio-economic or anthropologic aspects and their synergies.

Using the MAXENT climate suitability model, Schroth et al., (2016) predicted that by 2050, maximum temperature over the dry season will be more limiting than water availability resulting in high spatial vulnerabilities in forest-savanna transition and least vulnerable areas in the Southern part of West Africa. While higher altitudes and relatively lower temperatures favour future scenarios of cocoa production, Läderach et al., (2013) suggest site-specific strategies to build resilience.

2.1.2 Cacao production: flowering, pod development and harvesting

In Ghana cacao cropping occurs in two seasons: a minor season occurring between mid-

May and mid-July and a major season from September and December (Glendinning, 1972). Flowering occurs in peaks where flowers are few and spasmodic during the Harmattan dry season between January and March and then blooms heavily at the onset of the rains in April (Glendinning, 1972b). Unpollinated flowers fall within two days on average depending on season and flower bloom declines at the peak of the main-crop and increases as pods are removed (Glendinning, 1972; personal observation). Successful pollination leads to flower set within a day although to a lesser degree, flower setting occurs on second day (Entwistle, 1958; Glendinning, 1972b). The flower is very small, approximately, 1cm diameter, with a style indistinguishably split into five stigmatic lobes which together with the stigma is receptive to pollen (Entwistle, 1958; Glendinning, 1972b). The ovary is surrounded by five staminodes which overtop the style and separate it from the anther. The anthers are enclosed in petal hoods (Glendinning, 1972b) and appear to be a morphological selection barrier for cacao pollinators. Cacao pods bear 40 or more beans and the amount to pollen grains transfer is linked to the number of fertilized ovules (Cope, 1962).

Cocoa farming is an extremely laborious business which involves a year-long cycle of farm management such as weed and pest control, fertilizer application, pruning, harvesting, fermentation and drying of beans before sales. During the harvest season (at the onset of dry season/early winter), the seeds (beans) are removed from harvested fruits (pods, Fig 1A), fermented (Fig 1B) and sun dried (Fig 1C) before selling to buyers. The dry fermented cocoa beans are then processed into three main products: cocoa butter, cocoa liquor, and cocoa powder. These products are sold to third party markets including the confectionary, cosmetics, or pharmaceutical industries to make finished products such as chocolates, candies, beverages, wine or cosmetics

(Gavrilova, 2021).

Figure 1: (A) Communal cocoa harvesting. Here, I joined the family of a volunteer farmer in this study to help with harvesting. Traditionally, harvesting involves all family members and sometimes neighbours and friends. Farmer and or family will reciprocate the service to neighbours during their harvesting period. (B) Cocoa undergoing natural fermentation on the farm. Harvested beans are piled on the cacao farm floor. Due to the sweetness of the fresh beans, it attracts several insects including flies and bees, so farmers cover fruit pile with a net. It is not clear whether the diverse insects themselves aid in the fermentation process. Fermentation is a crucial stage that afford cacao its delicate rich flavour notes. (C) Sun drying of fermented cocoa bean. After fermentation, beans are spread on locally made rollable wood mat in the open sun. The drying beans are covered with opaque polyethylene sheet at the onset of rains or at night. Farmers frequently rotate beans to ensure uniform drying which over time turns the beans brown, leaving a notable cocoa aroma. The moisture content and the extent of sun burn (brownness) determines the grade assigned to the bean. The official market price quote for farmers, is usually based on the premium grade such that, failure to achieve acceptable grade cost farmers in revenue losses regardless of the yearly labour input. The rate of drying is unpredictable and depends on the local weather conditions such as humidity, duration of daily sunshine and the frequency of precipitation.

Photo credit: Acheampong Atta-Boateng.

2.1.3 Overview of Ghana cacao sector

Cocoa production in Ghana began in 1879 (GIPC, 2022). Ghana became the world's leading cocoa producer in the 1960s and cocoa production was the largest foreign earner at 45%, until Côte d'Ivoire overtook Ghana in production (Essegbey and Ofori-Gyamfi, 2012). Currently, cocoa production makes up 19% share of foreign revenues at USD 2.8 billion (GIPC, 2022). Agriculture constitutes 19.6% share of Ghana's gross domestic product (GDP) following industry, 32% and 42% in the services sector (Statista, 2024a). Agriculture is the largest employer at 33% with GDP growth rate at 8.42%, of which the cocoa sector performed at 10.39% from a 2013 reference baseline (MOFA, 2022). Cacao is the largest crop cultivated in Ghana by landcover at approximately 1,913,000 ha, achieving 87% yield at 0.87 Mt/ha according to 2021 estimate by the Ministry of Food and Agriculture (MOFA, 2022). The Ghana Cocoa Board (COCOBOD) is the government regulatory body which through its subsidiary, the Cocoa Marketing Company, buys cocoa from COCOBOD licensed buyers who in turn directly source cocoa from farmers (Ecobank, 2014).

The Ghana cocoa market is regulated by COCOBOD, which set a fixed, annual the government purchasing cocoa price for farmers. The intended upside of fixed cocoa price is that farmers are shielded from price volatility on the global commodity market in the fiscal year. However, on the downside, farmers do not benefit from market gains such as demand driven surges in price. Contrary to the Ghana market volatility protection rationale, global cocoa prices have

seen mean steady growth since 1959 (based on 65 years available data), with the only anomalies in price drop occurring in March 2000 and two dramatic price surges in July 1977 and more recently, March 2024 (Trading Economics, 2024a). Thus, only a single incidence in the cocoa trading history among the compelling market odds justify the farmer-price hedging versus the long-standing free market system. In other words, only the government stand to benefit from the price fixing policy. For instance, during the first quarter of the year 2024, an El Niño event (irregular climate event caused by the warming of tropical Pacific Ocean) caused shifts in weather patterns that resulted in cacao yield losses, and eventually, increased global cocoa commodity demand and price surge (Global Research, 2024). While financial market traders and investors with the means to hedge forward in 'thin exposure' on the cocoa commodity 'futures' and 'options' saw exponential financial gains (Global Research, 2024), farmers with fixed price were the big losers. Meanwhile, the predetermined price alongside predictable production outcome allows the government of Ghana to leverage cacao production as a financial instrument such as Eurobonds to fund economic activities (source: Peace FM, 'Kokrokoo'-local radio political morning program). Despite the ~$2.6 billion cocoa revenue, the prospects of an open, competitive, and free cocoa market whereby the State acts solely as a non-competing regulator, whose tax revenue share of a vibrant cocoa value-chain is incentivized by market growth, is yet to be realized.

Oil palm dominates Ghana's industrial commodity production at about 2,154,078 Mt, followed by cacao, at 1,047385 Mt and rubber at 27,344 Mt (MOFA, 2022). Nevertheless, oil palm production between 2012 and 2021 declined by 1.9% compared to cacao and rubber that grew in production by 25% and 35.4% respectively over the same period. Despite the encouraging growth, Ghana's cacao sector has not been without controversy. For instance, Ghana's announcement to

end the export of raw cocoa beans for onward processing in Switzerland in coincidence with the European Union blockage on intellectual property grounds of the World Trade Organization's (WTO) proposal for worldwide COVID-19 vaccine production, caused market waves (Ecobank, 2021). Although Ghana is Switzerland's primary cocoa supplier (Sostizzo, 2017), and the second largest global cocoa producer, the proposed export direction was independent of the WTO's vaccine advocacy, and rather part of Ghana's broader developmental ambition to add value to all raw material exports (Ecobank, 2021). The initiative is carried out by incentivizing the private sector to establish domestic cocoa processing factories to add to the rapidly growing sector. As of the year 2021, the domestic cocoa sector supported 20 manufacturers including: six in diversified cocoa products; seven chocolate processors; two in cocoa liquor production; a cocoa butter company; a 'cocoa mass' producer; a 'cocoa nibs' producer; and three cocoa powder manufacturers (MOFA, 2022).

2.2 Yield gap and socio-economic implications

The yield-gap of a crop is the difference between the current crop yield and a benchmarked yield such as the potential yield, Y_p or theoretical yield, Y_t (FAO and DWFI, 2015). The main difference between Y_p and Y_t is that Y_p relates to yield of a cultivar growing in its best adapted conditions, and likely to vary spatially. Spatial variation is determined by factors that are unique to a locality and implicate local crop productivity. This includes microclimate, soil chemistry and soil microbial load or the incidence of parasitic symbionts that are spatially non-uniform. Y_t is the model predicted yield within biophysical limits and is defined by parameters of

interest such as photosynthesis or biomass and likely to over-estimate what is possible in the field. In cacao, actual yield, Y_a, varies from less than 100 to over 3,000 kg ha^{-1}, averaging between 340 and 540 kg ha^{-1} globally (Cook, 2018). In Ghana, the reported Y_a is between 337.9 and 400 kg ha^{-1} (Laven and Boomsma, 2012; Aneani and Ofori-Frimpong, 2013), while Y_p is 1,891.3 kg ha^{-1}, and the farmer-based Y_p is 1,875.1 kg ha^{-1}, giving an estimated yield gap of 82.1% (Aneani and Ofori-Frimpong, 2013).

The yield gap per given land use area means there is a productivity deficit on the same land. Logically, when the trade-off for closing the yield gap is less than the added yield outcome, it may lead to a positive socio-economic benefit directly in the form of increased harvest or financial return, assuming demand-supply driven price volatility remain constant. At a given market price, the wide variation in yield as shown by Cook (2018) implies that for instance, farmer 'A', with 3,000 kg ha^{-1} yield will earn 300% more income than farmer 'B' with 100 kg ha^{-1} yield output. Where the total farming cost of 'A' is less the 300% income range, farmer A will be expected to have a better socio-economic reality based on capital returns and relatively more spending income than farmer 'B'.

Farmer-based Y_p is often lower than Y_p which is experimental, due to subjective farmer behaviour such as failure to prune or apply a biocide on time. Because it has been possible to produce up to 3000 kg ha^{-1} (Cook, 2008), this has been put forward as a theoretical maximum that is achievable, at least under some circumstances. Best practices, including efficient and effective use of agricultural inputs, may at least partially close the gap between Y_p and Y_a although factors such as farmer skills, use of innovation, the climate, the state of the soil and other biological resources, as well as the prevalence of pests and diseases, must be considered (FAO and DWFI,

2015). Although the yield of farmer 'A' can be said to be the maximum attainable crop yield by best practices, it represents the farmer-based Y_p which is equivalent to the attainable yield, Y_a. The yield gap, Y_p is relatedly, the causal sum of yield deficit resulting from factors that are yet to be resolved. Consequently, agricultural development that results in increased production output eventually improves socio-economic outcomes of society through poverty reduction and food security (Babenko and Vaselyeva, 2017). The scenario of farmer 'A' and 'B' highlights arguments by Babenko and Vaselyeva (2017) that, closing the yield deficit of farmer 'B' will improve farmer B's socio- economic outcome.

2.2.1 Link between cacao yields and livelihoods

Cocoa production supports 4-6 million farmers globally, and over 40 million workforce that depend on the cocoa industry for their livelihoods (WCF, 2019). The estimated USD100 billion annual revenues from production (Potts et al., 2014a) and additional USD 50 billion value from the commodities trading market (Gavrilova, 2021), supports critical social needs such as healthcare and children's education for some of the world's poorest cacao farmers (Morel et al., 2019b; Frimpong et al., 2020) and directly or indirectly addresses the United Nations Sustainable Development Goals on poverty, food security, access to education and good health as well as wellbeing (United Nations, 2015).

Although interventions that tend to address yield deficits often prioritize solutions that focus on biophysical constraints to productivity, a broader perspective that considers the complementary importance of biocultural influences, such as the nature of livelihood practices, belief systems and institutions is often lacking (Hirons et al., 2018). Studies have shown that the

livelihood benefit of cacao yield intervention depend on underlying socio-economic status (Morel et al., 2019b). For instance, Morel et. al (2019) found a disparate outcome in yield increases whereby wealthier households benefited proportionally more from ecologically intensive interventions such as improving understory litter, while poorer households benefited more from capital intensive interventions such as the use of pesticides and fertilizers that needed capital investments (Morel et al., 2019b). Furthermore, Morel et al (2019) argued that income from cacao yields alone were limited in addressing the livelihood needs and as such, require the complementary support of the state. Scholarly works about the interconnections between the cacao micro and macroeconomy, with respect to livelihood is limited, given that in cocoa producer countries such as Ghana, cocoa production is an important contributor to GDP, thus, GDP per capita. Moreover, besides farmer's self-reliant support from labour earnings, State investment in community development such as proving healthcare, transport or educational infrastructures can be better executed when increased productivity relatively increases cocoa sales and tax revenue. For instance, from cocoa revenues, the Ghana COCOBOD has established healthcare and educational scholarship schemes selectively for cacao farmers and their respective household to improve their access to healthcare and education (COCOBOD, 2024).

2.2.2 What is limited about this understanding?

Cacao 'boom and bust' (Ruf, 1995) occurs when production increases ('boom') on newly cultivated converted forest but declines in yield ('bust') over time due to farm selection pressures like pest, diseases, and depleted soil, thereby causing a cycle of forest conversion and biodiversity loss (Clough et al., 2009). Although it has been suggested that both production and conservation

needs can be resolved by addressing yield-gaps while benefiting farmer income (Rice and Greenberg, 2000; Waldron et al., 2012a), it is uncertain for instance, whether more profit gains from addressing yield gaps will not motivate further investments to convert more forests into farmlands for more profits. However, unlike in large commercial farming practice, the 'boom and bust' cycles associated with smallholder farming suggests that declining farmland productivity will drive shifting cultivation/swidden or fallow agriculture, such that farmers may likely remain on their farmlands if an intervention prolonged the boom scenario albeit the added year-round labour demand and the investment cost of cultivating new farmlands.

Increasing cacao demand leads to increasing monoculture practice and plantation expansion into forest areas, which threaten biodiversity loss and emissions (Ruf and Schroth, 2004). In as much as production losses remains the biggest threat of the cacao industry, the overarching impact of unmet demand and declining supply may exacerbate a win-loss scenario (Hirons et al., 2018). In the cacao sector, the production end of the value chain tends to bare most risk during crisis contrary to the value-added end of market chain. For instance, by the end of the first quarter of year 2024, the global market saw a historic rise in cocoa commodity price from about $3,000/per ton to about $10,120/per ton (Nasdaq, 2024b). This was attributed to climate shocks which resulted in the decline of cocoa supply from West Africa, the region responsible for nearly 75% share of global cacao production. Farmers lost revenues from the ENSO affected yields. Meanwhile, the production deficit caused high commodity demand, resulting in significant returns to traders on the financial market and major European suppliers with cocoa holding infrastructure and investment to hedge. Unlike farmers who sell at fixed prices besides yield losses, the processing end-chain have optional pricing mechanisms to pass cost to chocolate consumers.

This case highlights Hirons et al (2018) concerns on the importance of equity towards climate resilience in the cacao sector by focusing efforts to address the resilience of 'losers' to climate shocks.

Another aspect of cacao yield-livelihood linkage concerns limitations of the income in addressing realistic livelihood needs. In July 2019, the government of Ghana and Côte d'Ivoire negotiated an addition of $400/ton on cocoa prices called the Living Income Differential (Gilbert, 2024). While such additional incomes may directly increase farmers financial status, studies show that increased farmer income from cocoa can only address limited livelihood needs such as cost of education, food security and acquisition of personal asset (Morel et al., 2019b). Farmer income is constrained in the provision of other livelihood needs such as access to clean water, reliable healthcare which require community-level infrastructure investments from government institutional stakeholders (Morel et al., 2019b). Thus, resolving yield gaps will essentially improve aspect of livelihood conditions affected by inadequate farmer or household income but may not address livelihood needs derived from the community level development.

2.3 Pollination limitation in crops

Pollination occurs when a pollinating agent transfers pollen grains from an anther to a stigma of the same or different flower of the same species. The pollinating agent can be a biological organism such as insects or bats, or inanimate, like wind or by water. Self-pollination describes pollination within the same plant while cross-pollination involve pollen transfer to a different flower.

In cropping systems, pollination is likely achieved by insects especially in trees (Garcia

et al., 2021) and high value crops. Most cereals or grains such as corn and wheat are wind pollinated. Although most literature focus on animal-pollination (Friedman and Barrett, 2009), globally, we derive majority of food calories (van der Sluijs et al., 2016) from the 10% fraction of angiosperms that are wind pollinated (Friedman and Barrett, 2009). Pollination limitation occurs when the full reproductive potential (i.e fruit or seed set) of a crop is not expressed due to limited pollination services (Aizen et al., 2008). Pollination failure can result from many factors including: inadequate pollinating agents due to pollinator population declines in entomophilous crops (pollinator-limitation) (Reilly et al., 2020); by landscape factors (Ricketts et al., 2008a) or flower-related behaviour (pollen-limitation) (Aizen and Harder, 2007). While biotic pollination is directional and dependent on the behaviour of the animal vector (Whitehead, 1983), wind pollination (anemophily) is passive, and depend on pollen grain characteristics, aerodynamics, suitable floral characteristics, receptive stigma morphology and orientation, pollen release timing and environmental conditions that coordinate floral cues (Whitehead, 1983; Dowding, 1987). Thus, these factors alone or in combination are generally likely to impact pollination limitation in crops. Pollination limitation, relative to the successful reproductive outcome begs the question of the appropriate definition in the case where successful pollen transfer proceed to failed fertilization (fusion of male (pollen) and female (ovules) or the case whereby successful fertilization precedes failure of seed or fruit set. Pollination limitation (PL) is pollen-based when insufficient, too much, too mixed, or poor pollen quality is delivered to the stigma, whereas PL is pollinator-based when there are too few or too inconstant pollinators (Wilcock and Neiland, 2002). Increased risked of pollination failure is associated with plants when they are too specialized or selective; with populations, when they are too sparse, small, or genetically uniform; and with communities when they are too fragmented, genetically impoverished or under rapid modification (Wilcock and

Neiland, 2002).

2.3.1 Why important?

Sufficient pollination provides several benefits including crop yield, crop shelf-life enhancement and food waste reduction (Klatt et al., 2014). Insufficient pollination is suggested to intensify demand for agricultural land, thereby increasing the pressure on agricultural land supply and impacting global environmental change (Aizen et al., 2009; Garibaldi et al., 2011). In a study on 87 crops, PL resulted in a 3% to 8% decline in global agricultural production over 46 years (Aizen et al., 2009). Furthermore, incomplete, and variable pollen delivery is found to decrease yield and temporal stability of global agriculture more in crops that depends on pollinators (Garibaldi et al., 2011). For instance, an estimated 72% of the 1,594 total crops cultivated across the tropics (Roubik, 1995) and Europe (William, 1994), benefit from animal pollination. Thus, the loss of pollination limited services will inevitably result in both economic and ecological impact (Potts et al., 2010).

2.3.2 Evidence across crop species of economic importance

In India, pollinator absence reduced 54% of the value of fruit production in eggplants (Bhattacharya and Basu, 2018). In a study across 131 farms in the United States, wild bees accounted for $1.2 Billion annual production value of highbush blueberries *(Vaccinium corymbosum)*, apple *(Malus pumila)*, sweet cherry *(Prunus avium)*, tart cherry *(Prunus cerasus)*, almond *(Prunus dulcis)*, watermelon *(Citrullus lanatus)* and pumpkin *(Cucurbita pepo)*(Reilly et al., 2020), and production from pollinator-dependent crops was valued annually at $50 billion

(Calderone, 2012; Bauer and Sue Wing, 2016). In sub-Saharan Africa, pollination accounted for 62% yield in cotton while in sesame, pollinator absence resulted in crop yield gap of 32% and 59% (Stein et al., 2017). Specifically in Kenya, pollination services accounted for 40% production value in smallholder crops such as green gram (*Vigna radiata*), beans, cowpea (*Vigna unguiculata L. Walp*), sunflower (*Helianthus annuus*), tomato (*Solanum lycopersicum*), bambara groundnut (*Voandzeia subterranean L.*), passion fruit (*Passiflora ssp.*), and capsicum (Kasina et al., 2009). In the United Kingdom, insect pollination services in greenhouse systems accounts for £27 million (tomatoes), £0.64 million (sweet pepper) among field crops; £ 41.9 million (oilseed rape), £9.3 million (blackcurrant), £5.6 million (strawberry), £3.1 million (raspberry), £ 5.6 million (cherry) and £ 87 million (apple) (Mburi et al., 2006). Across six European countries, PL decreased harvestable yield by 8% in sunflowers, 6% in oilseed rape and a mean yield loss of 2.8% across 105 commercial fields (Holland et al., 2020).

2.3.3 How has it been accessed?

The goal of establishing pollination limitation (PL) is to determine whether reproductive yield will be limited without pollination. As such, pollination limitation can be determined indirectly by assessing either pollen-based limitation or pollinator-based limitation. Pollen-based PL assumes absence of pollinator-based limitation and that successful seed or fruit set depends on the viability of pollen that results in successful fruit set. Pollinator exclusion experiment is used to determine pollinator-based PL (Bhattacharya and Basu, 2018). Here, a part of the crop under investigation is excluded from natural pollinators (Bhattacharya and Basu, 2018). PL has also been determined by comparing yield response to open pollination (i.e pollination by natural biotic

agents) relative to full or proportional pollination controlled by artificial ("hand") pollination (Groeneveld et al., 2010a; Toledo-Hernández et al., 2020a, 2021b). These methods can only provide insight in pollinator-based PL while they do not account for pollen-based PL. As pollen recognition and rejection in cacao is late acting (Ford and Wilkinson, 2012) in the ovaries during fertilization (Cope, 1962), it can be argued that pollen-limitation in cacao may not be considered as PL. Contrary to several species where pollination failure occurs before fertilization, I distinguish PL in cacao from the conditions of self-incompatibility and therefore restrict PL to pollinator-limitation. Meaning, selfing can purely be considered as a genetic limiting factor in cacao and therefore pollen-limited methods are not discussed or addressed in this thesis.

2.4 Pollination in cacao

A study in Indonesia on whether pollination deficit, on its own, is a factor limiting cacao yield found that enhanced pollination intensity (between 10 and 40%) increased yield by 100% (Groeneveld et al., 2010b). In the study, pollination service was more limiting to yield than abiotic resources including light, water, and nutrient. The study provides a surprising insight into the drivers behind cacao yield gaps, however, there remains research to be done to determine whether the findings apply to other growing regions. Unfortunately, studies on cacao pollinators, their ecology and the relationship of pollination service to yield remain very limitted (Toledo-Hernández et al., 2017).

Although studies on cacao pollination ecology are limited (Toledo-Hernández et al., 2017), there appear to be opportunities for plantation management to increase effective pollination. Recent studies have shown that hand pollination exercises can be a cost-effective approach that

can reduce existing yield gaps due to pollination service deficit (Toledo-Hernández et al., 2020; Toledo-Hernández et al., 2023). For example, Groeneveld et al (2010a) found pollination deficit at their study sites in Central Sulawesi, Indonesia and found that supplemental hand pollination had the largest measurable effect on cocoa yield of the factors tested (Table 4). Previous work has shown that (1) distance to native vegetation (Young, 1986; Clough et al., 2011), (2) understory light environment (Young, 1986), (3) soil moisture (Lahive et al., 2019b), (4) litter layer depth and quantity of decaying vegetative material (Frimpong et al., 2011), and (5) season (wet vs dry) (Young, 1986) can affect the pollinator community composition and total pollinator abundance in cacao plantations (Woodcock et al., 2019). While Young (1986) found a negative correlation between distance to shade tree and pod numbers in cacao plantations in Costa Rica, Frimpong et al (2011) found no relation to shade trees, nor with distance to forests in Ghana. However, both studies found high cacao pollinator abundance under banana stems and pod husks, even under high light understory environments (Young, 1986; Frimpong et al., 2011).

2.4.1 What is understood about cacao pollination generally and specifically in Ghana

The first studies on cacao pollination originated in Trinidad and Tobago during the early 20th century after which research contributions from Ghana peaked in the mid 20th century (Caracciola, 1910; Pound, 1933; Posnette, 1950; Entwistle, 1957). In more recent times, challenges in cacao yield have prompted new research revealing new insight on pollination from emerging growing regions such as Sulewesi, Indonesia (Toledo-Hernández et al., 2020a, 2021b).

Cacao has been shown experimentally to be pollination limited under field conditions

(Groeneveld et al., 2010b; Toledo-Hernández et al., 2020a). For instance, cocoa yield increased above natural pollination level with increasing hand pollination rates (Groeneveld et al. 2010). Pollination limitation in cocoa (Toledo-Hernández et al., 2020b) is thought to be due to a combination of insufficient insect pollinator abundance and/or biodiversity (Toledo-Hernández et al., 2021b), which is expected to be a result of local biotic and abiotic habitat characteristics affecting pollinator species' survival and reproduction (Zakariyya et al., 2016; Forbes and Northfield, 2017a). Further, the self-incompatibility mechanism which occurs during cacao pollination (Cope, 1962), and the short life span of individual flowers (unfertilized flowers abscise ~22–24 hrs after flower opening (Swanson et al., 2008)) are likely to affect the rate of effective pollination.

Insufficient pollination was first linked to low crop setting in self-incompatible cacao as early as the 1940s at Aburi, in Ghana (Posnette, 1940). In Peru, a three-fold crop yield was reported in 1960 following a hand pollination exercise (Hurtado, 1960). From earlier studies, pollination frequencies were typically low (1% to 2%) during heavy flowering at the onset of the rainy season but peaked at about 50% around July and August when flowers were scarce (Posnette, 1942; van der Knaap, 1955). Moreso, pollination occurred during the day (Posnette, 1942) and in Ghana, 87% of pollination was found to occurr between dawn and 0900 hrs, and 12 % in the afternoon between 1200 and 1500 hrs (Entwistle, 1958).

2.4.2 Biotic and abiotic factors of cacao pollination

A balance of abiotic and biotic factors and their mutualistic interactions have been suggested to mediate pollination and fertilization success of cacao (Bridgemohan and Mohammed,

2019). However, studies report increased number of pollinated flowers relatively increased yield compared to factors such as light, moisture and soil nutrients (Groeneveld et al., 2010a).

Abiotic factors such as light environment and seasonality have been reported to influence flower visitor abundance and taxonomic diversity (Vansynghel et al., 2022a). In their study, light environment through canopy shading and seasonal moisture as the abiotic factors explained flower visitor abundance and diversity, further confirming findings by Vansynghel et al., (2022b). Thus, abiotic conditions act to provide conducive conditions for biotic actors to effectively provide pollination services.

There is a reason to acknowledge that activities and relationship among biotic actors themselves help pollination services. For instance, low fruit set of cacao pollinating midges (Vansynghel et al., 2022a) suggest the possibility of the involvement of complementary species that may be directly or indirectly associated with pollination service. However, no study to date have provided evidence that can be linked to a network of multiple flower visitors that are interlinked with a collective biological function of significance.

2.4.3 Taxonomy, diversity, and ecology of cacao pollinators

A typical cacao pod contains about 40 or more beans, meaning a pollinating agent must deposit about 40 pollen grains on the cacao flower style (Glendinning, 1972b). The style is fenced by staminodes, and the anther is enclosed in a petal hood which requires the pollinating agent to be small enough with specialized behaviour (Glendinning, 1972b). As early as 1910, ants, flies and thrips were identified as candidate pollinators and concluded thrips were the likely pollinating agents (Caracciola, 1910). Pound (1933) found evidence to supports thrips pollination and Cope

(1940) also found positive correlation between pollination and ants and thrips on cacao flowers. Furthermore, Billes (1941) found direct evidence of thrips pollination but concluded it to be unlikely effective as wing vibrations during flight take-off shook off most of the pollen.

Nonetheless, Cobley (1942) altogether rejected ants, flies, and thrips as important cacao pollinators. Aphids were found to be positively (Stahel, 1928; Billes D.J., 1941) and negatively (Cope, 1940) correlated with pollination although Entwistle (1958) could not confirm these findings in flower enclosure studies.

Pound (1933) first reported Cecidomyid midges on cacao flowers in Trinidad but did not appear as pollinator (Entwistle, 1958). Pollinating agents were examined based on the possible quantity of pollen grains they could transport (Glendinning, 1972b). While cacao flower visiting insects were common, Billes (1941) noted that pollination occurred in random bursts, discounting the importance of these insects, and drew more attention on the *Forcipomyia* midges of the Ceratopogonidae family. Between the early 1940s and 60s, *Forcipomyia* midges have not only been accepted as cacao pollinators but were also confirmed across three tropical continents in West Africa (Posnette A. F, 1950), East Indies (van der Knaap, 1955), Costa Rica, and the Philippines (Sauders, 1958). Research on *Forcipomyia* midges expanded, providing further insight into its pollination mechanism (Billes D.J., 1941; Posnette, 1950) which for instance, is attained solely by the female *Forcipomyia spp.* (Billes D.J., 1941; Posnette A. F, 1950).

Cacao flower visitors are diverse and originate from a vast range of taxa. Early collection of cacao flower visitors that were linked to pollination, including *Forcipomyia quasi-ingrami* Macfie and *Laseohelea nana* Macfie, were described by J.W. S Macfie and remarked by biologist A.F Pognette as “cacao pollinators of economic importance” (Macfie, 1945). Although cacao

reproductive ecology saw vibrant research throughout the early half of the 20th century, the accepted pollinators were mainly associated with midges of the Ceratopogonidae and Cecidomyiidae families (Kaufmann, 1973, 1975a; Winder, 1978). In a more recent review, Toledo- Hernández et.al (2017) reported that nearly half of cacao pollination services were achieved by members from the two dipteran families. Nevertheless, increasing evidence of diverse cacao flower visitors (Toledo-Hernández et al., 2017, 2021b; Chumacero et al., 2018; Vansynghel et al., 2022b) suggest that cacao pollination services may be nuanced than thought and the functional role of the variety of flower visitors remain a curious subject open for discoveries.

Cacao flower visitors are diverse and vary in abundance, across climate, geography, and landscape habitat (Forbes and Northfield, 2017b). For instance, in Bolivia, parasitoid wasps (Hymenopteran) were the most abundant flower visitors in both wild and cultivated cacao groups (Chumacero et al., 2018). At central Sulawesi, Indonesia, ants (Formicidae) were the abundant flower visitors followed by various Diptera (Toledo-Hernández et al., 2021b). In seasonally dry, semi-arid Northern Peru, aphids (Hemiptera) were the most abundant flower visitors, followed by ants (Hymenoptera). Furthermore, thrips (Thysanoptera), followed by various Diptera were the most abundant in moderately humid southern Peru (Vansynghel et al., 2022a). Vansynghel et al. (2022) suggested that of the flower visitors reported, the Thysanoptera group rivals the Dipterans as candidate cacao pollinators. Of the surveyed flower visitors, the major taxa in decreasing order of abundance are Diptera, Hymenoptera, Homoptera, Coleoptera, Thysanoptera, Lepidoptera, Collembola, Neuropteran and Arachnidae (Toledo-Hernández et al., 2017). Earlier survey over a decade near the Bobiri forest reserve (appx. 205km from current study area) in Ghana reported only Diptera and Hymenoptera as cacao flower visitors (Adjaloo and Oduro, 2013). While this

suggests a likely temporal shifts in cacao flower visitor biodiversity in Ghana, recent survey in Peru indicates that cacao flower visitor diversity and abundance can vary by location in the same region (Vansynghel et al., 2022b). Differences in cacao flower visitor abundance and diversity have also been reported Bolivia (Chumacero et al., 2018) and Indonesia (Toledo-Hernández et al., 2021b). In Southern Peru, thrips were found to be the abundant flower visitor although this was not the case in Northern Peru (Vansynghel et al., 2022b).

In cacao flower visitor investigations, flower visitors can be monitored, captured, or surveyed by techniques including the Mc Phail flower trap (Frimpong et al., 2011) and the sticky-glue flower trap (Chumacero de Schawe et al., 2018). Different factors can play important role in pollinator behaviour and pollination services. The importance of pollinator habitat to pollination services have been highlighted (Forbes and Northfield, 2017b). Cacao pollinator response to cacao flower further suggests that olfactory cues may play pollinator role in pollinator behaviour (Arnold et al., 2019). Furthermore, leaf litter is reported as the best breeding substrate for the most described cocoa pollinators, Ceratopogonid midges, and is associated with high cocoa yields (Adjaloo et al., 2013).

2.4.4 Why need for more studies on cacao pollinators?

Although it has long been accepted that the female *Focipomya* midges are implicated in cacao pollination over the past eight decades, and fit the behaviour required to ascertain pollination services (Billes D.J., 1941; Macfie, 1945; Posnette A. F, 1950; Glendinning, 1972b; Toledo-Hernández et al., 2017) yet, the functional role of the several other species that consistently visit cacao flowers and or have been subjects of debate remains unresolved (Caracciola, 1910; Billes

D.J., 1941; Chumacero et al., 2018; Vansynghel et al., 2022b) especially since the well-known midges seem to achieve a fraction of observed pollination (Toledo-Hernández et al., 2017), and no collective association has been linked among flower visitors. Part of the puzzle might be related to technical challenges although recently, studies that have attempted to directly identify cacao functional pollinators by quantifying pollen carried on the insects' bodies have been unsuccessful, even for Ceratopogonidae and Cecidomyiidae samples, although they are commonly associated with cacao pollination (Vansynghel et al., 2022a). The combination of a highly diverse and variable suite of cacao flower visitors, and the lack of a direct correlation between flower visitation and effective pollination, suggests that cacao pollination may be a more nuanced and complex process than previously described. More recently, an integrated micro-computed tomography and geometric morphometrics was used to elucidate the linkage between flower visitation and pollination function (Wolcott et al., 2023). However, the technique at best serves only to narrow the likelihood of pollination service of candidates and likely applicable as a complementary technique to a more robust approach. Nonetheless, the conclusion from Wolcott et al (2023) provides contrasting results for the ceratopogonid midges analysed than previously known. Thus, the confounding misery that could be the key to the sustaining the multi-billion USD cacao enterprise continues to remain a mystery. While hand pollination practice improves cacao yield, it comes at a labour cost (Toledo-Hernández et al., 2020a). Improving our understanding of the biology of cacao pollination especially the lesser-known functionality of flower visitors may help us develop improve the economic footprint of benefit of efficient pollination services at no labour cost.

2.5 Genetics of cacao reproductive biology

The genetics of cacao is atypical of angiosperms, exceptionally complex and suggested to be of recent evolutionary origin (Pandey, 1960). Below, I begin with broad background and describe the genetically nuanced nature of cacao reproduction. Nearly 70% of flowering plants exhibit a genetic system that suppresses inbreeding by allowing pistil (female flower tissue, comprising stigma, style, and ovary) to 'recognize' and then 'reject' self-related pollen (male flower tissue) to prevent self-fertilization in a phenomenon called self-incompatibility (Hiscock, 2002; Hiscock and Mcinnis, 2003). This recognition and rejection of the phenotypically identical pollen is controlled at the *S*-locus (Franklin-Tong and Franklin, 2003). If pollen is compatible, fertilization proceeds, leading to fruit set, therefore incompatibility can be a direct cause of yield loss. There are two forms of self-incompatibility (SI); the Gametophytic SI and Sporophytic SI (Hiscock, 2002). Gametophytic SI (GSI) occurs when the incompatibility *S* phenotype of the pollen is expressed by the haploid genome (Franklin-Tong and Franklin, 2003). In the Sporophytic SI (SSI), the *S* phenotype of the pollen is determined by the parental diploid (Hiscock, 2002; Hiscock and Mcinnis, 2003). GSI is the most common form of SI among angiosperm while SSI evolved more recently (Hiscock and Mcinnis, 2003). The main difference is that in the GSI, the *S* alleles are expressed co-dominantly in the pistil while in the SSI system, the dominance of *S* alleles can be expressed in the pistil and in the pollen (Hiscock, 2002). Moreover, in cases where genetic data do not satisfy GSI and SSI requirements, the pollen phenotype is suggested to be determined during micro-sporogenesis of both the pollen's own genotype and the parent plant (De Nettancourt, 2001). While self-compatibility (SC) and SI distinctly exist across plant groups, several species groups express both SC, SI and in some cases, unilateral incompatibility, which is the case where

the pollen of the SC species is inhibited in the styles of the SI species but without inhibition in the reciprocal scenario (Lewis and Crowe, 1958). The SI x SC inhibition is considered general at the families and genera taxonomic levels, although exceptions of SC are notable at the species or variety level (Lewis and Crowe, 1958).

SI in cacao was first reported in Trinidad (Pound, 1932). The early genetic hypothesis of cacao SI posited that cacao SI was sporophytic, and was based on five alleles that exhibited dominance with genes occurring at the same locus (Knight and Rogers, 1955).The incompatibility was found to be expressed through a sporophytic control of non-fusing gametes in which the reaction occurred after pollen tube have penetrated the ovaries, resulting in fertilization failure (Knight and Rogers, 1955; Cope, 1958). Thus, unlike many species where pollen rejection occurs early before or during pollen-tube decomposition, cacao SI is a gameto-sporophytic system expressed only at the level of the embryo sac thus, late acting or ovarian and the selfing efficacy is found to vary between clonal varieties (Ford and Wilkinson, 2012; Lanaud et al., 2017a).

Besides the determination of the pollen phenotype by the gametophyte and sporophyte factors in the ovarian gametophytic-sporophytic systems of cacao, it also conditions the incompatibility reaction of the ovules (de Nettancourt, 2001). Earlier investigations on cacao SI reported that cacao expressed three forms of incompatibility expressed experimentally in 25%, 50% and almost 100% non-fusion ovules in the ovary (Cope, 1958, 1962). Hence, gametes that expressed similar dominant alleles could not fuse, and *S*-locus actions occurred before and after meiosis, with two other loci that produced non-specific precursors to which *S* alleles imparted their specificity (Cope, 1962). Consequently, the consensus is that the regulation of syngamy (fusion of gametes) on self and cross pollination in cacao involved the *S, A* and *B* genetic loci (de Nettancourt,

2001).

2.6 Landscape and farm features of cacao production system

Native cacao is an understory forest tree (Arévalo-Gardini et al., 2021) that originated from Amazonia and as such have led many to assume that the closeness to forest landscape might enhance yield. Studies have found a strong relationship between natural habitat area and pollination services (Kremen et al., 2004). Hence, conserving the habitats of pollinator within agricultural landscapes has been found to maintain pollination service, which further increases the size, quality and stability of harvests for 70% of global crops (Ricketts et al., 2008b).

The increasing importance of pollination services in cacao systems have prompted the need to improve cacao farms into sustainable landscapes that improves biodiversity and conservation (Bos et al., 2007a; Clough et al., 2009; Wanger et al., 2018; Toledo-Hernández et al., 2021b). However, there exist knowledge gaps in our understanding of the landscapes factors that impact cocoa production. Recent studies on the effect of landscape and farm-level factors on cacao flower visitation found that the habitat surrounding the cacao farm and canopy cover increased the abundance of Diptera and ants but not litter (Toledo-Hernández et al., 2021b). Meanwhile, plantation floor litter such as rotting banana trees and piles of harvested cocoa shells, are both known to be the preferred larval habitat for cacao's chief pollinators (Glendinning, 1972; Winder and Silva, 1972; Young, 1982; Adjaloo et al., 2013). Moreover, rotten biomass on plantations and the proximity of litter pile to cacao tree has been associated with pod output (Morel et al., 2019b).

In coffee, the proximity of plantation to forest has been found to increase pollinator visitation (Ricketts, 2004; Klein et al., 2008). Contrary in other studies, the distance of cacao

plantation to forests was found not have effect on pollination service or cacao flower visitation rates (Klein et al., 2008; Toledo-Hernández et al., 2021b; Vansynghel et al., 2022a). Although a positive relation of forest proximity to yield was observed in an herbivory predator exclusion experiment (Gras et al., 2016), the response was unclear and was not associated with the predation manipulation nor pollination (Gras et al., 2016) and might likely be associated with shading. Ecological studies of cacao systems are at its infancy, and in this thesis, I attempt to expand on this developing field of study by investigating the linkage of landscape factors related to the complexity of vegetation surrounding plantations, plantation floor litter, as well as plantation light environment to cacao yield and the functional diversity and abundance of its flower visitors.

3 REVIEW OF METHODOLOGY

This section reviews material and methods, methodological concepts, programs, and protocols applied to achieving the goals of all the thesis papers. In addition, each respective paper in the thesis has a methods section that describes the methods applied to answer the questions addressed in each paper.

3.1 Establishing field experimental site

Eight sites were established for field experiments near Tarkwa-Breman in the Wassa-Amanfi district in the Western region of Ghana (Table 1, Figure 1). The individual plantations were selected as study sites based on the complexity of vegetation surrounding the plot and the presence or absence of non-cacao shade trees within the plot. The former was hypothesized to affect biodiversity richness, and the abundance and distribution of biotic components (pollinators). The latter is an indicator of the light environment which is also expected to affect the biotic composition of the understory. Surrounding plot vegetation was classified into two categories: '*homogenous (simple)*', when the plot is surrounded by a single species or without complex stratification e.g., farm or single species plantation or grass field; and '*heterogenous (complex)*', when the vegetation

surrounding a plot constitute multi-strata, high floral diversity e.g., secondary forest, wetland, or a highly diverse vegetation patch. The assumption of this selection criteria is that complex vegetation is biodiverse and may provide a range of habitat or refugia for diverse pollinating agents thereby hypothetically increase pollinator visitation and eventually pollination services in the surrounding farms.

A plot of size 40 x 40 sq. meters was marked within each plantation and the total density of cacao trees was determined by tagging all the trees within the plot and removing tags to count (in the absence of a hand-held counting device). The average diameter at breast height (dbh) per plot was determined by measuring the dbh of all trees within 2m left and right of the diagonal transect of the plot with a dbh tape. The total number of trees with circumference larger than 150 cm was also recorded.

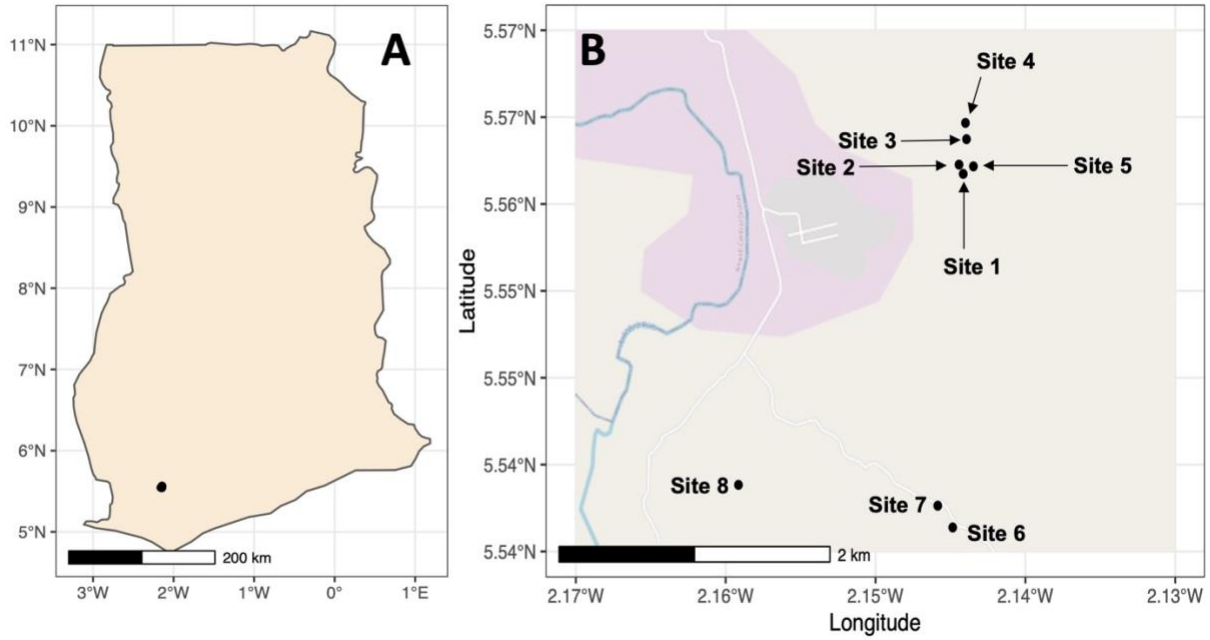

Figure 1: Location of study location in South-western Ghana (Tarkwa-Breman, 5.56173/-

2.144153 lat/long) in the Prestea Huni-Valley District (A). Map of experimental sites (B). The purple regions represents the Tarkwa-Breman community town. Blue line represent a river and white lines represents road networks.

Table 1: Plot locations and characteristics

Site #	Site code	Place/location	Latitude	Longitude	Vegetation surrounding plot	Shade trees
1	1_nscf	Tarkwa-Breman	05°33.704'	-002°08.649'	Heterogenous	No
2	2_sscf	Tarkwa-Breman	05°33.736'	-002°08.666'	Heterogenous	Yes
3	3_nscf	Tarkwa-Breman	05°33.824'	-002°08.636'	Heterogenous	No
4	4_ssff	Tarkwa-Breman	05°33.880'	-002°08.640'	Homogenous	Yes
5	5_nsff	Tarkwa-Breman	05°33.730'	-002°08.608'	Homogenous	No
6	6_ssff	Anti-korkoh	05°32.483'	-002°08.691'	Homogenous	Yes
7	7_nsff	Anti-korkoh	05°32.558'	-002°08.751'	Homogenous	No
8	8_sscf	Amezugbe	05°32.630'	-002°09.549'	Heterogenous	Yes

3.2 Plantation floor deadwood

Because we expect the quantity of plantation floor deadwood to affect the local arthropod community composition and abundance, we measured the number of logs and structures such as fallen trees, old tree trunks and large branches of diameter greater than 5cm, as well as the total number of piles of cocoa husks on the plot. The age of cocoa trees, chemical inputs and information on plantation management practices such as time of farm input application, choice of commercial farm input brand, and weed control were also obtained by administering a questionnaire to farmers/farm owners (See section 3.3.1).

3.3 Plantation light environment

Light environment in each plot was measured by measuring the amount of light that penetrates through the aboveground canopy using the canopy-scope score (Brown et al., 2000). The score is effective for measurements that are averaged within a plot (Hale and Brown, 2005a). Thus, in this study, a 5-point average score was obtained with measurements from the middle of the plot and the four points near corners of the 40 x 40 sq. meter plot.

Figure 2: Higher understory light environment in a plot without shade trees (A). Lower light environment in a plot with many shade trees (B). Several factors other than the presence of shade trees impact understory light environment of cacao plantations. All photos were taken at the same time. Photo credit: Acheampong Atta-Boateng.

3.4 Field team and logistics

To execute the field sampling campaign, I recruited students from the local town and trained them to perform hand pollination, flower counting, monitoring fruit development, trapping arthropod and preparing trapped arthropods into final specimens for further analysis. The field assistants were supported by a field manager who was an undergraduate biology degree major. See figure 3 for hand pollination team resting after a tiring field day.

Figure 3: Field crew after gathered after setting up and marking plots.

3.5 Sampling methods and data collection

3.5.1 Farm management survey

Farm owners or farm managers were interviewed on their choices of agronomic practices.

Survey Questionnaire Data Sheet

Ghana Farmer Survey Form

Date: ……

Farm ID: ……..

Farm owner/manager code: ……

Farm name: ……

Farm location: ……

Agronomic management activities

Q1 What agronomic activities do you typically practice/apply on your farm? List all practices that apply e.g. pruning, weeding.

- ……. …….
- ……. …….
- ……. …….
- ……. …….

Agrochemical inputs

Q 2 Do you apply agrochemical input(s) on your farm?

[YES / NO]

If no, skip questions below.

Q 3 Do you apply agrochemical input to control weeds?

[YES / NO]

If yes, list all the brands that you use.

- ……. …….
- ……. …….
- ……. …….
- ……. …….

Q 4 Do you apply agrochemical input to control pests?

[YES / NO]

If yes, list all the brands that you use.

- ……. …….
- ……. …….
- ……. …….
- ……. …….

Q 5 Do you apply fertilizer input on your farm?

[YES / NO]

If yes, list all the type/brands of fertilizer that you use, when it is/they are applied on the farm and how it is/they are applied on the farm in the table below.

Table 2 Template sheet to collect data on fertilizer input management.

Fertilizer type/brand	Application time	Mode of application
1.		
2.		
3.		
4.		
5.		
6.		

3.5.2 Hand pollination experiment

Thirty-six trees, with dbh ranging from 35/πcm to 65/πcm were selected and marked based on a systematic sampling technique (Figure 4 & 5). Selected trees were tagged and labelled as replicates of hand pollination treatments from 0%, 20%, 40%, 60%, 80% and 100%. Thus, this represented six replicates per treatment per sample site. The hand pollination treatments indicate the proportion of flowers that are pollinated by hand. The zero percent is the control treatment in which pollination occurs only by a natural pollinator. For each tree, the total number of flowers present within two meters height from the base of the tree were counted and the number to be pollinated calculated. For example, if the tree is marked 20% and 100 flowers were counted within two meters height from the base of tree, 20 flowers will be hand pollinated. The remaining flowers were completely removed.

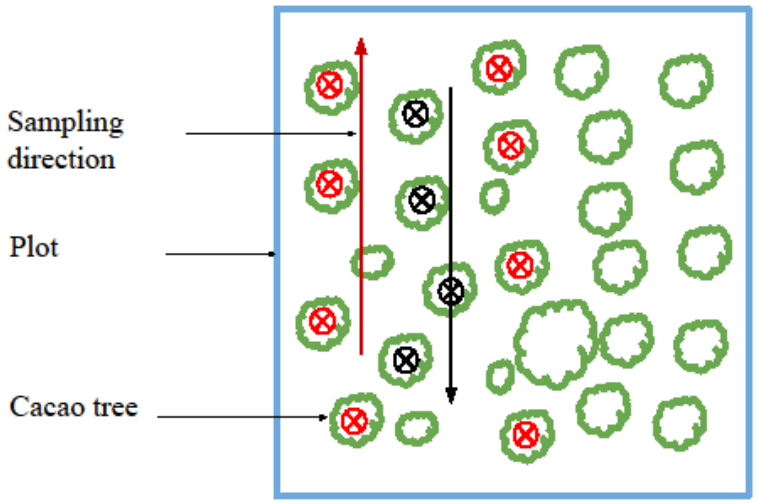

Figure 4: Illustration of how trees were selected and designated for hand pollination treatment experiment. The red and black arrows indicate opposing directions of zig zag sampling movement. From a starting point, trees that fall within the sampling criteria are tagged until the total number of a replicate set (0, 20, 40, 60, 80 & 100) is complete. The next replicate continues until we reach the end of the plot and then we turn 180 degrees in the opposite direction. This is repeated until all the treatment replicated are represented on the plot. The illustration is not drawn to scale but also indicates that the trees are not planted in straight coherent rows.

To hand pollinate flowers, flowers from a different cacao tree not marked for hand pollination were collected. Pollen from stamen of flower were tested for dryness and brought into contact with a viable stigma of candidate flower using a pair of hand tweezers. Successful pollination is indicated by immediate split in the apical portion of the stigma, observable with a hand lens. The remaining unpollinated flowers below two meters were removed from the tree. Hand pollination was repeated daily when field conditions allowed from the beginning of August to the end of October during the wet season and from the beginning of January to third April during the dry season. During subsequent visits, the number of flowers successfully pollinated,

number of cherelles[1] formed from pollinated flowers, number of cherelles failed both at early and late stage, as well as cherelles that mature into cacao pods were recorded. Pollinated flowers and cherelles were marked by pin tags. A total of 14 persons were trained after a two-day workshop and multiple field trials and demonstrations to assist in hand pollination and insect sampling studies. During the dry season, new recruits were similarly trained.

[1] Cherelles are fruitlets formed after successful pollination. Cherelle loss forms approximately 95% fruit loss after successful pollination.

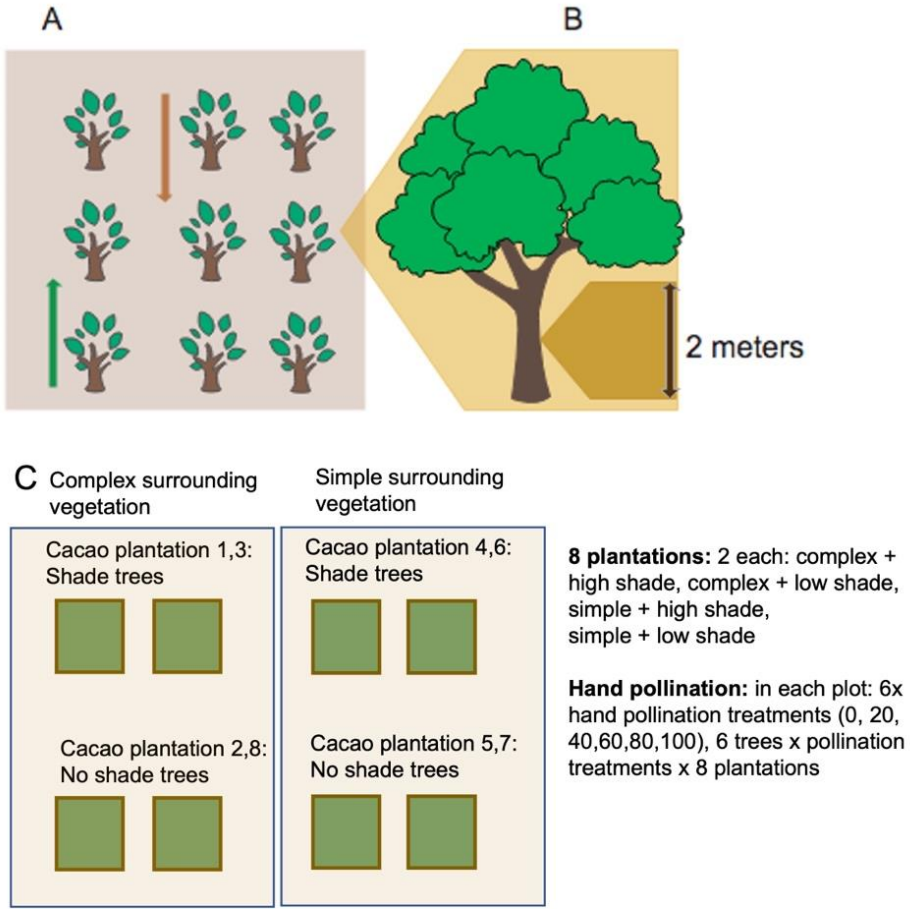

Figure 5: Plot and tree level sampling: (A) Systematic random sampling approach for selecting trees in each plantation study site for hand pollination treatment. Arrows point to direction of sampling. Six mature trees with diameter at breast height between 35-65/πcm were selected and marked for each treatment: 0%, 20%, 40%, 60%, 80%, and 100% hand pollination. (B) Hand pollination treatments were applied from 0 to 2m height from the ground on the tree.

Table 3: Data sheet for recording hand pollination attributes

Plot	Tree ID	Total # of flowers	% pollination	# actually pollinated	# failed pollination	# Cherelle set	# failed early cherelles	# failed late cherelles	# mature fruit
1	1								
1	2								
1	3								
1	4								
1	5								
1	6								

Figure 6: Hand pollination exercise in a plot.

3.6 Flower visitor sampling

To distinguish flower-visitors from non-flower-visiting insects, a minimum of 30 flowers were sampled per plot. Six flowers from five selected trees were glued with a colourless insect trapping glue (Tangle-trap® sticky coating, Tanglefoot). Insects trapped on flowers were collected after 24hr of glue application and carefully placed together with the flower into an Eppendorf tube. Collected samples were over topped with 98% ethanol with the aid of a medical syringe and needle and tightly sealed for storage, pending identification (Fig 7, 8). Insects and descriptive field data were collected over six sampling weeks during the wet season (summer) and the process was repeated for the dry season (winter) (Table 4).

Figure 7: Gluing of flowers, (left photo). Sampling of trapped insects after 24 hours of gluing (right photo).

Table 4: In each plot, glue was applied to 30 flowers on each of the six trees and the following data were recorded.

Site	Vegetation complexity	Canopy trees	Total # pod piles	Amount of woody debris	# failed captured	# pollinator species
1	Complex	Present		High		
2	Simple	Present		High		
3	Complex	Absent		Low		
4	Simple	Absent		Low		
5						
6						
7						
8						

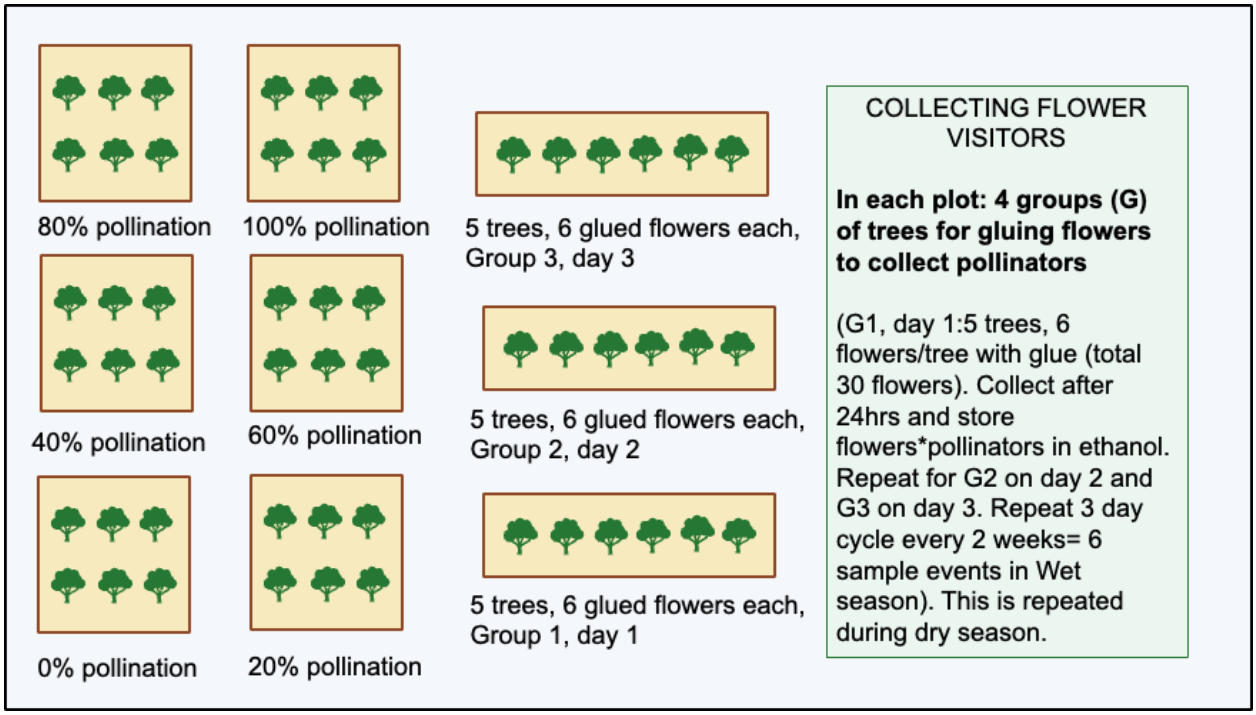

Figure 8: Insect visitor sampling protocol.

3.6.1 Specimen morphotyping and identification

All collected flower visiting samples were shipped to Oxford, UK. For identification, first, the specimen was placed in a petri dish and inundated with ethanol to increase visibility. Specimens were then observed under a dissecting scope attached to a halogen light source at the Plant Sciences Department Herbarium (Fig 9, top). Absence or presence of flower visitors were recorded. Using expert help and available manuals, specimen are identified into major taxonomic groups. Further analysis was conducted to gather more information at higher resolution at the Museum of Natural History using high resolution Leica model stereo microscope with imaging software (Fig 9, bottom).

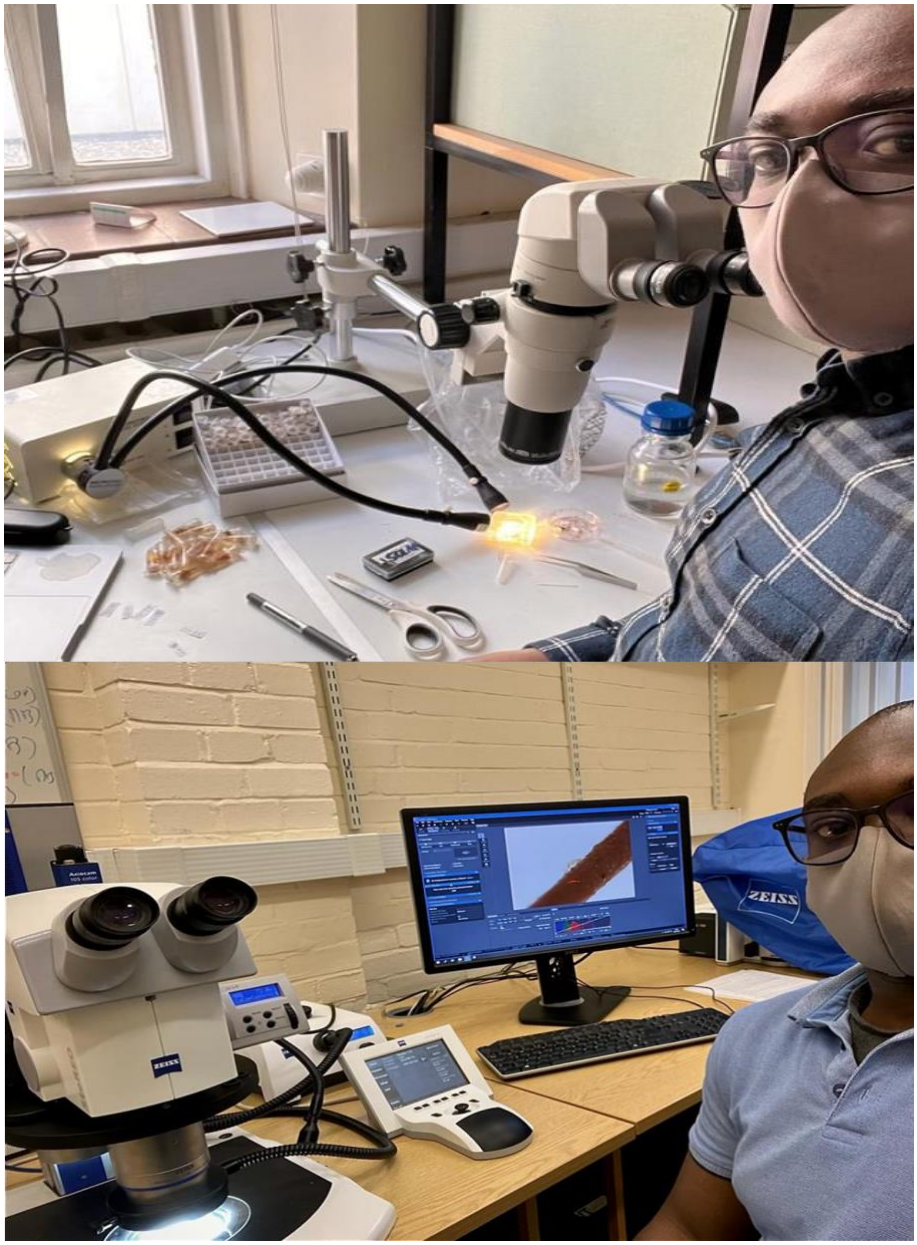

Figure 9: (top) A dissecting microscope at the Department of Biology (Plant Science) Herbarium. (bottom) Using a stereo microscope at the Oxford University Museum of Natural History.

3.7 Data processing

3.7.1 Missing data imputation

Cacao trees flower continuously throughout the season. Unpollinated flowers abort after 48hrs. Thus, hand pollination and corresponding yield response data (fruit set, cherelles, and matured pod) collection occurred each day when possible, during weekly visitation. Unfortunately, there are days in which we could not access experimental plots due to overflooding after heavy rains, or traditionally barred days. As part of the customs and traditions, it is a taboo to visit farms or forests during certain days of the week or important cultural events. Tarkwa-Breman is located in the Prestea-Huni valley and wetlands enclave. Thus, villages get completely inundated, and roads become impassable by vehicles except canoes. These interrupted field sampling campaigns leading to data gaps. Given the statistical modelling software package, complete data without missing values was needed test pollination hypothesis, constructing pollination-limited yield curve, and estimating open pollination and yield gaps. I therefore implemented an unbiased data imputation technique to impute all missing data.

3.7.1.1 Imputation assumptions

The first approach is to decide the category of missing data. There are three potential scenario assumptions underlying missing data imputation:

a) MCAR (missing completely at random)- where the probability of being missing is the same for all cases.
b) MAR (missing at random)-where the probability of being missing is the same only within group of observed data. MAR holds when the probability to be included in a sample depends on some known property.
c) MNAR (not missing at random). Here, the probability of missingness varies for reasons

unknown to us.

In the current data, conditions of missingness are known, which are the constraining field conditions. Thus, I conjectured that the probability of being missing is the same for all cases of missingness, thus the data is missing completely at random. This implies that the causes of the missing data are unrelated to the data. This rationale would also apply to a scenario where an instrument stopped recording data because the battery died, for example.

Secondly, the context from which data is drawn is considered. The problem of total flower bloom counts from trees presents plausible conditions for careful consideration. Naturally, flower bloom in cacao declines over time. The rate may depend on two main factors: biophysical conditions relevant to reproduction physiology, and whether pollination success led to fruit set such that resources are allocated to fruit development instead of flowering. Thus, I assumed that a high pollination rate will reduce the flower blooming period. As a result, conditions for imputation strategies that I considered included:

1. Causal effects of experimental unit: where individual causal effect requires data imputation in the framework of causal effects whereby the effects are studied in a unit level-heterogeneity in treatment effects.
2. Fully conditional specification: where variables may have effects on other effects.

3.7.1.2 Data imputation in irregularly sampled cacao flower bloom counts

Against the outlined background, I used the Predictive Mean Matching (PMM) method specified in the Missing Imputation by Chained Equation (MICE) algorithm (Buuren et al., 2022) in the R programming environment to impute missing data for both the wet and dry season data. PMM calculates the predicted value of a target variable according to the specified imputation model. For each missing entry, the method forms a small set of

candidate donors (typically with 3, 5 or 10 members) from all complete cases that have predicted values closest to the predicted value for the missing entry. One donor is randomly drawn from the candidates, and the observed value of the donor is taken to replace the missing value. The assumption is that the distribution of the missing cell is the same as the observed data of the candidate donors. PMM is found to be a robust method and performs as well as theoretically superior methods, produces the least biased estimates, and works well for a variety of data types (Marshall et al., 2010; Kleinke and Reinecke, 2013).

I generated a random imputation number, *m,* and used a multiple imputation simulation technique to estimate a population mean. Imputation procedure is valid by a "*confidence proper"* for a complete data statistic if certain approximated conditions hold. This was done by first experimenting on a randomly generated dummy data. Then I used actual field data without missing values and manually created missingness with the observed data to act as a control. This allowed me to test the confidence of the imputation strategy. In the actual experimental data, both dry season and wet season data had similar number of columns and rows as variables and observations respectively. The variables included ***plot*** (factor), ***treatments*** (factor), ***tree id*** and ***total flower counts*** (continuous) with over 33 sampling time variables. See Figure 10 for missing data patterns.

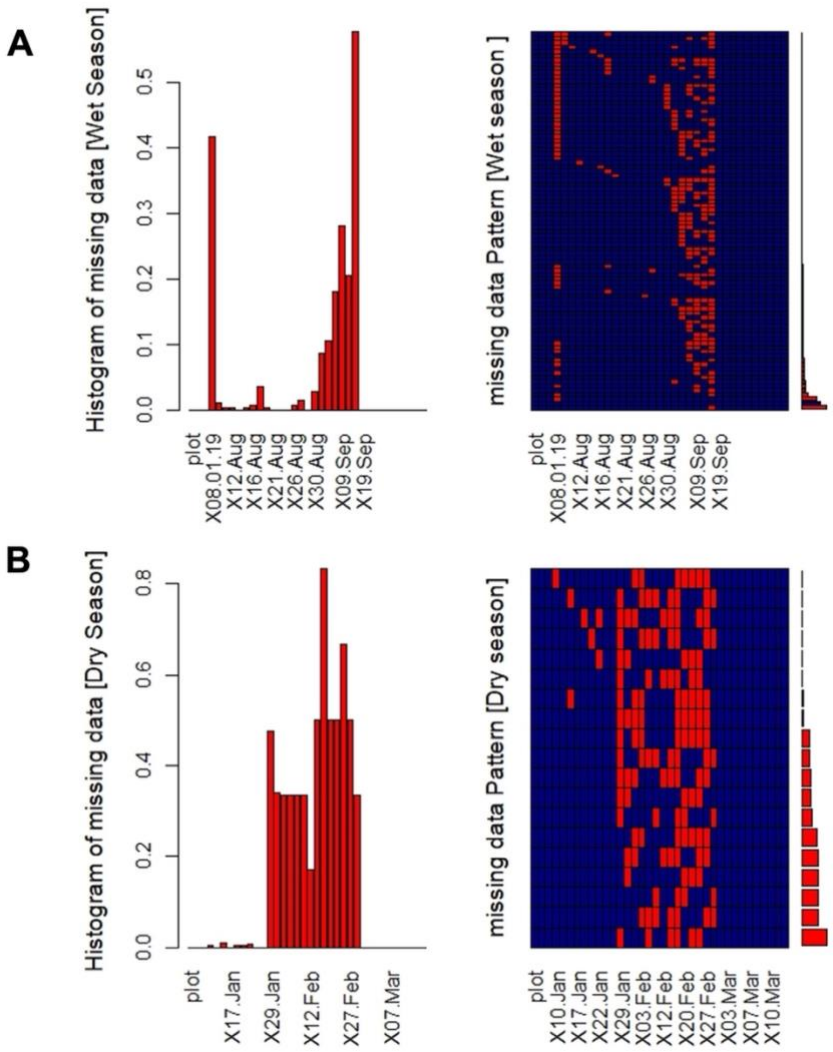

Figure 10: Histogram (left) and missingness pattern from (A) wet season data and (B) dry season data.

3.7.2 Imputation diagnostics

3.7.2.1 Severity of missing data and predictor variables

Influx-outflux pattern was applied to data to identify variables with higher outflux, which is an indication of predictor power (Fig 11). Variables with higher influx depend strongly on the imputation model. When points are relatively close to the diagonal, it shows that influx and

outflux are balanced. The variables in the upper left corner (Fig 11a) have more complete information, so the number of missing data problems for this group is relatively small. The variables in the middle (Fig 11 a, b) have an outflux between 0.5 and 0.8, which is small. Thus, missing data problems are more severe, but potentially this group could also have important variables. The lower (bottom) variables have an outflux with 0.5 or lower, so their predictive power is limited. Also, this group has a higher influx, and, thus, depend more highly on the imputation model.

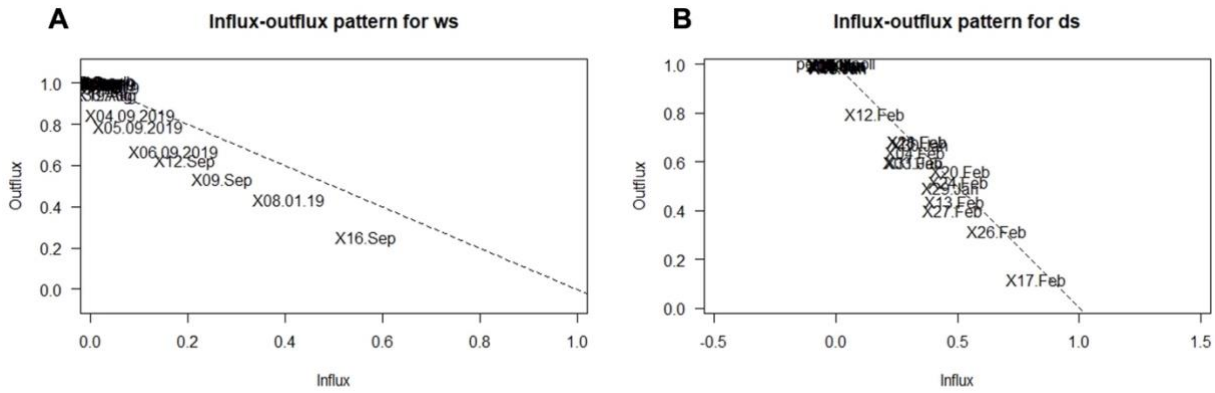

Figure 11: Severity testing of missing data and predictor variables for (A) wet season data and (B) dry season data.

3.7.2.2 Markov Chain Monte Carlo (MCMC) convergence

I used 40 iterations of random samples to generate trace lines to study convergence. Here, a well predicted imputed variable is expected to have well mingled Means and SD. Figure 12 shows MCMC convergence for the imputed missing data for the sampling time variable on 28th February 2020. This was performed for all the data variables with missing data.

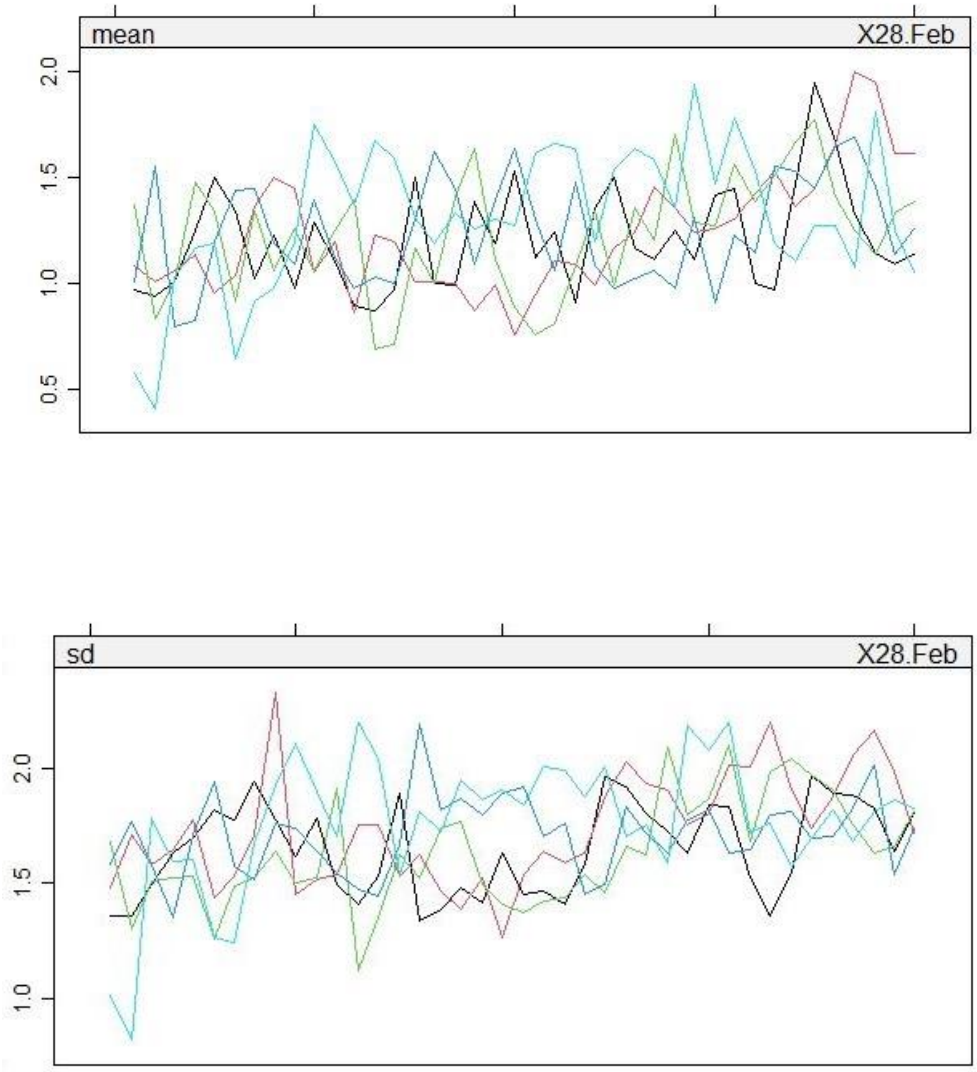

Figure 12: MCMC convergence testing for imputed missing data for the sampling date on 28th February 2020. (Top) mean of MCMC convergence and (bottom) Standard Deviation of MCMC convergence.

3.7.2.3 Imputation plausibility and MCAR assumption

This analysis tests whether the imputed data have 'plausible' values, that is, values that could have been observed if they had not been missing. Here, I check imputations (predicted missing values) and compare them against the observed values. If the data are assumed to be missing

completely at random (MCAR), then the imputations should have the same distribution as the observed data. Figure 13 shows six iterations of predicted missing values. The red colour data points are imputed data. The imputed data well predicts observed values for variables with missing data.

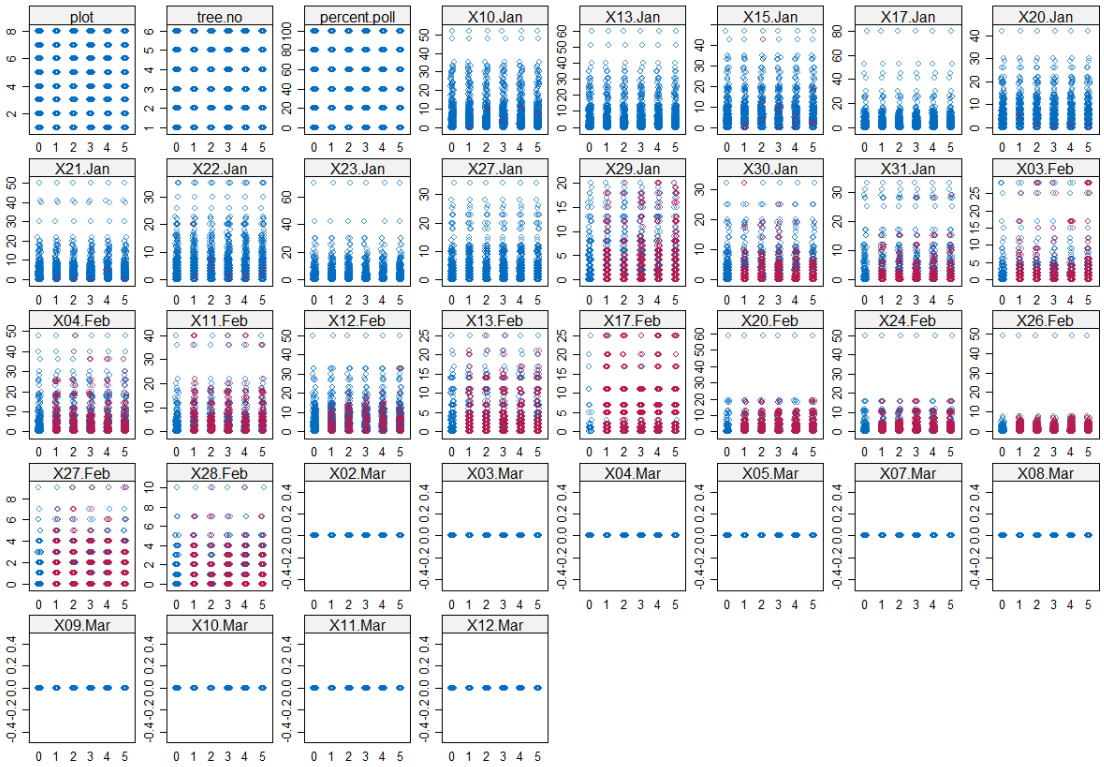

Figure 13: Strip plot of imputed data. Red shows imputed data. Blue stands for observed data.

3.7.3 Imputation distribution and selection

After imputation, I compared the distribution of options of imputed data and selected the imputation iteration distribution that closely fit the distribution of the observed data (Fig 14). The selected imputation was extracted and saved in a .csv file.

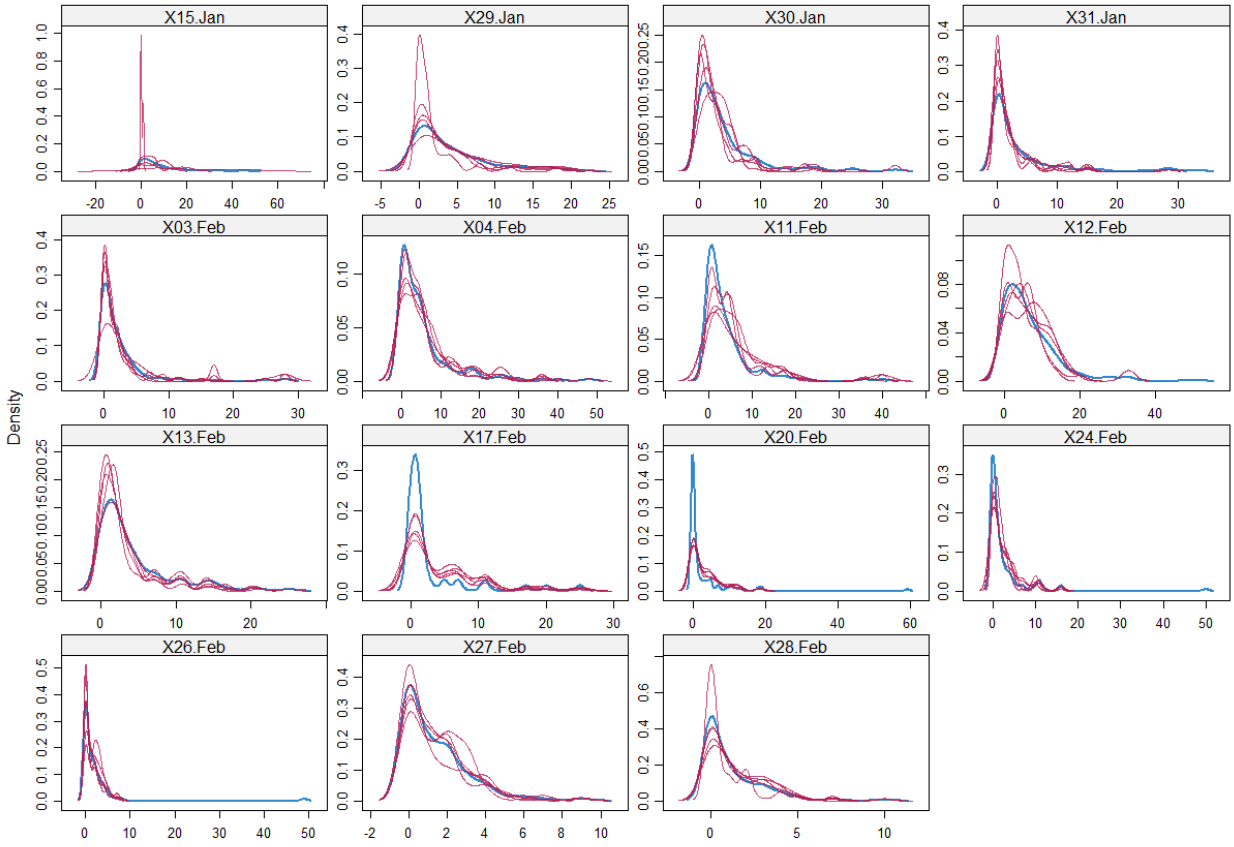

Figure 14: Distribution of observed and imputed data iterations.

3.8 Statistical modelling

Throughout the study, I worked with count data which fit a poisson or negative binomial distribution. Statistical models were selected based on rigorous assessment of suitability with data. In cases where testing assumptions required a restricted data distribution, data were transformed appropriately. Detailed analytical approaches are discussed in the methods section of the various papers in this thesis.

3.9 Network analysis

Network analysis was used to evaluate the flower visitor interactions and elucidate the structural complexity of the arthropod assemblage of cacao flower visitors. Here, I converted species abundance data into nodes and edges to perform topological analyses and generate new variables that represents attributes of designated data nodes and edges. The same generated data is accessed by visualization algorithms that present interaction data as intuitive connections among subjective parameters. For instance, in figure 15, the green shaded circles are nodes. Their colour intensity, position, size, and nature of connectivity can be used to infer their nature in relation to other nodes or the entire network and to further define their attributes such as their influence and strength in the network. In figure 15, the node circled with pale red shows a high degree of influence and will score the highest in a centrality metric. However, the nature of its relationship with the other nodes can be distinguished by red edge. Again, the individual nodes may score on different metrics just by attributes displayed by the size of node or colour intensity.

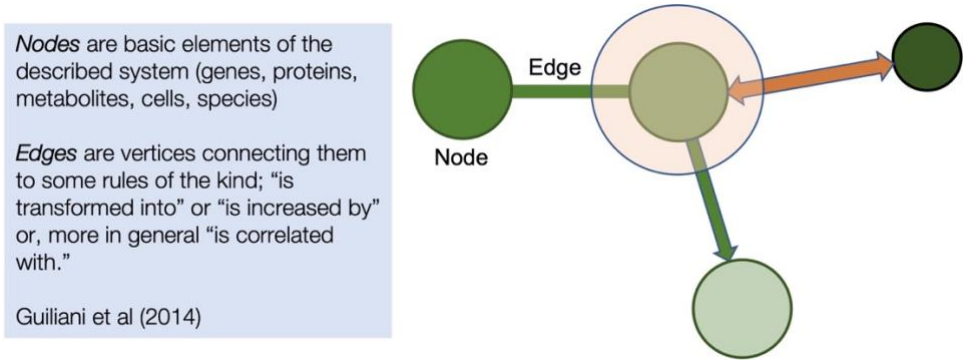

Figure 15: Illustration of basic network structure.

In this thesis, I considered six common centrality metrics; Betweenness Centrality, Bridging Centrality, Bridging Coefficient, Closeness Centrality, Eigenvector Centrality, Degree Centrality, alongside the Hyperlink Induced Topic Search and *k*-core Decomposition topological metrics to elucidate the network characteristics and ecological functions of cacao flower visitors. I used the modular open source Gephi v0.10.1 software which combines topologic statistics data alongside OpenGL visualization engine, to perform network analysis. Here is a brief definition of selected network metrics (see paper three for additional details):

I. ***Bridging Coefficient*** BC, is a centrality metric that determines how well a node is located between two high degree nodes. It is denoted as:

$$BC_{(f)} = \frac{d_{(f)}^{-1}}{\sum_{i \in \mathrm{N}_{(f)}} \frac{1}{d_{(f)}}} \qquad [1]$$

where $d_{(f)}$ is the degree of node f, $\mathrm{N}_{(f)}$ is the set of neighbours of node f. In this paper, node f represents all flower visiting taxa.

II. ***Closeness Centrality*** relates to the distance between nodes and favours the node that is has the shortest connecting distance or reach (Wai and Thu, 2015).

III. ***Degree*** is the number of direct connections a node has, and a high value shows network actors with greater connective opportunities, that are less dependent on other nodes (Wai and Thu, 2015).

IV. ***Eigenvector centrality*** is a modularity matrix algorithm for community structure detection and centrality measure that identifies vertices of a network graph that occupy central

positions in the communities they occupy (Newman, 2006).

V. **A Network *Hub*** indicates a high-quality node that links to other high-quality nodes. This can reveal connections of biological significance. The Hub measures the quality of the node links. The ***Hyperlink Induced Topic Search*** (HITS) algorithm (Kleinberg, 1997) is used to rank networks into hubs or authorities. ***Component number*** and ***Component strength*** are attributes of node influence and are used as measures of Hub influence.

4 ACHIEVING A LIVELIHOODS-CONSERVATION WIN-WIN BY REDUCING THE YIELD GAP IN CACAO PRODUCTION

The main challenge of *Theobroma cacao* (cocoa) production is sustaining production without environmental cost. In Ghana, lack of sophisticated technology leaves farmers with the option of increasing production outcomes through farm expansion at environmental cost. Meanwhile, cacao has a yield gap. Addressing and providing avenues to close the yield-gap will increase yield outcome and farmer income therefore making existing farms more productive. This can further reduce the incentives to expand farm areas into forests.

To achieve this, I first identify what the reported yield constraints of cacao are, which fall under three themes: biotic, abiotic and management factors. Then, using existing data from literature and data from my study site, I synthesize and evaluate which of the outstanding yield-limiting factors, if mitigated, would be most likely narrow the yield gap.

ACHIEVING A LIVELIHOODS-CONSERVATION WIN-WIN BY REDUCING THE YIELD GAP IN COCOA PRODUCTION

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4.1 Abstract

Cacao farming is a major cause of deforestation in producer countries such as Ivory Coast, Ghana, and Indonesia with detrimental consequences for biodiversity conservation. As cacao production is generally lower than the maximum attainable yield, addressing this 'yield gap' would enable farmers to meet increasing global cacao demand, maintain ecosystem services provisioning, and assure the socio-economic wellbeing of farmers. In this study we ask what are the key biotic, abiotic and management factors that impact cacao yield, and the key opportunities to increase yield, with the aim of guiding future research and policy action. We find that pollination services, nutrients and diseases (biotic), and water (abiotic) are the main factors that impact yield across mostly Asia and West Africa. Given the availability of irrigation practices, biocides and fertilizers, pollination services the main opportunity to close yield gap.

Keywords: pollination, agroecosystems, cacao, biostimulants, land-use change

4.2 Introduction

Cacao (*Theobroma cacao* L.) is an essential ingredient in the confectionery, dairy, wine/distillery, perfumery/cosmetics, and pharmaceutical industries (Gavrilova, 2021). Cacao production supports 4-6 million farmers globally, and an additional 40-50 million people who depend on the cocoa industry for their livelihoods (World Cocoa Foundation, 2019). The estimated USD100 billion annual revenues from production (Potts et al., 2014a) and additional USD 50 billion value from the commodities trading market (Gavrilova, 2021), supports critical social needs such as healthcare and children's education for some of the world's poorest cacao farmers (Frimpong et al., 2020). Increasing cacao demand has led to increasing intensive production methods and plantation expansion into forest areas, which causes biodiversity loss and increases greenhouse gas emissions (Ruf and Schroth, 2004). During the end of the first quarter of 2024, decline in cacao productions in West Africa due to climate shocks resulted in about 200% historic price spike of the cacao trading index (CJ:NMX) (Nasdaq, 2024b). While stockholders earned significant market returns, the impacted production meant revenues losses for farmers whose income due to the pre-fixed prices solely depends on the quantity of harvest output in Ghana. Addressing the conflict between biodiversity conservation and climate change on the one hand, and market demands and the economic welfare of producers on the other hand, requires creative approaches to cocoa production that sustains predictable yield outcomes.

Addressing the yield versus biodiversity and ecosystems services trade-off is to close the 'yield gap' in existing plantations using farming methos that ecologically diversity rather than simplify agricultural land, which has been shown to protect ecosystems services while

promoting crop production (Tamburini et al., 2020; He et al., 2023). The yield-gap of a crop is the difference between the current crop yield and a benchmarked yield such as the potential yield, Y_p or theoretical yield Y_t (FAO and DWFI, 2015). Y_p relates to yield of a cultivar growing in 'ideal' conditions, and consequently varies with location, while Y_t is model predicted yield within biophysical limits defined by parameters of interest such as photosynthesis or biomass. Globally, actual or realized cacao yield varies from less than 100 to over 3,000 kg ha^{-1}, averaging between 340 and 540 kg ha^{-1} globally (Cook, 2018). In Ghana, the reported yield is between 337.9 and 400 kg ha^{-1} (Laven and Boomsma, 2012; Aneani and Ofori-Frimpong, 2013), while Y_p is 1,891.3 kg ha^{-1}, the relative farmer Y_p is 1,875.1 kg ha^{-1}, based on an estimated yield gap of 82.1% (Aneani and Ofori-Frimpong, 2013). Farmer-based Y_p is often lower than Y_p which is experimental, due to farmer subjective behaviour such as failure to prune or apply weed on time. Because it has been possible to produce up to 3000 kg ha^{-1}, this has been put forward as a theoretical maximum that is achievable, at least under some circumstances. Closing the cacao 'yield-gap' in existing plantations that are gradually transformed into diversified agroforestry systems can offer a 'win-win' for conservation and improved farmer livelihood. Previous reviews of factors impacting cacao yiels have focused on abiotic factors such as water use (Carr and Lockwood, 2011), soil nutrients (Aneani and Ofori-Frimpong, 2013; Wessel and Quist-Wessel, 2015a), and regional production capacity (Wessel and Quist-Wessel, 2015a); or biotic factors such as plantation age (Vaast et al., 2016; Niether et al., 2020b), physiological responses to environment (Lahive et al., 2019a), and pests and diseases (Ploetz, 2016a, Maas et al., 2016); or agronomic practices, including the choice between diversified plantation systems, such as agroforestry, and intensive, monoculture systems (Vaast et al., 2016; Niether et al., 2020b).

In addition, there is strong evidence from hand pollination experiments that suggests that yield may be limited in part by insufficient pollination (Groeneveld et al., 2010a; Toledo-Hernández

et al., 2020; Toledo-Hernández et al., 2017). Understanding the cacao yield gap is critical for identifying management interventions to increase yield and meet socio-economic goals, while simultaneously protecting and enhancing biodiversity and ecosystem services. However, studies on cacao yields are limited and geographically unevenly distributed, showing there is more work to be done to understand the factors limiting cocoa yield (Forbes et al., 2019). In this study we synthesize key reported biotic and abiotic factors that impact cacao yield across growing regions from literature. To understand non-biotic/abiotic sources of yield gap, we surveyed selected plantations in one of the most productive cacao growing regions in Ghana to understand relationship of yield with farm-specific attributes and farm management practices.

4.3 Materials and methods

4.3.1 Literature review

A literature review was conducted on factors affecting cacao yields. Published, peer-reviewed papers were retrieved from Google Scholar and the Web of Science search engines using the search terms 'COCOA OR CACAO YIELD', 'COCOA OR CACAO YIELD FACTORS'. Articles were further screened to select studies that reported yields in units per land size of relative percent yield attribute. In some cases, several articles were discovered through cross referencing or manually fine-tuning search query by specifically adding "biotic', 'abiotic', 'physiology', 'pollination', 'management' or factors that had been mentioned in cross-referenced papers. Abstracts of the articles returned by the searches were read, and papers that reported empirical yield values, factors found to affect yield, and provided some analysis of knowledge gaps were read in full. Reported yield values and associated factors were collected in a database for analyses.

4.3.2 Case study: Study area

To supplement the literature review, empirical data on plantation management and yield was collected at eight study sites near Tarkwa-Breman in the Wassa-Amanfi district in the Western region of Ghana (Table 1, Figure 1). The sites were selected from plantations based on the complexity of vegetation surrounding the plantation and the presence or absence of non-cacao shade trees within the plantation. The former was hypothesized to increase local biodiversity richness and to affect the species diversity, abundance, and distribution of cacao pollinators. The latter affects the light environment which also affects the abiotic and biotic understory environment. Surrounding plot vegetation was classified as: '*homogenous (simple)*', when the plot was surrounded by a single species with or without complex stratification e.g., farm or single species plantation or grass field; or '*heterogenous (complex)*', when the vegetation surrounding a plot constituted multi-strata, high floral diversity e.g., secondary forest, wetland, or a highly diverse vegetation patch. The assumption of this selection criteria is that complex vegetation is biodiverse and may provide a range of habitat or refugia for diverse pollinating agents thereby hypothetically increase pollinator abundance, diversity, visitation and eventually pollination services in the neighbouring cacao plantations.

A study plot of size 1600 m^2 was marked within each plantation (eight study plots total, Table 1) and the total density of cacao trees was determined by tagging all the trees within the plot and removing tags to count. The average diameter at breast height (dbh) per plot was determined by measuring the dbh of all trees within 2m left and right of a diagonal transect of the plot. The total number of cacao trees per 1600 m^2 plot was counted to determine the cacao tree density. The total number and species of trees with dbh larger than 150 cm in the plot was also recorded. These were mostly shade trees of non-cocoa species. Plantations with shade required a minimum of four trees that relatively covered at least half of the plantation and

represented partial shading. Plantations without shading had their canopies completely exposed to sunlight.

Within each of the eight study plots, 36 trees were sampled by systematic random sampling technique. The total number of matured pods and the diameter at breast height (dbh) was measured for each sampled tree. Tree dbh was categorized into three diameter classes; “low”, “mid”, and “upper”, determined by the interquartile ranges, median and mean of dbh data from all eight plantations. From data, tree circumference range for “low” dbh class was ≥ 7 < 11 cm: “mid”, ≥ 11 < 14 and “upper”, >14 cm. DBH= tree circumference/π.

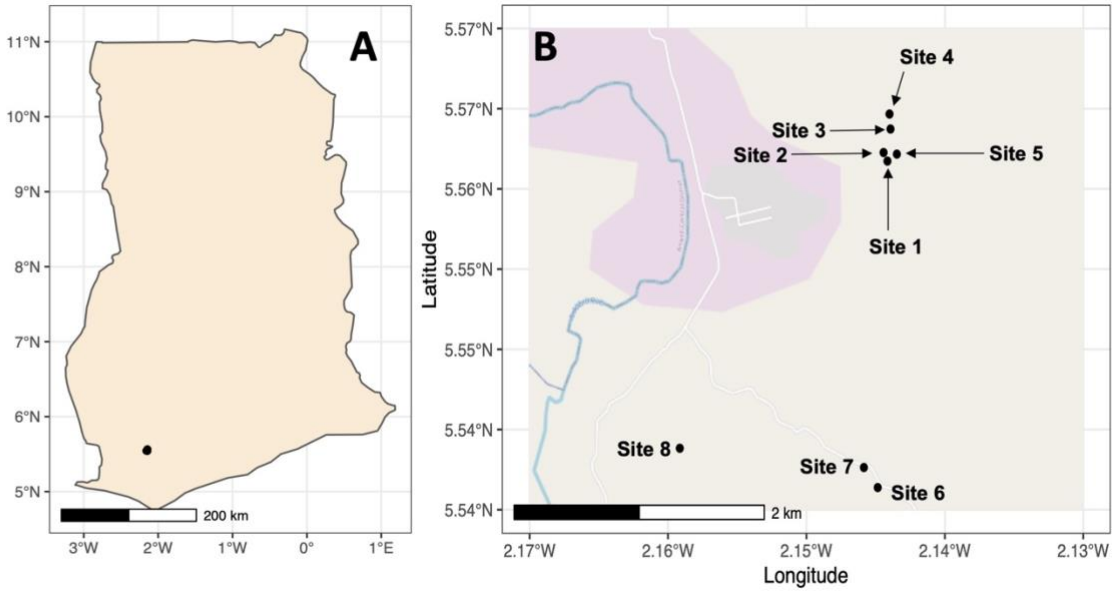

Figure 1: Location of study location in South-western Ghana (Tarkwa-Breman, 5.56173/-2.144153 lat/long) in the Prestea Huni-Valley District (A). Map of experimental sites (B). The purple regions represents the Tarkwa-Breman community town. Blue line represent a river and white lines represents road networks.

Table 1: Plot locations and characteristics

Site code	Location	Latitude	Longitude	Surround vegetation	Shade tree present	Tree density/ha	Mean dbh (cm)	Mean plot light environment	Litter depth (cm)
1_nscf	Tarkwa-Breman	05°33.704'	-002°08.649'	Complex (Heterogenous)	Yes (1)	2750	3.42	6, low shade	0.88
2_sscf	Tarkwa-Breman	05°33.736'	-002°08.666'	Complex (Heterogenous)	No (0)	2056	3.53	3, high shade	5.99
3_sscf	Tarkwa-Breman	05°33.824'	-002°08.636'	Complex (Heterogenous)	Yes (1)	1288	4.17	3, high shade	5.44
4_ssff	Tarkwa-Breman	05°33.880'	-002°08.640'	Simple (Homogenous)	No (0)	1325	4.36	9.2, low shade	6.52
5_nsff	Tarkwa-Breman	05°33.730'	-002°08.608'	Simple (Homogenous)	Yes (1)	1925	3.52	6.8, low shade	6.84
6_ssff	Anti-korkoh	05°32.483'	-002°08.691'	Simple (Homogenous)	No (0)	1113	4.09	6, low shade	6.4
7_nsff	Anti-korkoh	05°32.558'	-002°08.751'	Simple (Homogenous)	Yes (1)	1150	3.99	9.8, low shade	6.08
8_sscf	Amezugbe	05°32.630'	-002°09.549'	Complex (Heterogenous)	No (0)	2413	4.24	9.4, low shade	6.72

4.3.3 Survey of plantation and management practices

The farmers who manage the plantations were surveyed to understand farm level decision making and the main routine of on-farming activities ('cultural practices'). All farm managers had access to a large common market where they obtain farm inputs. Data was collected on farm input choices for pest control, weed control and fertilizers. For farm inputs, farmers were asked about the type of input type (brand) and the time and mode of applying inputs (See questionnaires at section 3.5.1, Chapter three).

4.3.4 Collection of field data

To understand the importance of farm level characteristics, we determined the relationship among qualitative variables such as farm (plantation) and light management as well as quantitative variables including the total number of large branches (>5cm), cacao tree density per plot, the number of old tree trunks, diameter at breast height (dbh), total number of pod (husk) piles, and the total number of tall (non-cacao) trees per plot, the degree fresh branches on plantation floor.

4.3.5 Statistical analysis

All statistical analyses were conducted using the R programming software. ANOVA was performed using the base R 'Stats' package version 4.1.1 to determine the effect of tree size class on pod output on 288 trees with 'total matured pod' output as the dependent variable and 'plantation' and 'dbh' with three levels of factors: low-size, mid-size class and upper-size class, as independent variables. The relationship between on-farm attributes and management

practices with pod output, was evaluated using correlation matrix by Angular Order of the Eigenvectors, 'AOE' parameter with R package 'corrplot' version 0.92 (Wei et al., 2017). Correlations were determined based on positive or negative correlation and correlation coefficient, *r*, which determine the strength of the paired relationship at $p<0.05$ confidence.

4.4 Results and discussion

Section 4.4.1 to 4.4.2, below, provides an overview of the factors and management interventions that are standard practice, and for which the yield impacts are largely well-understood. Each of these factors is discussed in detail below. Section 4.4.3 summarizes previous sections and 4.4.4 uses a case study from a survey from eight plantations and discusses on-farm characteristics and farmer subjective management interventions that may limit yield or offer avenues to increase yield.

4.4.1 Established factors impacting cacao yield

In the published literature, the best-understood factors affecting yield can be categorized as abiotic (light (including pruning), water, soil nutrients, and fertilizer use) or biotic (pests, diseases, parasites, and pesticide use), and the interactions between these factors Table 4). Each of these factors is discussed in detail below.

4.4.1.1 Abiotic factors: Light

A number of studies have shown that light availability is positively associated with cacao yield and can have a positive interaction with fertilizer input (Cunningham and Lamb, 1959; Hurd and Cunningham, 1961; Asare, 2016; Asare et al., 2017), whereas shade can be negatively correlated with yield (Clough et al., 2011). However, although higher light environment can provide higher yields, for instance 2.4-fold observed in Côte d'Ivoire

(Lachenaud and Mossu, 1985), there is often a trade-off with economic life span of the trees and there are some management challenges in the long-term such as the need for pest control in full-sun exposed monocultures (Ahenkorah et al., 1974a; Wanger et al., 2018). Thus, a balance between high and low light availability has been advocated for sustained optimal yields (Owusu, 1978). For instance, Murray (1958), showed a positive linear relationship between light and yield that peaked at 50% light intensity (partial light) beyond which yield declined, unless supplemented with nutrients. In line with Murray's (1958) findings, shaded cacao systems can be financially profitable despite relatively lower yield because of the economic lifespan of the plantation, lower average cost in agrochemical inputs and higher average gross benefit per hectare (Obiri et al., 2007; Jezeer et al., 2017). In addition to the trade-offs between yield and plantation lifespan, there are also trade-offs between high light environments for cacao yield, and lower-light agroforestry systems and 'cacao forests.' For example, agroforestry cacao systems and 'cacao forests' may promote biodiversity and ecosystem services (Johns, 1999; Clough et al., 2009; Suárez Salazar et al., 2018), maintain water resources and increase drought tolerance (Schwendenmann et al., 2010). In contrast to the potential benefits of shade noted above, where plantations experience frequent flooding, open canopies are required for soil evaporation to reduce the impact of the flooding (Raz-Yaseef et al., 2010), and the high moisture, low light and low temperatures in shade plantations can also promote fungal infection (Rotem and Palti, 1969). The optimal balance between sun and shade has yet to be determined (Melnick, 2016), but it appears that there may be an optimal light environment to achieve yield, profitability, and environmental benefits.

4.4.1.2 Abiotic factors: Water

Investigations on the effect of water availability on the yield of field grown cacao yield has been investigated through irrigation treatment, Studies on the effect of water

availability as a factor limiting cocoa yield found irrigation is associated with up to 40% of yield in Ghana (Hutcheon et al., 1973a). Although empirical studies of yield loss or gain under drought or irrigation treatments are limited (Carr and Lockwood, 2011; Gateau-Rey et al., 2018), simulation model suggest a 50% cacao yield gap due to water limitation in Brazil, Congo, Costa Rica, Malaysia, Nigeria, and Venezuela (Zuidema et al., 2005). In Sulewesi, Indonesia, desiccation significantly reduced bean yield by 10%, however, water relations of cacao depend on the development stage of cacao (Moser et al., 2010). Water availability at the early pod development stage is more important than during the late growth stage (Bridgland, 1953; Ali, 1969). Also, the amount or quantity of water available may affect cacao yield. For instance, while rainfall is reported as most important factor influencing cacao yields (Wood and Lass, 2001), flooding negatively impact yield in lowlands in Brazil (Bertolde et al., 2012). Irrigation at 470 mm resulted in dry bean yield up to 2.7 t ha^{1} in northern Australia (Diczbalis et al., 2010). In a study with Amelonado variety, yield increased from 12-17% during average rainfall and a yield deficit of 40% during severe drought in Ghana (Hutcheon et al., 1973b). However, this may not be consistent for all other varieties as genetic variation also affect water use or stress sensitivity to yield (Lahive et al., 2019b). In the drought tolerant cultivars, mulching and appropriate shading have been suggested to mitigate drought in Ghana (Acheampong, 2010).

4.4.1.3 Abiotic factors: Soil nutrient

Studies on whether soil nutrient availability, on its own, is a factor limiting cocoa yield have found that soil nutrient contributed 19% of cacao yield in Ghana (Edwin and Masters, 2005). In a temporal soil enrichment study, yield increased with time from 62% up to 116% (FAO, 2005). Furthermore a 20-year comprehensive study reported a negative effect of nitrogen (N) fertilization on cacao yield (Ahenkorah et al., 1987). However, phosphate deficit

caused yield decline in less than 10 years whereas increased light environment exacerbated nutrient limitation (Ahenkorah et al., 1974a). These contrasting findings emphasize the importance of nutrient specificity in yield-nutrient studies. In a multi-factor comparative yield study in Indonesia, N had no significant effect on cacao (Groeneveld et al., 2010a). The authors though acknowledged that soil N was not limiting in the area of study. The reduced sensitity of nutrient treatment factor relative to pollination service deficit could be explained by the high availability of soil N at the study site. Similarly in Ghana, soil P but not soil N was found to limit yield (Ahenkorah et al., 1987). This suggests the importance of geographical variability and the need for data from contrasting cocoa producer regions. In a review by (Appiah et al., 1997) low input of fertilizer accounted for yield decline and was explained to have replenished years of depleted soil nutrients in the largest cocoa growing region in Ghana. Thus, the specific soil nutrient deficit and age of cacao farm may also be important factors of yield-nutrient relationship in cacao.

4.4.1.4 Biotic factors: Pest, diseases, and parasitic flora

Pests and diseases are a major factor limiting cocoa yield (Fulton, 1989; Wessel and Quist-Wessel, 2015b), and studies found a two-fold decline in annual yields due to increased incidence of diseases and pests between 2001 and 2016 (Bowers et al., 2001; Ploetz, 2016a). The effects of predominant diseases and pests such as the 'black pod' and 'witches' broom', has been recently found to account for 33-38% of global cacao yield losses (ICCO, 2017; Marelli et al., 2019; Gutiérrez et al., 2016). In Ghana, black pod caused yield loss of 30% in 1985(Akrofi et al., 2003), and can reach up to 60-100% yield loss (J.T., 1988). The *Phytopthora megakarya* strain of black pod was once reported as the main yield-limiting factor of cacao production in Ghana (Opoku et al., 2000) and cause 80% yield loss in Cameroon and Gabon (Deberdt et al., 2008a). In a 12 months study, Ashiru and Jacob (1971a) reported that

physiological wilt and biotic damage caused 75% Cherelle loss per tree with diseases and pests including small mammals accounting for most.

Reports on the yield impact of phytopests such as epiphytes or parasitic plants are limited in the literature. However, there is evidence of their direct and indirect impacts on cacao productivity through competition for resources such as light (Akrofi and Acheampong, 2016). Akrofi and Acheampong (2016) reported two classes of epiphytes: vascular and non-vascular of which 14 species of vascular have been identified in cacao farms in Ghana while non-vascular species mainly consisted of mosses, liches, and liverworts. A study through epiphyte removal treatment experimentally concluded that epiphytes had no effect on yield (Sporn et al., 2007). However, Sporn et al., (2007) acknowledged that the species considered were not vascular epiphytes, requiring further work on how vascular epiphytes in particular influence pod yield especially in the context of potential competition for translocated or stored carbohydrates.

Generally, the impact of diseases on yield varies by production region: for example, there have been reported losses of 50-80% in Cameroon, 30-50% in Ghana and Togo and 10-30% in Côte d'ivoire (Duguma et al., 2001; Ploetz, 2016b). Furthermore, diseases are largely confined to geographic regions. However, the supposed predominant regional diseases: black pod (Central & Southern America), swollen shoot virus (West Africa), witches' broom (Southern America), vascular streak (Asia) and frosty pod (Central & Southern America) may not be the principal yield constraint at the local level, as there are usually other competing pathogens (Evans, 2007; Ploetz, 2007, 2016a).

4.4.1.5 Interactions among yield impacting factors

Each of the highlighted factors, although important individually, may also be working

in concert with other factors to impact cocoa yield. For example, various studies have found interactions between light and water availability (Zuidema et al., 2005), and light and nutrient or soil quality (Ahenkorah et al., 1974a, 1987; Isaac et al., 2007; Yulianti et al., 2018). Moreover, factors may be interdependent. For instance, under light and nutrient interaction, light becomes limiting at low intensities while nutrient availability becomes limiting at light intensities above 50% (Murray, 1958). As a result, light and nutrient availability are argued not to be considered independently. Also, studies in Bahia, Brazil on farm level effect of soil water, dbh of shade trees, percent dead trees and ground cover found none of the factors to be significant independently (Gateau-Rey et al., 2018). However, in the analysis of Gateau-Rey et al., (2018) their interactions were significant including interactions of total tree dbh of shade trees and longitude ($p = 0.04$); total dbh of shade trees, number of shade trees, and longitude ($p = 0.01$) as well as the interaction of total dbh of shade trees, number of shade trees, longitude, and ground cover ($p = 0.05$).

A potential benefit of the interactions between critical cocoa yield-limiting factors is that it is sometimes possible to address the limitations together. For example, one of the most effective approaches, in the medium to long term, to address cocoa tree physiological performance, nutrient requirements, climate change impacts and pests and pathogen infestations is ecological diversification of the plantation (Kremen, 2020; Pérez-Neira et al., 2020). Although shading in cacao agroforests has sometimes resulted in yield reduction (Cunningham and Lamb, 1958; Clough et al., 2011), partial shading at 40% conversely increased biodiversity, farmer income and effective income due to reduced labor and input cost from ecosystem services (Waldron et al., 2012b). Similarly, Niether et al. (2020) report that while cocoa yield in agroforestry systems is about 25% less than monoculture systems, it contributes 10-fold more of total systems yield, including higher animal diversity. The

relationships between nutrient requirements, climate change impacts and pests and pathogen are also borne out in the classic cacao 'boom and bust' cycle associated with new plantation establishment (Ruf, 1995; Clough et al., 2009). To begin, production increases ('boom') on newly cultivated converted forest lands because fertile soil, shading and low weed competition(Clough et al., 2009) but declines ('bust') over time due to increasing pests and diseases, depleted soils, and sensitivity to climate shocks. Understanding and addressing the factors that limit yields during the 'bust' phase can potentially prolong the boom periods and mitigate the bust periods, alleviating the socio-economic challenges facing cacao farmers as well as conservation concerns in cacao production. Overall, these studies demonstrate that both production and conservation needs can be addressed, while benefiting farmer income, although it is important to note that farmer skills and use of innovation, local climate, and the local prevalence of pests and diseases will impact the outcomes of any intervention (FAO and DWFI, 2015).

To summarize abiotic and biotic constraints that impact cacao yield, the factors that strongly (50% or greater increase in kg/ha yield), positively affect cocoa yield include light, water availability, nutrient availability, pollination and weed control. Factors that strongly, negatively affect cocoa yield include drought, pests, and diseases (Table 2). Most of the research on biotic factors was reported from West Africa (Ghana, Côte d'Ivoire, Nigeria and Cameroon), whereas much of the research on abiotic factors was from South America (Brazil and Columbia) and Asia (Indonesia).

Table 2 Summary of global cacao yield effects of key biotic, abiotic and management factors. Growing regions (excluding Colombia) together forms 88% share of global cacao production (Statista, 2024b). Plus (+) and minus (-) signs denotes yield increase/addition and yield decrease/ decline. Red and blue numbers indicate 50% or greater gain or loss in kg/ha yield respectively. Where yield is reported in a range, the highest attainable is recorded. Where yields are not originally reported, percent yield of treatment factor is calculated from a reference treatment (control). Physiological capacity (biotic factor) as the defined as the inherent physiological limit on how many pods a cacao tree can produce under ideal growth conditions.

			Asia	**South America**	**South America**	**West Africa**	**West Africa**	**West Africa**	**West Africa**
			INDONESIA	BRAZIL	COLOMBIA	GHANA	CÔTE D'IVOIRE	NIGERIA	CAMEROON
Factor	Factor affecting yield	Treatment	Yield effect (%, kg ha $^{-1}$)						
Abiotic	Light & water	Pruning, no irrigation	-	-	-29%[1]	-	-	-	-
	Light	Shading	+40% [2]	-	-	-	-	-	-

	Water	Irrigation/rainfall, drought	+10% [3], -62% [5]	-89% [4]	-	-	-	-	-
	Water & light	Irrigation & soft pruning	-	-	+83% [1]	-	-	-	-
	Water & light	100% irrigation & high pruning	-	-	+9% [1]	-	-	-	-
Biotic	Pest and disease (in general but mostly black pod & witches' broom)	Agrochemicals	-	-	-	-30% to -50% [6,7]	-10% to -30% [6,7]	-	-50% to -80% [6,7]

Black pod	Fungicide	-	-	-	-	-	-	-2.4%, -2% (1& 2 yrs) [8]
	Biocontrol	-	-	-	-	-	-	-66%, -33% (1&2 yrs) [8]
Rodents	-	-45% [9]	-	-	-20% [9]	-15% [9]	-40% [9]	-40% [9]
Parasitic plants	Epiphyte removal	0% [10]	-	-	-	-	-	-
Genetic variety	Four varieties	-	-	-	+42% [11]	-		-
Nutrient	N, P&K	-	-	-	+19%[11], [a]+61.7/+99.8/ +116/+106% (1,2,3 & 4th	-	-	-

						yrs.) [12]			
	Pollination service	Hand pollination	+100% [2], +161% [13], [b]2600 kg/ha/yr [14]	-	-	-	-	-	-
	Physiological capacity		-	+71% [15]	-	-	-	-	-
Management	Weed control	Weeding frequency, weedicides	-	-	-	+55 kg/ ha [16]	-	-	-

[a] Percent yield estimate over four recurring years. [b]Calculated mean yield estimates from four cacao clones in one study. [c] Indirect yield loss based on fraction of diseases and direct yield parameter. [1](Meneses-Buitrago et al., 2019), [2](Groeneveld et al., 2010b), [3](Moser et al., 2010), [4](Gateau-Rey et al., 2018), [5] (Keil et al., 2008), [6] (Bakala and Kone, 1998), [7](Ploetz, 2016), [8] (Deberdt et al., 2008b), [9] (Hebbar, 2007), [10] (Sporn

et al., 2007), [11] (Edwin and Masters, 2005), [12] (FAO, 2005), [13] (Toledo-Hernández et al., 2020a), [14] (Forbes et al., 2019), [15] (Bos et al., 2007b), [16] (Aneani and Ofori-Frimpong, 2013).

4.4.2 Less understood factors impacting cacao yield

Section 2 focuses on management interventions that are less established, such as pollination management, management of physiological capacity, and genotype management and modification.

4.4.2.1 Pollination

A study in Indonesia of whether pollination deficit, on its own, is a factor limiting cocoa yield have found that enhanced pollination intensity (between 10 and 40%) increased yield by 100% (Groeneveld et al., 2010b). In the study, pollination service was more limiting to yield than abiotic resources including light, water, and nutrient. This research provides a surprising insight into the drivers behind cacao yield gaps, but there remains research to be done to determine whether the findings apply to other growing regions. Unfortunately, studies on cacao pollinators, their ecology and the relationship of pollination service to yield remain very limitted (Toledo-Hernández et al., 2017).

4.4.2.2 Pollination opportunities and research gaps

Although studies on cacao pollination ecology are limited (Toledo-Hernández et al., 2017), there appear to be opportunities for plantation management to increase effective pollination. Recent studies have shown that hand pollination exercises can be a cost-effective approach can reduce existing yield gaps due to pollination service deficit (Toledo-Hernández et al., 2020). For example, Groeneveld et al (2010a) found pollination deficit at their study sites and found that supplemental hand pollination had the largest measurable effect on cocoa yield of the factors tested (Table 4). Previous work has shown that (1) distance to native vegetation

(Young, 1986; Clough et al., 2011), (2) understory light environment (Young, 1986), (3) soil moisture (Lahive et al., 2019b), (4) litter layer depth and quantity of decaying vegetative material (Frimpong et al., 2011), and (5) season (wet vs dry) (Young, 1986) can affect the pollinator community composition and total pollinator abundance in cacao plantations (Woodcock et al., 2019). While Young (1986) found a negative correlation between distance to shade tree and pod numbers in cacao plantations in Costa Rica, Frimpong et al (2011) found no relation to shade trees, nor with distance to forests in Ghana. However, both studies found high cacao pollinator abundance under banana stems and pod husks, even in high light understory environments (Young, 1986; Frimpong et al., 2011). To better understand pollination yield gaps, and factors that affect pollination services across cocoa producing, yield levels achieved by current pollinators and the ecology of pollinators in growing areas are critical avenues for further research inquiry.

4.4.2.3 Physiological capacity

We define physiological capacity as an inherent physiological limit on how many pods a cacao tree can produce under ideal growth conditions and assume that there may be tree level variation in this functional property. One mechanism by which cacao trees limit pod production is through fruit abortion, also known as 'Cherelle Wilt' (CW), a process where trees shed immature fruits, ideally improving the quality of the remaining fruits (McKelvie, 1960; Costa et al., 2006; Iwanami et al., 2012; Alvim, 1954; Ashiru and Jacob, 1971b; Aneja et al., 1999). In several tree crops, fruit abortion process is enhanced as a selection mechanism to improve fruit quality in commercial planaations (Celton et al., 2014; Byers et al., 1986; Williams, 1979; Miller, 1988; Bound et al., 1998; Dennis, Jr., 2000).

CW accounts for 75% of losses between the flower and mature pod stages and is thought to be mainly the result of physiological limitation (Melnick et al., 2013; Melnick, 2016), although it

can also be caused by biotic damage by pest, diseases, or rodents (Ashiru and Jacob, 1971). Studies into the mechanisms of CW found application of exogenous compounds decreased CW induction by 66% (Naundorf and Gardner, 1950), 3-fold (Gardner and Naundorf, 1950), and 96% (Naundorf and Yillamil, 1950). While the incidence of CW declined, authors did not compare the changes in CW induction rates to the number of matured pods with untreated controls. Moreover, a separate study that attempted to relate CW to yield in cacao found poor correlation (McKelvie, 1960). Thus, to date, the relationships between resource allocation, CW, and yield remains an open area of research.

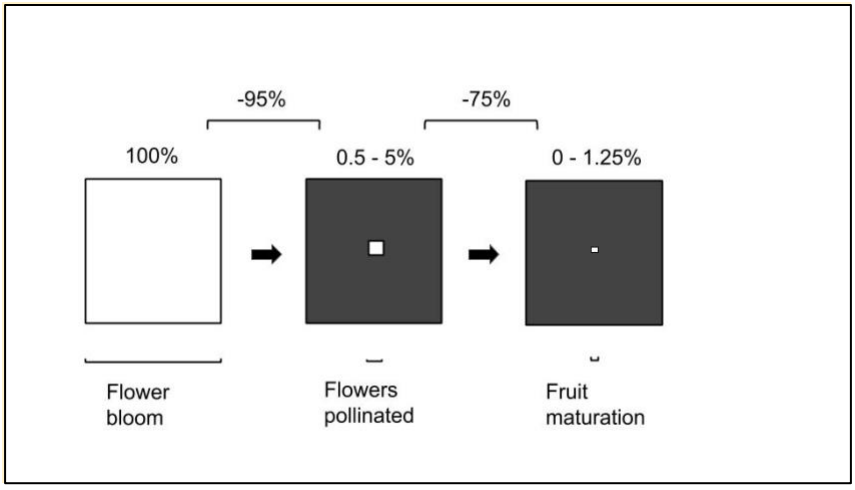

Figure 2: Illustration of potential sources physiological limits to yield from anthesis, pollination phase and cherelle development in the reproductive phase of cacao. Reducing size in white square box indicates percent quantity of described attribute (not to scale): 100% = flower bloom; 0.5-5% = Flowers pollinated; 0-0.1.25 = Fruit maturation. Negative percent values represent estimated losses and potential avenues for research and management interventions to minimize yield gap. Data source: (Aneja et al., 1999; Melnick, 2016).

4.4.2.4 Physiological capacity opportunities and research gaps

The SUCROS-Cocoa physiological model, generalized for all cacao varieties, provides some insight into the potential relationships between resource allocation, CW, and

yield. The model finds that the most yield-limiting factors are irradiation, irrigation, and maintenance respiration (Zuidema et al., 2005). Thus, interventions that supplement light, water, and resources necessary for plant respiration processes have the potential to increase pod yield. In particular, a lesser-known class of agricultural inputs, biostimulants, has the potential to improve nutrient use efficiency, tolerance to abiotic stress, and therefore crop quality. The European Union Fertilizing Products Regulation and the European Biostimulants Industry Council define biostimulants as a material with substance(s) and or microorganisms which when applied to plant or rhizosphere stimulate plant natural processes to improve one or more of plant's nutrient use efficiency, tolerance to abiotic stress, and crop quality, independent of its content (Ricci et al., 2019; See du Jardin, 2015; Yakhin et al., 2017). For example, non-hormonal biostimulants (n-hB) have been found to reduce abiotic stress (Atta-Boateng and Berlyn, 2021). Although the life span cost to higher yielding cacao relative to shaded farms is explained by nutritional stress (Ahenkorah et al., 1974a), n-hB could leverage this nuance by minimizing the need for soil nutrient replenishment; improving nutrient use efficiency; and managing hormonal and vascular induced fruit abortion in cacao. The effect of biostimulants for promoting growth, genetic vigour, stress tolerance, nutrient uptake and pest resistance are well documented in other species (Russo and Berlyn, 1990, 1991, 1992; Sivaramakrishnan and Berlyn, 2000; Richardson et al., 2004; Saa et al., 2015; Yakhin et al., 2017). Biostimulants therefore present an as-yet untested opportunity to increase yield in cacao plantations.

4.4.2.5 Tree genotype and self-incompatibility

Apart from the general importance of each of the factors described above, individual tree response to light, water, planting density, soil nutrients, pests and diseases, and pollinator availability as well as physiological capacity is directly affected by tree genotype (Lockwood

and Yin, 1996; Daymond et al., 2002; Acheampong et al., 2013; Ofori et al., 2015; Pereira et al., 2017). Studies on the effect of tree genetics on yield responses in two contrasting growth conditions in Ghana showed moderate heritability towards yield efficiency and a relatively larger non-additive genetic effect (Padi et al., 2017). Usually, traits with higher proportion of additive genetic variation can be modified easily by selective breeding. Genetic variability of yield among cacao genotypes have been suggested to be attributed to the ratio of yield to vegetative growth (Daymond et al., 2002). As a result, selective breeding for improved partition has been suggested (Daymond et al., 2002).

After successful pollination, a male gamete from pollen must fuse with a female gamete from an ovule to form an embryo, which develops into fruit. In cacao, a phenomenon called self-incompatibility occurs when the male and female bearing the same dominant incompatibility allele fails to fuse (Glendinning, 1972a). While studies of the complexity of self-incompatibility is active research area in cacao genetics, the mechanism of non-fusion gametes that leads to fertilization failure in cacao have been found to be saprophytically controlled (Cope, 1958; Lanaud et al., 2017b). Although self-incompatibility directly determines fruit set, there is limited studies that account for the relative yield cost of cacao self-incompatibility.

4.4.2.6 Genome Editing and Cocoa – opportunities and research gaps

Genome engineering technology such as CRISPR-cas9 has the potential to address agriculture and the overarching environmental challenges (Doudna and Charpentier, 2014). While genome editing may address technical challenges of specific yield gap challenges such minimizing the carbon cost of premature fruit abortion or increasing pest and diseases resistance, a socio-economic implementation gap can impede technological intervention (Toledo-Hernández et al., 2021a). However, for commodities like cacao largely cultivated by

smallholder farmers, the socio-economic gap can limit the beneficial genome editing technologies. Although there is limited report on yield gap addressed by specific genome edited cacao, interventions such as grafting, plant nurseries alongside agroforest management have been suggested as potential socio-economic implementation solution in cacao (Toledo-Hernández et al., 2021).

4.4.3 Research Gaps from previous section – a summary

From the review above, cacao yield is impacted by a range of biotic, abiotic, physiological and management factors. There is evidence that some of the factors impact cacao yield independently but may differ in their impact when interacting with other factors.

More work is needed to elucidate factors that drive pollination limitation across different production regions, how pollination efficiency varies regionally, how the biodiversity of pollinators across varies across cacao producer regions and the effect on relative yield outcomes and how landscape and abiotic factors interact with pollinators function. Although fruit abortion is uncommon among fruit trees and farmers tend to induce this in practice to increase selective allocation to quality fruits, it is still unclear if this is the strategy in cacao or that it is a negative physiological initiation that can be minimized to increase yield output. Similarly, while the genetic selfing trait of cacao may provide a selective advantage for a desirable biological reproductive outcome or an evolutionary meaning, the relevance to been quality and the broad cacao economy remain blurry. Understanding the fundamental biological meaning underpinning cacao genetics and physiology can expand opportunities to close the respective yield limits. Unlike large commercial plantations, the global cacao industry depends primarily on smallholder farmers producers from low-income economies often lacking formal

training. Regardless of the biophysical factors that affect productivity, farm level management choices may impact yield, nevertheless often neglected in yield analysis. Although culture and traditions may vary across cacao growing regions, comparative studies on the impact of inter-regional management practices on yield and opportunities for knowledge sharing where management practice have proven successful can be invaluable.

4.4.4 Case study: on-farm characteristics and management implication on yield

The literature review revealed that light, water availability/drought, nutrient availability, pest and disease control, and pollination are important factors limiting cocoa globally (Table 2).

All these factors can be strongly affected by agronomic practices, making farm management one of the most critical factors determining both cocoa yield and conservation outcomes (Abdulai et al., 2020). Farm management: both the activities performed on the farm and how farmers make decisions about what to do, is also one of the less understood factors that may have impact on cacao yield. To address this gap in our understanding, we interviewed cocoa farmers at study sites in Ghana to understand the relationship between farm management practices, farmer decision making, farm attributes, and yield.

Survey data was collected from eight selected cacao plantations from three local communities in the Prestea-Huni valley Municipality of Western Ghana (Table 3).

We found that plantation variables explained variability of pod output ($P>F$, 1.7×10^{-8}). Although all the farms are in the same district and some from the same community, the eight selected study sites varied in terms of shade management, cacao planting density, and

management of farm litter. Moreso, four out of the eight plantations had shade trees and the remaining four had their canopies fully exposed to sunlight. The planting density of cacao trees ranged from 178 to 440 trees per hectare (Table 1). Farm management practices differed across plantations as seen in the differences in the amount of pod piles remains, as well as the clearing of fallen fresh or large branches, felling large trees and keeping of old tree trunks. For instance, plantation #4 had 36 living tall trees and one old remnant tree trunk compared to plantation #6, with two tall trees but 36 old tree trunks (Table 3). The presence of tree trunks either implies plantation owner removed trees or that the trees were felled before the farm was acquired in plantation #6. However, in the case of plantation #4, it can be argued that the availability of 36 trees and the incidence of only one felled tree could have been a choice by the plantation manager. In the latter case, the management choice affects the intensity of canopy and understory irradiance. Despite the proximity of some of our plantations in the study (Fig 1), we found differences in management practices across our study sites, with respect to pruning, pest and disease management, fertilizer use including brand preference, mode, and frequency of application (Table 4).

Table 3: Management practices of selected farms from the Prestea Huni-Valley municipal, Western Ghana. SEM=Standard Error of Mean.

Plot #	Forest proximity	Location	Shade management	Planting density (± SEM)	Plantation floor				
					Pod pile	Fresh branches	#Tall trees	#Branches (>5cm)	Old tree trunks
1	Close	Tarkwa-Breman	Yes	440 ± 32	0	Absence	2	29	7
2	Close	Tarkwa-Breman	No	329 ± 32	0	Absence	1	36	2
3	Close	Tarkwa-Breman	Yes	206 ± 32	15	Absence	3	35	4
4	Far	Tarkwa-Breman	No	212 ± 32	2	High	36	8	1
5	Far	Tarkwa-Breman	Yes	308 ± 32	1	High	1	36	5
6	Far	Anti-korkoh	No	178 ± 32	2	High	2	4	36
7	Far	Anti-korkoh	Yes	184 ± 32	0	High	5	6	36
8	Far	Amezugbe	No	386 ± 32	0	Low	4	7	36

Table 4: Farm input and routine management practices by farmers of eight selected plantations in the Western region of Ghana.

Farm ownership	Farm activity	Weedicides (Local brand names)	Pesticides (Local brand names)	Fertilizer		
				Type (s)	Application time	Mode of application
1-5	1. Weeding 2. Spraying 3. Pruning 4. Fruit removal 5. Removing parasitic plants	1.Condemn 2.Adwuma wura 3.Run-off	1.Confidor 2.Acestor 3.Akate master	1.Asaase wura 2.Adehye 3.Cocoa feed	March August	Girdling/circling around trees
6-7	1. Farm inspection 2. Weeding 3. Spraying 4. Fruit removal 5. Maintenance	1.Gramoquick 2.Sharp	1.Akate master 2.Confidor	1.Asaase wura 2.Adehye 3.Cocoa feed	April May	Sprinkling solid fertilizer on farm
8	1. Weeding 2. Pruning 3. Spraying	1.Gramoquick 2.Sharp 3.Condemn	1.Fungicides 2.Acerstor 3.Confidor	1.Asaase wura 2.Adehye 3.Cocoa feed	May	Sprinkling solid fertilizer over farm

Another on-farm characteristic observed was mixed-sized cacao trees across plantations. This might be the result of planting new trees in existing plantations although seedlings of the same generation might have different growth trajectory. Tree age-size class is known to be associated with productivity (Steppe et al., 2011). However, there are limited studies that have related cacao yield to tree size class. We hypothesized there would be no difference in pod yield by tree size class across all plantations. The lower-sized class trees had largest variability that favours relatively higher total pod output (Fig 3), explanatory strength of tree size for variability in pod outcome is weak (P>F, 0.0597; Table S5), thus we refuse to reject the null hypothesis.

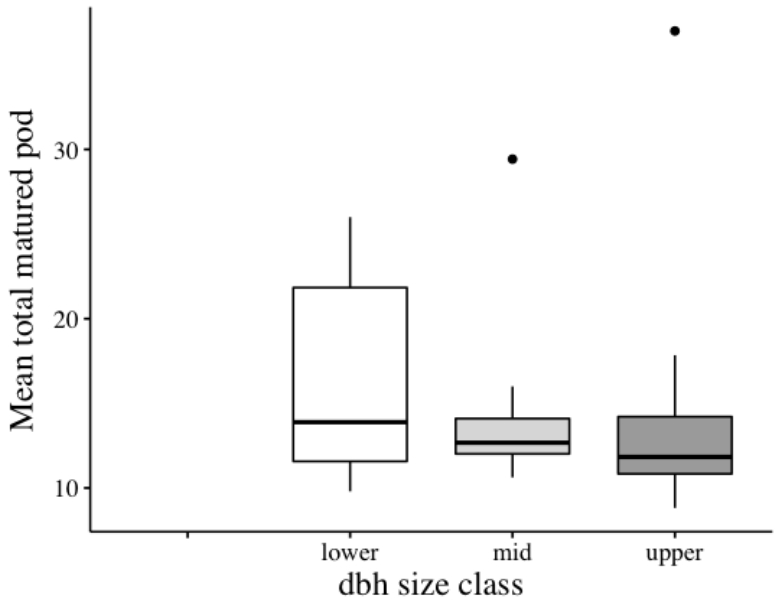

Figure 3: Pod output of cacao by tree size class.

Table 5: Analysis of variance model of size effect on cacao tree fruit output

Variables	*Co-efficient*	Df	Sum sq.	Mean sq.	F-value	Pr(>F)
Intercept	*21.32*					
dbh size class		2	547	274	2.847	0.0597
mid	*0.558*					
upper	*-1.01*					
Plantation	*-1.5248*	1	3239	3239	33.716	1.73e-08 ***
Residuals		280	26897	96		

We considered farm characteristics as a proxy of plantation management and correlated with total pod output. Overall, we found weak correlations between pod yield and cacao tree density (r = 0.28; Fig 4), plantation (r = 0.32; Fig 4), old tree trunk (r = 0.19; Fig 4), dbh (r = 0.12; Fig 4), tall trees (r = 0.09; Fig 4). Although weakly correlated, planting density was positively related with pod yield and has been shown in other studies to directly affect the plantation light environment, water and nutrient availability, pest and disease prevalence and availability of pollinators and considered an over-arching factor that determines cocoa yield (Souza et al., 2009).

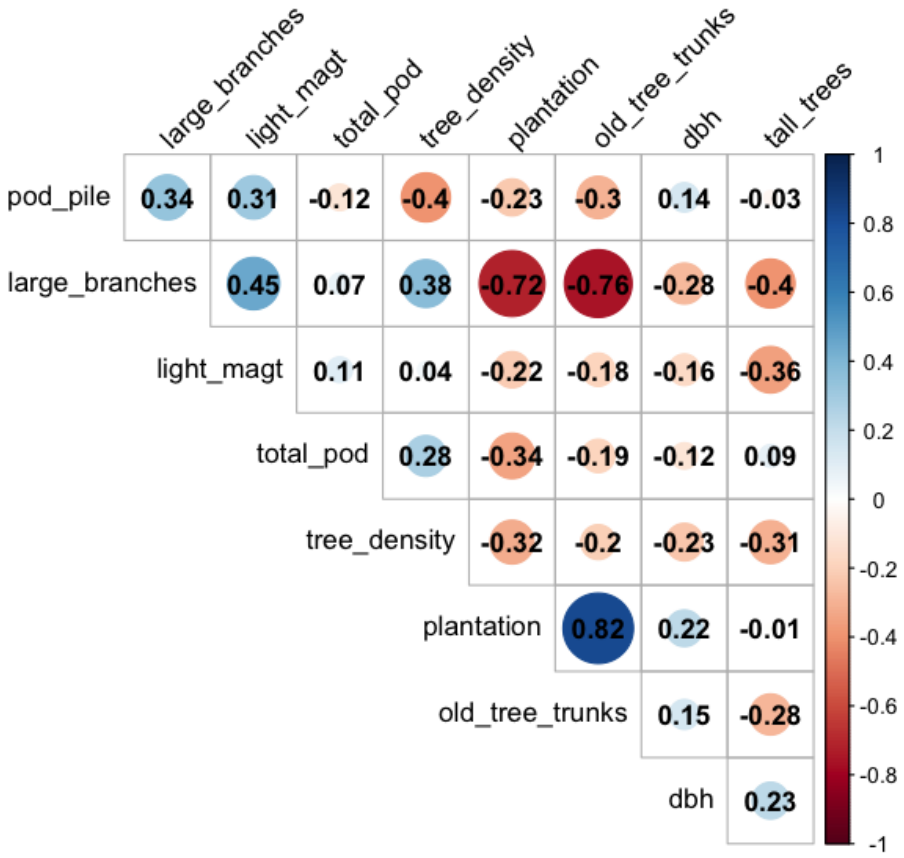

Figure 4: Correlation plot of farm specific characteristics to total pod output at 95% confidence level. Colours indicate direction of correlation (positive =blue, negative= red). Colour depth and size indicates correlation coefficient. Size of bubble indicate correlation coefficient. Absence bubble shows not significant at P<0.05.

Analysis of the relationship between plantation management variables (shade management, cacao planting density, litter management) with pod yield found weak correlations between pod yield and cacao tree density (r = 0.28), plantation (r = 0.32), old tree trunk (r = 0.19), dbh (r = 0.12), tall trees (r = 0.09). Plantation planting density, shown in this study as positive but weakly correlated with pod yield has been shown to directly affect the plantation light environment, water and nutrient availability, pest and disease prevalence and availability of pollinators (Souza et al., 2009). As such, it is considered an over-arching factor important to cocoa yield (Souza et al., 2009). ANOVA model from tree size class effect on pod yield from

288 trees, found no significant relationship between tree size class and pod output (Table 5) although the mean pod output for smaller size trees was higher than for larger tree sizes (Fig 3). Our findings are in line with recently published work which has shown that agronomic management explained on-farm variability in cacao yield more than environmental factors (Abdulai et al., 2020). Earlier litter studies in Ghana have shown that cacao yield increased with tree proximity to pod pile (Morel et al., 2019a). In this study, we did not measure the proximity of pod pile to a tree. Instead, we measured the total number of pod piles distributed across the entire plantation floor, in addition to other plantation floor attributes and found weak association of all with pod yield (Fig 4).

4.4.5 Literature vs case study: the known and unknown yield gap drivers

Overall, this case-study, although limited by sample size suggests that the differences in farm management decision making and the choices of practice can be a source of on-farm variation in cacao yield and should be considered in future studies alongside abiotic and abiotic factors that impact yield. In related studies, agronomic management was found to explained on-farm variability in cacao yield more than environmental factors (Abdulai et al., 2020).

4.5 CONCLUSION

This paper evaluates the biotic, abiotic and plantation management factors that limit cacao yield. The biotic and abiotic factors were assessed from published literature while management factors were determined from a case study across eight selected farm plantations in Ghana.

The main findings of the study shows that pollination (biotic), water and light interaction (abiotic), Cherelle wilt (physiological) and farm-level management are key major factors that contribute existing yield gaps. While irrigation and shade management alleviate water and light

constraints, there exist intervention gaps for increasing pollination efficiency and increasing the proportion of cherelles that convert into mature fruits. More research is needed to close knowledge gaps in cacao reproduction biology, tree allocation physiology and effective strategies to rationalize cacao farm management that maximizes yield. Addressing these factors and closing yield gaps can increase farmer income to and improve their livelihoods. High yielding cacao production can sustain the cacao industry against the uncertainty of future climate threats while stabilizing market volatilities due to production deficits.

Closing yield-gaps through sustainable cocoa production can provides long-term win-win economic benefits for all stakeholders in the cacao value-chain while providing the resilience needed to withstand the uncertainties of climate shocks.

5 POLLINATION LIMITATION IN CACAO: EMPIRICAL EVIDENCE FROM WESTERN GHANA

Paper one, suggests that closing cacao yield gap can increase livelihood outcomes of smallholder cacao farmers and potentially alleviate the environmental consequence of forest conversion into cacao farms. The paper shows that among several cacao yield constraints, pollination and physiological limits might account largely for existing yield gap. It is noteworthy to mention that interventions such as agrochemicals, irrigation and shade trees exist for managing pests, drought, or excessive sunlight respectively. Unfortunately, the controlling factors of pollination deficit or excessive fruit abortion is poorly understood. Studies that examined pollination and physiological limits of cacao in Sulawesi, Indonesia concluded that cacao is co-limited by pollination and physiology. In this paper, we test pollination limitation in Ghana and evaluate the landscape and abiotic factors that drive pollination limitation in the study area.

POLLINATION LIMITATION IN CACAO: EMPIRICAL EVIDENCE FROM WESTERN GHANA

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5.1 Abstract

Cacao production accounts for over $100 Billion annual revenues in the chocolate industry but also forest loss, impacting biodiversity conservation efforts in growing regions. There is evidence that cacao production is lower than the theoretical maxima on most plantations. Addressing this 'yield gap' would not only enable farmers to meet the rising global cacao demand but could also improve the socio-economic wellbeing of farmers and farming communities, increase productivity of existing farmlands and alleviate the need for tropical forests conversion to farmlands. Pollination limitation appears to be one of the causes of the yield gap in some plantations, suggesting that increasing pollination services could help to

close the yield gap. However, pollination limitation in cacao is poorly understood. Here we test the pollination-limitation hypothesis with a hand pollination experiment conducted during both wet and dry seasons in South-western Ghana, the second largest producer of cacao in the world. Further, the biotic and abiotic predictors of pod and flower outputs are tested in mixed-effect linear models, and their implications for managing cacao systems are discussed. Using a pollination-limited yield curve, we estimate the natural pollination levels at the study area to be under 30% and a 70-80% pollination-limited yield gap. This implies that interventions that target the biodiversity and abundance of cacao pollinator population will not only optimize ecosystem services in cacao systems but will also be critical to the global cacao economy.

Keywords: pollination limitation, cacao, pollination service, biotic, abiotic, hand pollination

5.2 Introduction

Theobroma cacao (cocoa) is an economically important crop produced for confectionery and cosmetics, largely for the Western European and the rapidly developing Asian markets (Voora et al., 2019b). It is cultivated mainly by smallholder farmers in low-income economies across the global tropics, mainly in Latin America, West Africa, and Southeast Asia (Franzen and Borgerhoff Mulder, 2007). Cocoa is an important economic commodity. In 2017, global production of cocoa beans was valued at USD 6.62 billion (FAO, 2022), and the global chocolate industry was valued at USD 106.19 billion (Voora et al., 2019b). For comparison, global production of tea was valued at USD 15.9 billion (FAO, 2022). It has been suggested that there is a gap between the achieved and maximum potential crop yield, a 'yield gap', in cocoa production (Aneani and Ofori-Frimpong, 2013; Abdulai et al., 2020). Closing this yield gap would increase production, and therefore income, for the smallholder farmers who produce most of the cocoa globally. Closing the yield gap could have

the additional benefit of reducing or avoiding the need for expansion of the area of cocoa production, which often has negative biodiversity impacts (Panlibuton and Meyer, 2004; Weber et al., 2007). Further, farmer profits may not fall with market price as demand of cocoa products is inelastic (Andreyeva et al., 2010) regardless of consumer economic status (Smith et al., 2018).

To close the yield gap, meet the growing global demand for cocoa (Voora et al., 2019b), and protect future production in a changing climate, it is essential to understand the factors that limit cocoa production, and determine the gap between achieved yield and the theoretical physiological or ecological maxima. The physiological maximum refers to the yield attained under optimal growth conditions where there are sufficient nutrients, light, and moisture. The ecological maximum refers to the yield attained when biotic interactions with the crop are optimized, including soil microbial interactions, plant facilitators such as shade trees or nitrogen fixing plants, and pollination services.

Among the many biotic and abiotic factors impacting cocoa yield (Groeneveld et al., 2010a; Ploetz, 2016; Meneses-Buitrago et al., 2019), pollination limitation has been shown to be one of the most important (Groeneveld et al., 2010a; Toledo-Hernández et al., 2020a). Those findings are in line with wider understanding of the major factors limiting production for other insect pollinated crops such as pear, macadamia, and eggplant (e.g. Basu et al., 2011; cet al., 2011; Bhattacharya and Basu, 2018; Grass et al., 2018; Holland et al., 2020).

Pollination is the transfer of pollen (which contains male gamete) from the anther to a stigma which contain the ovules (which contains the female gamete). Pollination is the primary step for seed formation and its failure can be attributed to poor pollen quality or delivery, too few or inconstant pollinators, too specialized or selective plants, fewer or too uniform genetic population (Wilcock and Neiland, 2002). Understanding pollination limitation

is important for plant conservation efforts and maintaining crop yields (Wilcock and Neiland, 2002). After pollen deposition on the stigma, the pollen grains germinate to form a pollen tube which transfers the male gametes (sperm cells) to the ovule to fertilize the egg cell, but when hindered, fail to set fruit (Lord and Russell, 2002). Due to the importance of the genetic diversity in flowering plants, majority of plants supresses pollen from the same flower (self-pollination) by a genetic system that recognizes and reject self-related pollen in a phenomenon called self-incompatibility (Hiscock, 2002; Hiscock and Mcinnis, 2003). Self-incompatibility (SI) in cacao is late acting or occurs in the ovary (Ford and Wilkinson, 2012), and is expressed through a sporophytic control of non-fusing gametes in which the reaction occurred after pollen tube have penetrated the ovaries, resulting in fertilization failure (Knight and Rogers, 1955; Cope, 1958). Thus, even after successful pollen transfer between flowers by a pollinating agent, fertilization failure due to complex genetics of selfing results in failure of fruit set. As fewer S alleles in a population leads to fewer mating opportunities, population crossing using artificial pollination of cacao clones from five different geographical regions confirmed increased inter-compatibility between groups above 30% fruit set threshold, suggesting the use of inter-compatibility information in plantation design to maximise yield (López et al., 2021).

It is recognized that there are likely to be regional differences in the abiotic and biotic factors that have the greatest impact on cocoa yield, thus the results from the study reported here, conducted in Ghana, might be mainly be applicable to West Africa, the most important cocoa producing area in the world (Young, 1986; Forbes and Northfield, 2017; Chumacero de Schawe et al., 2018; Toledo-Hernández et al., 2020b, 2021b).

This study is based on two hypotheses: There will be a yield gap due to (1) physiological limitation, or (2) pollination limitation (Fig 1), and we ask the following specific questions:

1. Is there evidence of a physiological yield gap?
2. Is there evidence for a pollination yield gap?
3. If there is a physiological or pollination yield gap, is it affected by:
    a) vegetation surrounding the plantation: simple (homogenous composition) or complex (heterogenous composition)?
    b) plantation light environment (a function of cocoa tree density and presence of non-cocoa shade trees)?
    c) plantation floor leaf litter depth?
    d) seasonal moisture regimes (wet vs dry season)?
4. What is the natural pollination level and pollination yield gap of the study sites?

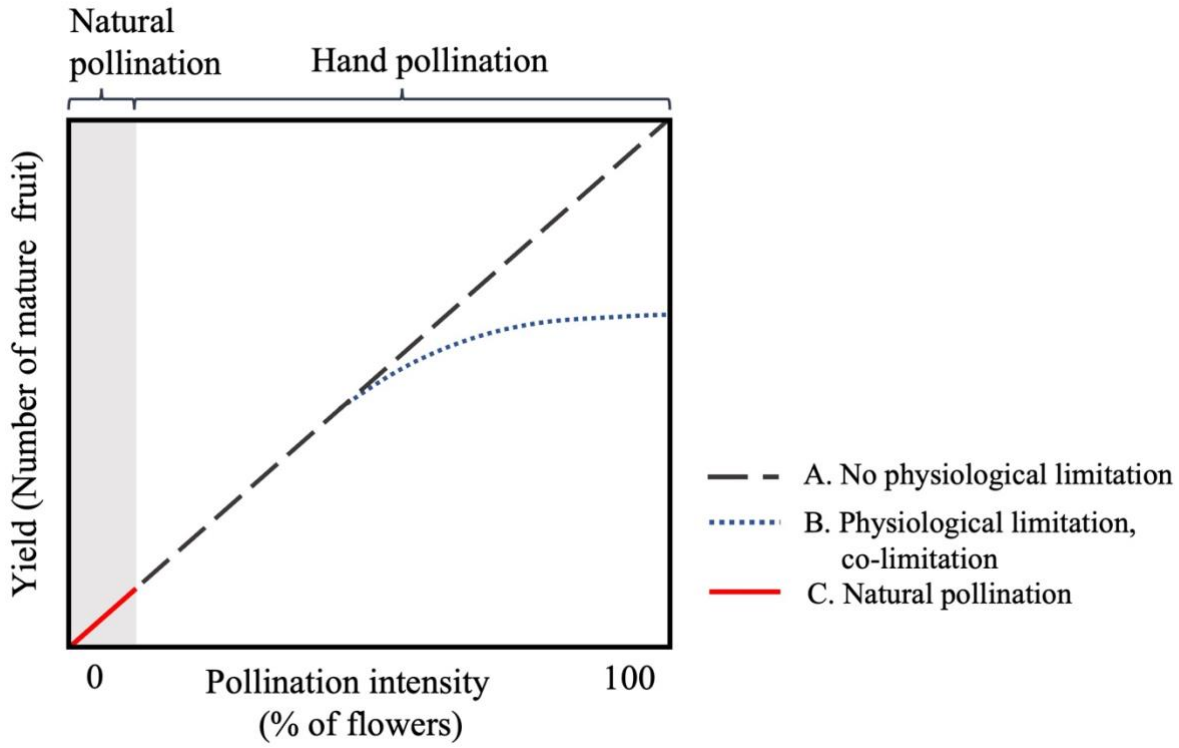

Figure 1: Yield gap in cocoa with respect to physiology and pollination. This figure represents idealized scenarios, with increasing percent hand pollination shown on the x-axis. Modified from Groeneveld et al., (2010).

Hypothesis 1: There will be a yield gap due to physiological limitation.

Cherelle wilt is cocoa's fruit self-thinning process, in which about 75% of immature fruit wither before maturation (Melnick, 2016). This phenomenon is thought to be a result of physiological constraints related to abiotic factors such as light, moisture and soil nutrients (Groeneveld et al., 2010b), as well as timing and regulation of resource allocation for leaf production and fruit development (McKelvie, 1956; McKelvie, 1960). For yield to be shown to be physiologically limited, the response to increasing pollination rates must cease at a physiological maximum beyond which no further increases in pollination will result in increased yield (Fig 1). Physiological limitation has been shown by McKelvie (1960), who found that nutrient status as well as tree size were the main drivers of yield, and Groeneveld et al. (2010), who found that fruit set increased with increasing percent hand pollination (HP) rate up to a maximum limit of 40%, beyond which further increase up to 100% HP did not impact yield.

Hypothesis 2: There will be a yield gap due to pollination limitation.

Cocoa is insect pollinated, and if there were no physiological limitation, we would expect the number of fruits produced to increase linearly with the number of flowers that are pollinated (Figure 1, dashed dark line). However, cocoa has been shown experimentally to be pollination limited under field conditions (Groeneveld et al., 2010b; Toledo-Hernández et al., 2020a). For instance, cocoa yield increased above natural pollination level with increasing hand pollination rates (Groeneveld et al. 2010). Pollination limitation in cocoa (Toledo-Hernández et al., 2020b) is thought to be due to a combination of insufficient insect pollinator abundance and/or biodiversity (Toledo-Hernández et al., 2021b), which is expected to be a result of local biotic and abiotic habitat characteristics affecting pollinators' survival and reproduction (Zakariyya et al., 2016; Forbes and Northfield, 2017a). In addition, cocoa's self-incompatibility

mechanism (Cope, 1962), and the short life span of individual flowers (unfertilized flowers abscise ~22–24 h after flower opening (Swanson et al., 2008)) are likely to affect rates of effective pollination.

5.3 MATERIALS AND METHODS

5.3.1 Study sites

Eight privately owned plantations near Tarkwa-Breman in the Wassa-Amanfi district in the Western region of Ghana were chosen as study sites (Table 1, Fig 2). Two of the plantations had high shade and were surrounded by complex vegetation, two had low shade and complex vegetation, two had high shade and simple vegetation, and two had low shade and simple vegetation (further explanation below; Fig 4C). In each plantation, a 40m x 40m plot was established. All trees in the plot were counted to determine cocoa tree density per plot and the presence or absence of non-cocoa shade trees was recorded. The average cocoa tree diameter at breast height (dbh) per plot was measured with a dbh tape for all trees within 2 m distance on the left and right along the two intersecting diagonal transects of the plot. The total number and species of trees with dbh larger than 150 cm on a diagonal transect of plot was also recorded. These were mostly shade trees of non-cocoa species.

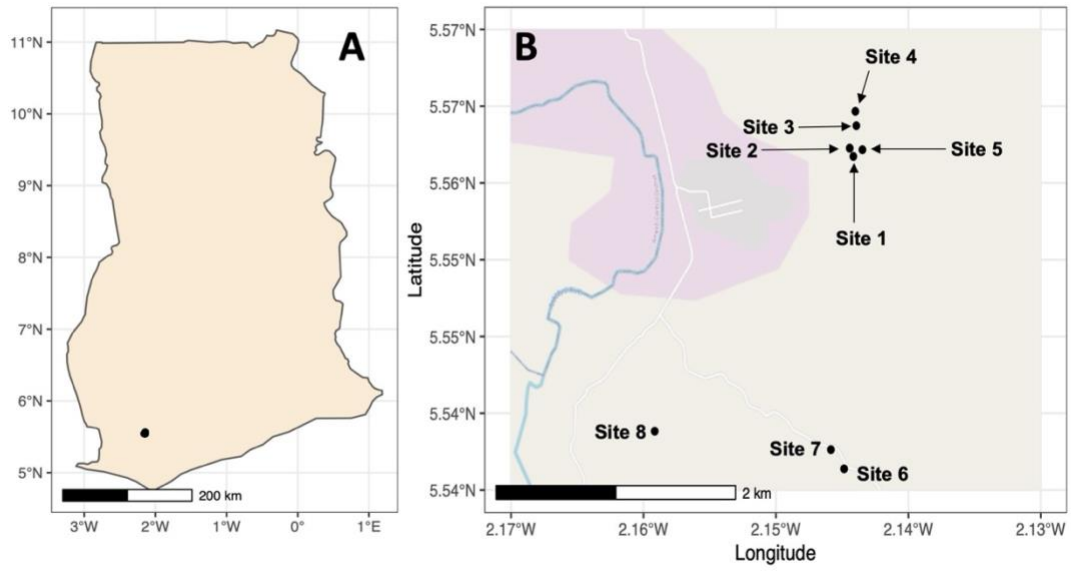

Figure 2: Location of study location in South-western Ghana (Tarkwa-Breman, 5.56173/-2.144153 lat/long) in the Prestea Huni-Valley District (A). Map of experimental sites (B). The purple regions represents the Tarkwa-Breman community town. Blue line represent a river and white lines represents road networks.

Table 1: Experimental sites and plot attributes.

Site code	Location	Latitude	Longitude	Surrounding vegetation	Shade trees	Tree density/1600m² plot	Population mean dbh of trees in plot (cm)	Mean understorey light environment	Litter depth (cm)
1_nscf	Tarkwa-Breman	5.561733	-2.14415	Complex (heterogenous)	Yes	440	14.4	6, low shade	0.88
2_sscf	Tarkwa-Breman	5.562267	-2.14443	Complex (heterogenous)	No	329	14.2	3, high shade	5.99
3_sscf	Tarkwa-Breman	5.563733	-2.14393	Complex (heterogenous)	Yes	206	15.4	3, high shade	5.44
4_ssff	Tarkwa-Breman	5.564667	-2.144	Simple (homogenous)	No	212	14.7	9.2, low shade	6.52
5_nsff	Tarkwa-Breman	5.562167	-2.14347	Simple (homogenous)	Yes	308	14.4	6.8, low shade	6.84
6_ssff	Anti-korkoh	5.541383	-2.14485	Simple (homogenous)	No	178	15.7	6, low shade	6.4
7_nsff	Anti-korkoh	5.542633	-2.14585	Simple (homogenous)	Yes	184	14.6	9.8, low shade	6.08
8_sscf	Amezugbe	5.543833	-2.15915	Complex (heterogenous)	No	386	15.2	9.4, low shade	6.72

5.3.2 Hand pollination experiment

In this study we use hand pollination to test for physiological limitation and pollination limitation, as well as a means of disentangling pollen limitation, lack or insufficiency of viable pollen received in the flower, from pollination limitation, a low fraction of flowers receiving pollination visits from a pollinating agent. Hand pollination treatments test pollination limitation only, as each tested flower receives more than sufficient pollen for pollination.

To test for physiological limitation (is the number of set fruit less than the number of hand pollinated flowers, **Question 1**), and pollination limitation (is the number of fruits set when open (naturally) pollinated less than the number of fruits set when 100% hand pollinated, **Question 2**), 36 trees, with dbh ranging from 35/πcm to 65/πcm were selected in each study plot. These represented large trees in the plots (for plot average dbh see Table 1) and represented a mean 14% sample of the total number of trees in the plots. As the tree density varied among plots, sampling proportions ranged from 8.1% to 20.2%.

In each plot, six replicate trees were tagged and labelled for each of six treatments: 0% (open/ natural pollination), 20%, 40%, 60%, 80% and 100% hand pollination (HP) (Figure 3). For each tree, the total number of flowers present up to 2m height from the base of the tree was counted on the day of treatment, and the number to be pollinated calculated. For example, if the tree was marked 20% and 200 flowers were counted within 2m height from the base of tree, 40 flowers would be hand pollinated. All hand pollinated flowers were marked with a pin so that they could be identified and recorded if flower abscises when pollination fails (Fig 3B) and tagged with double pin when cherelles successful mature into fruit (Fig 3A). For the 20%-80% HP treatments, all unpollinated flowers were removed from the tree to avoid the non-hand pollinated flowers from receiving insect pollination. Note that cocoa flowers open for 22-24hrs,

after which, if unfertilized, they abscise (Swanson et al., 2008). Thus, each day when conditions allowed, hand pollination experiment was repeated. The total count of flowers that were successfully pollinated or failed from previous days were recorded as well as newly formed cherelles (fruitlets) or cherelles that abscised.

Figure 3: Designated pins to mark pollinated flowers and successful fruit conversion. A single pin shows pollinated flower. Double pin shows developing fruit after fruit set.

Note that 0% (natural/open pollination) does not refer to pollination exclusion where flowers are shielded from pollinator visitation. Rather, open pollination represents the control where pollination occurs only by natural pollinators. This serves as baseline to allow us to test whether there is a difference in yield (matured pod count) in open pollination compared to maximum pollination (100% hand pollination) (Question 2). HP experiments were conducted at the peak of the reproductive stage of the season, where trees had existing developing fruits and profusely flowering (in the case of the wet season). HP experiments were conducted continuously until flowering ceased. The total number of pods already existing on the tree (assumed to be open pollinated) were counted (referred as, Pod_{int}) and allowed to stay on the tree while the additional pods that successfully mature from HP experiment was measured as

the experimental total pod yield (or also referred as Pod_{exp}). While the experimental total pod yield, Pod_{exp} was used to determine yield response to HP to test pollination hypothesis, both Pod_{exp} and Pod_{int} data were used to test evidence for physiological capacity given pollination response.

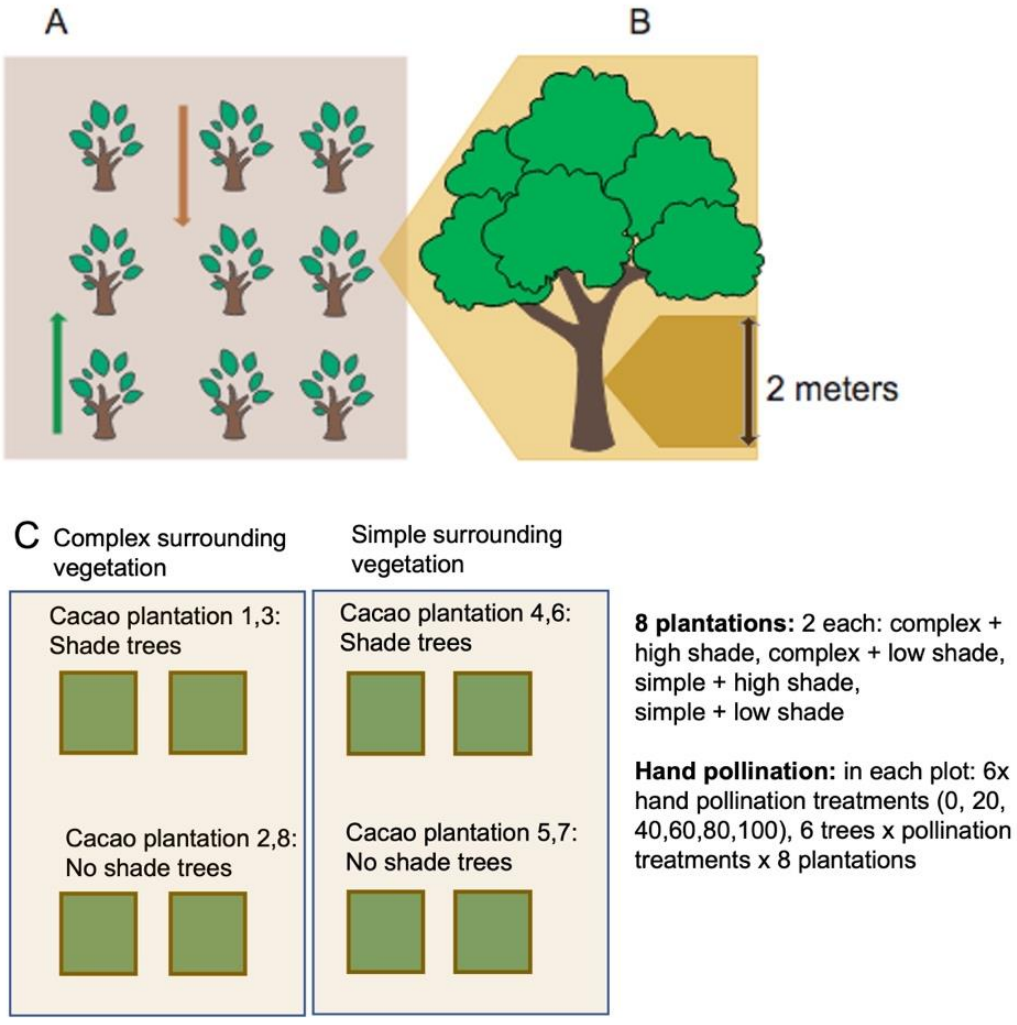

Figure 4: Plot and tree level sampling. (A) Systematic random sampling approach for selecting trees in each plantation study site for hand pollination treatment. Arrows indicate the direction of sampling. Six mature trees with diameter at breast height between 35-65cm were selected and marked for each treatment: 0%, 20%, 40%, 60%, 80%, and 100% hand pollination. (B) Hand pollination treatments were applied from 0 to 2m height from the ground on the tree. (C) Hand pollination: In each of the eight study sites there were six trees for each of the six hand pollination experiments (0, 20, 40, 60, 80, 100%). Therefore, for the whole experiment there were 8 sites x 6 treatments x 6 trees = 288 treated trees for each experimental season and 576 trees for the entire studies.

To hand pollinate flowers, nearby flowers with viable pollen were collected during early morning. To ensure pollen compatibility, pollen was collected from several freshly blooming flowers from adjacent trees and mixed. Pollen from stamens of flowers were tested for dryness and brought into contact with a viable stigma of the candidate hand pollination flower with the aid of a pair of tweezers. Successful pollination is indicated by immediate split in the apical portion of the stigma, observable with a hand lens. To address **Question 3d,** hand pollination was repeated on sampled flowers for a total of 22 days between August 01 and October 24, during the wet season, and 23 days between January 20 and February 28, during the dry season. The same experiment plots were used for the during the dry season, however, trees were unbiasedly resampled to minimize plot level errors.

5.3.3 Surrounding vegetation

Studies on the effect of pollinator habitat and pollination services show a strong relationship between natural habitat area and pollination services (Kremen et al., 2004). Also, proximity to native forest has been shown to increase pollinator visitation in coffee farms (Ricketts, 2004). However, in cocoa farms, proximity to forest has been shown to have no influence on pollinator visitation (Toledo-Hernández et al., 2021b). This may be due to the relatively small size of known cacao pollinators resulting in a relatively shorter flight distance or smaller foraging ranges. Thus, we sought to evaluate whether the vegetation immediately surrounding a cacao farm have effect on flower visitation rates and pollination service.

To test the effect of vegetation surrounding the cocoa plantation, including non-plantation trees but not limited to forest, on pollinator visitation (**Question 3a**), we classified vegetation surrounding plantation as either homogenous ('simple') or heterogenous ('complex') typologies. 'Simple' indicates a plantation surrounded by vegetation that

comprised of a single species or single stratified vegetation (or canopy) structure, such as a monoculture farm, meadow, or grassland. 'Complex' refers to a vegetation characterized by multi-stratified vertical layers and high floral diversity, especially secondary forest, wetland, or a highly diverse vegetation patch. Emphasise is placed on structure and species diversity to satisfy the assumption of complexity.

5.3.4 Plantation light environment

Light availability through shade management have been found to impact cocoa yield (e.g., Ahenkorah et al., 1974; Clough et al., 2011). Murray (1958) experimentally demonstrated a linear relation between light intensity and cacao yield whereby optimal yield was attained at 50% light intensity. To address **Question 3b**, we evaluated the effect of *understory light environment* and *canopy light* on cacao yield response to physiological or pollination limitation. *Understory light environment* is as a continuous variable and is the amount of light that penetrates downward through the aboveground canopy to reach the plantation floor and farm space. It is measured with a device called canopy-scope (Brown et al., 2000). Because the canopy-scope score is effective for measurements that are averaged within a plot (Hale and Brown, 2005b), for this study, a score was determined by averaging the understorey light measurements from the middle, and the near four corners of the study plot. *Canopy light* is a categorical variable with two factor levels: *shade* and *no shade. No shade* variable was designated to plots in which cacao tree canopies are fully exposed to the sun. *Shade* was designated to the plots that has at least six non-cacao overtopping trees that altogether cast a degree of partial shade on the plantation canopy.

5.3.5 Plantation leaf litter depth

Litter refers to non-living vegetative residue on the plantation floor. This usually constitutes falling fresh or dry leaves, small broken branches, rotten cocoa husks, and other plant remains that cover the topsoil. Leaf litter is reported as the best breeding substrate for the most described cocoa pollinator group, Ceratopogonid midges, and is associated with high cacao yields (Adjaloo et al., 2013; Morel et al., 2019b). To address **Question 3c**, litter depth per plot was determined by averaging the depth of litter (cm) on the soil surface from the plot centre and near the four corners of the plot with the aid of a meter ruler.

5.3.6 Statistical analysis

In the test investigating physiological limitation (number of fruits set less than the number of hand pollinated flowers, **Question 1**), the expectation is that if there is no physiological limitation, and if other fixed and random variables are accounted for, the relationship between yield and % pollination will be linear (Figure 1). We used yield data (number of matured pods) from 0% (open pollinated trees), and 20%, 40%, 60%, 80% to 100% HP treatments as the response variable. Because the response variable data followed a Poisson distribution, we fit a Generalized Linear Model using the mixed effect approach to account for nesting using the Template Model Builder automatic differentiation engine (glmmTMB) R package (Brooks et al., 2017). Pollination treatment, seasonality and landscape characteristics were designated as fixed effects, while tree and site or plot identity were designated random effects. The model algorithm required complete dataset therefore all missing data were imputed using the Multiple Imputation by Chain Equation algorithm package in R (van Buuren and Groothuis-Oudshoorn, 2011). In addition to the GLM above, we tested physiological limitation by determining the relative change in HP treated pod output with respect to initial tree output

prior to experiment was calculated as:

$$+\Delta Y_{pod} = \frac{Pod_{exp}}{Pod_{int}} \times 100 \quad [1]$$

Where Pod_{exp} is the total output of matured pods after hand pollination treatment and Pod_{int} is the total pod output of naturally pollinated flowers from inception of the reproductive season. Given the data is non-parametric, the Kruskal-Wallis test was used to test how relative percent pod yield gain, $+\Delta Y_{pod}$ in for HP treatment rates differ from open pollination (0%HP). Here, it is hypothesized that the physiological carrying capacity of the tree will limit how many pods a tree can carry to maturity beyond the peak fruiting stage. If there is physiological limitation, there will be no difference in $+\Delta Y_{pod}$ across all the HP treatments.

To test for pollination limitation (number of fruits set with open pollination is less than the number of fruits set with 100% HP, **Question 2**), we used yield data from open and full (100%) HP as the response variable, pollination treatment, plot, and landscape characteristics as fixed effects, and tree and plot identity as random effects in a generalized linear mixed model using the Template Model Builder automatic differentiation engine (glmmTMB) R package (Brooks et al., 2017). Because the response variable was count data with a Poisson distribution, we fit a negative binomial mixed-effects model with a log link function by quadratic parameterization where variance, $\sigma^2 = \mu(1 + \mu/\varphi)$ or linear parameterization with variance, $\sigma^2 = \mu(1 + \varphi)$ accounted for overdispersion. Model assumptions are satisfied when the dispersion ratio, which is the ratio of deviance to degree of freedom, is approximately 1. The deviance to degree of freedom ratio was estimated from the ratio of Pearson's chi-square to residual degree of freedom ratio, χ^2/ν (Brooks et al., 2017).

Models were selected by the stepAIC algorithm which performs stepwise model selection by AIC from the MASS package in R programming software (Ripley et al., 2018). All data was visualized using the ggplot2 R package suite (Wickham, 2016a).

5.4 RESULTS

Question 1: Is there evidence of a physiological yield gap?

Data across all eight sites suggests that increased percent hand pollination increases pod output (Fig 4A). If open pollination output (0% HP treatment) is the baseline value, HP treatments increased the number of matured pods by 155.8% (20%HP treatment), 181.7% (40%HP treatment), 210.6% (60%HP treatment), 255.3% (80%HP treatment) and 343.3% (100%HP treatment). Plotting the percent gain in pod output relative to 0%HP for HP treatments shows a strong linear relationship between %HP pod yield at $R^2 = 0.96$ (Fig 5).

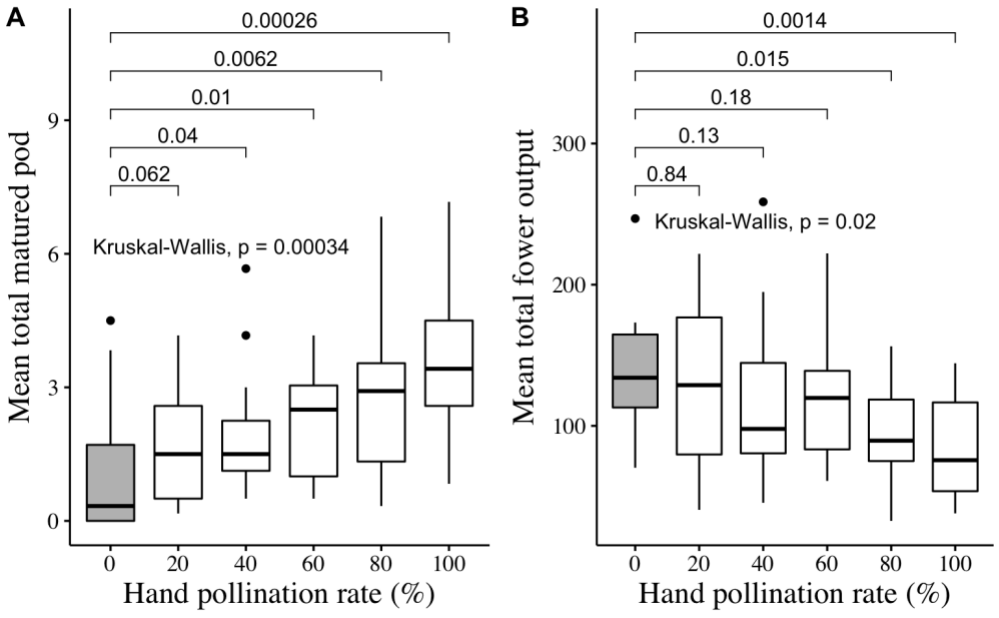

Figure 4: Comparison of mean response to hand pollination treatments (A) in total matured pod and (B) in total flower output from eight plantations across the wet and dry seasons.

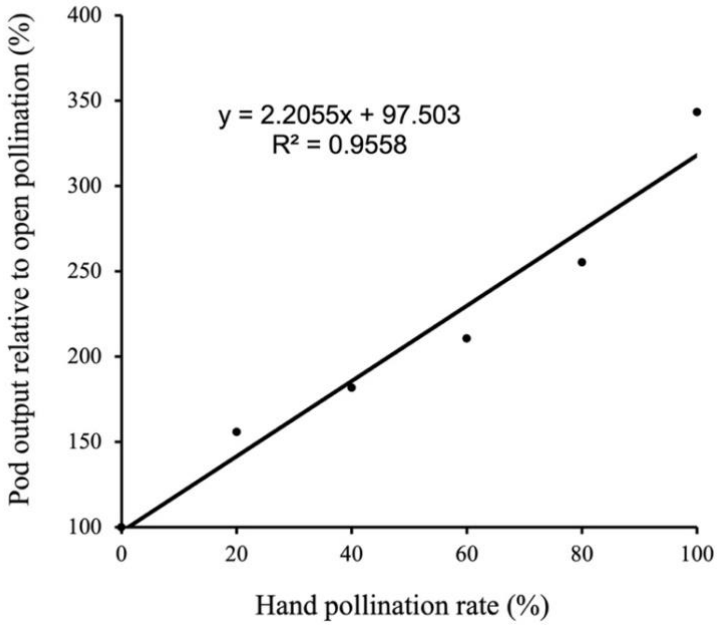

Figure 5: There is a strong linear relationship between % hand pollination and pod output from. Mean output for all hand pollination rates represent data from eight plantations. Note that the intercept, 0 indicates 0% HP (open pollination), and therefore represent natural insect pollination.

Unlike earlier work by Groeneveld et al., (2010), in this experiment, we did not observe a plateau curve where increase in hand pollination increased pod output up to a plateau where further increase in pollination no longer increased yield, suggesting that cocoa is not strongly limited by physiology at the study sites. However, the number of set fruit was never equal to the number of pollinated flowers. There are several potential explanations: the hand pollination treatment itself may have inadvertently damaged individual flowers (Kosterin and Bogdanova, 2014); wind and rain may have damaged pollinated flowers as observed on farm floors during mornings after heavy rain (personal observation); seasonality, where pollinated flowers drop after few days in the dry season due to decreased water availability (Frimpong-Anin et al., 2014).

In addition to the linear modelling approach, the effect of hand pollination treatment on the pod output was evaluated by calculating the additional percent gain in pod yield, $+\Delta Y_{pod}$ with increasing %HP with respect to peak open reproductive output. If cacao is physiologically limited, there should be no difference in $+\Delta Y_{pod}$ across HP treatments beyond peak reproduction. We found that there was a significant difference between the mean percent gain in pod yield after peak reproduction, $+\Delta Y_{pod}$, for all HP treatments (Table 2, Fig 6). Open pollination received only about 10.6±0.08 % gain in peak pod yield for 0%HP treatment. The mean $+\Delta Y_{pod}$ for HP treatment rates (20% -100%) all exceeded open pollination (Table 2). Furthermore, data distribution from boxplot (Fig 6) shows that more than half of HP treated trees had $+\Delta Y_{pod}$ much higher than open pollination such that the outliers, which represents the maximum pod carrying capacity of trees increased with increasing pollination rates beyond 500% and 800% in the case of 80%HP and 100%HP treatments respectively. This was consistent when across landscape variables (Fig 7).

Table 2: Percent gain in cocoa fruit yield in hand pollinated and open pollinated trees. 0% HP indicate zero hand pollination but may include natural pollination. SE is the standard error of mean.

Hand pollination treatment	Percent $+\Delta Y_{pod}$ (± SE)
Control (Open pollination)	10.59% (± 0.0768)
20% HP	39.04% (± 0.1477)
40% HP	30.08% (± 0.1826)
60% HP	33.84% (± 0.1454)
80% HP	54.98% (± 0.2027)
100% HP	93.59% (± 0.2715)

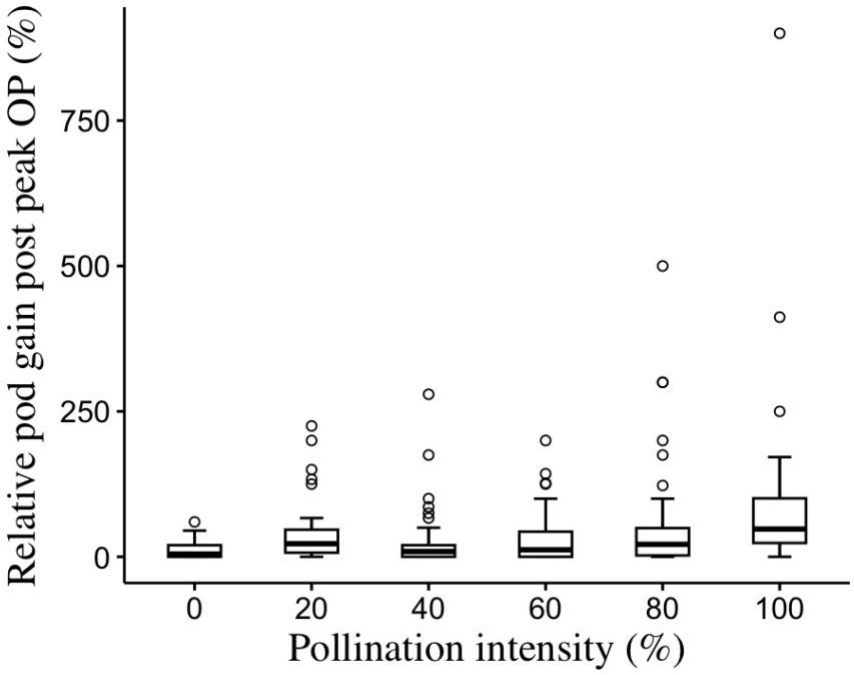

Figure 6: Mean percent gain in pod yield by trees (n=48) in plots after hand pollination experiment, each from eight plantations. Trees were sampled for pollination experiments in the wet season at peak reproduction phase where pre-existing pod were naturally pollinated. Datapoints indicate distribution of pod yield gain by individual trees for various PH treatment. The outliers here indicate maximum gain in pod yield per tree. P = 0.00004 (0-20%HP), p = 0.43 (0-40%HP), p = 0.023 (0-60%HP), p = 0.0017 (0-80%HP), p = 8^{-10} (0-100%HP). Global p-value, p =1.8^{-10}.

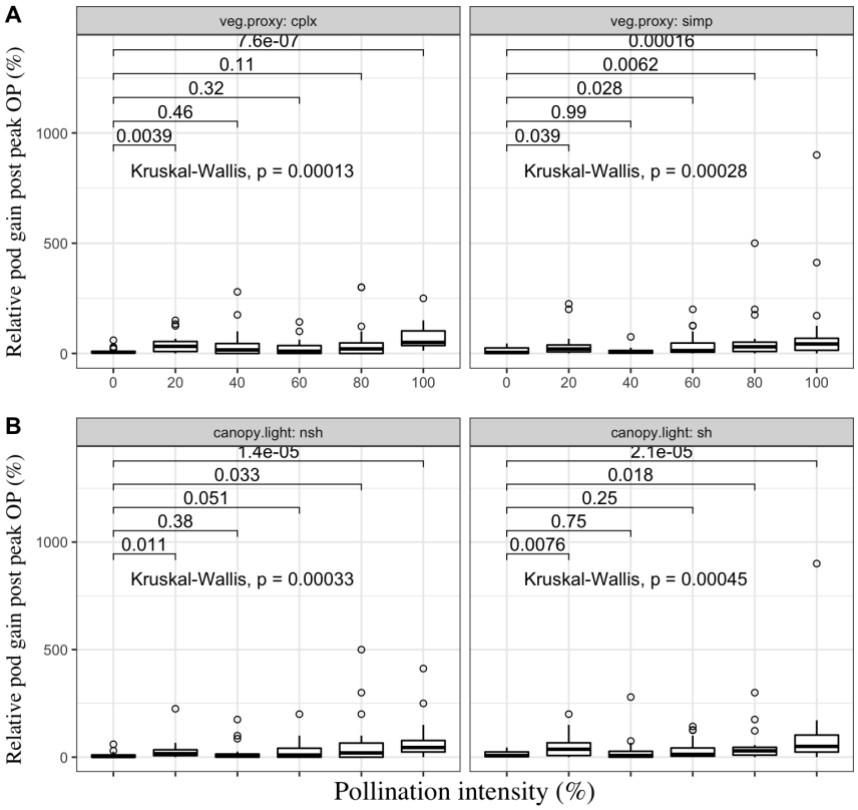

Figure 7: Additional percent gain in pod yield per plot relative to 0% HP, controlling for canopy light and surrounding vegetation.

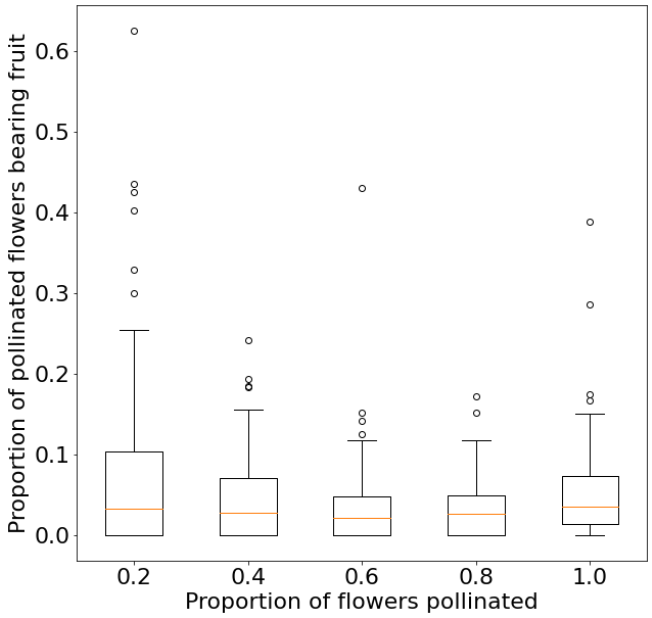

Figure 8: Proportion of hand pollinated flowers bearing fruit (matured pod). Orange colour represents mean proportion of pollinated flowers bearing fruit.

Finally, to further investigate whether pod yield is physiologically limited, we examined the proportion of flowers per tree that becomes matured fruit for each enhanced HP treatment group. Figure 8 shows similarity in the mean proportion of pollinated flowers that become mature fruit across all the enhanced HP treatments. This suggests that within reproductive biological boundaries, the cacao tree is somewhat maintaining a flower-pod conversion mechanism, and the differences in the actual pod yield is determined by the pollination rate. On this premise, we conjecture that cacao in the study area is pollination limited.

5.4.1 Pollination limitation

In our test of **Question 2:** Is there evidence for a pollination yield gap? Our null hypothesis was that there would be no significant difference between the pod yield with open pollination (0% HP) or 100% HP. The linear model analysis found a significant difference between 0% and 100% HP, with 100%HP producing more pods (Table 3, Fig 9B).

Table 3: Generalized Mixed Effects model (negative binomial by quadratic parameterization) test of 0% and 100%HP on pod production of cocoa. 100% HP represents continuous hand pollination of all flowers under 2 meter height on the sample trees over a period of 22 days in the wet season and 23 days in the dry season. Pollination treatment was a fixed effect in the model. The other fixed effects (plot and landscape characteristics), and random effects (tree and plot identity) were not significant in the final model.

Predictors	Co-efficient	Error	Z value	CI	P value	Dispersion ratio
Pod						1.00
(Intercept)	1.305	0.151	8.63	2.74-4.96	<0.001	
Pollination treatment [Natural]	-1.26	0.201	-6.12	0.19-0.42	<0.001	

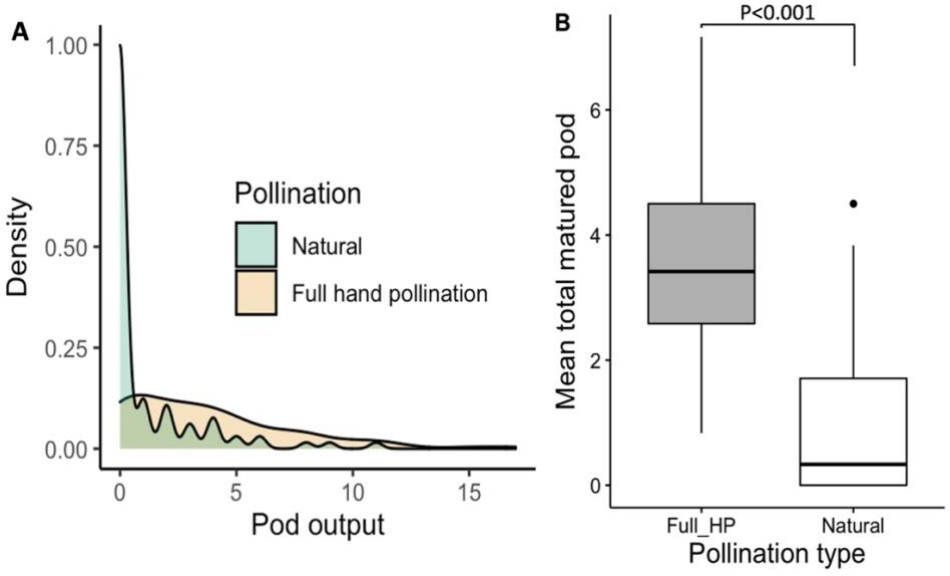

Figure 9: Variation in the mean matured pods output response (A) and total flower production (B) between 100% hand pollination and natural open pollination. 'Full_HP' received 100% hand pollination treatment. 'Natural' received 0% hand pollination treatment.

5.4.2 Pollination limitation as a function of biotic and abiotic landscape factors

To test which independent variables explain pod production in cocoa under pollination treatment rates, we fit a negative binomial regression model where total number of matured pod per tree was the dependent variable, and pollination treatments (0% and 100% HP), complexity of surrounding site vegetation (**Question 3a**), understory light environment and canopy shading (**Question 3b**), amount of litter (**Question 3c**), and seasonal moisture regime (**Question 3d**) were independent variables. The optimum model with the lowest AIC retained only pollination treatment (Table 4, PMOD 1). The next best model based on AIC had both pollination treatment and canopy light as explanatory variables (Table 4, PMOD 2).

5.4.3 Pollination response across landscape and abiotic factors

Pod output with 100% HP was higher than 0% HP across plots (Fig 10A), in the dry and wet seasons (Fig 10B), with simple and complex surrounding vegetation (Fig 10 C), and with and without shade trees (Fig 10D). The consistency of the distinct effect of full hand pollination compared to open pollination across all tested variables support the pollination limitation hypothesis in cacao.

Table 4: Generalized linear mixed model by Negative Binomial for predicting matured pod production (quadratic parameterization). MOD1 is the full model for predicting total number of pods. All models here have been corrected for overdispersion. The shaded region shows the optimal model, with the lowest AIC.

	Co-eff	*Error*	*p*	*AIC*	*Co-eff*	*Error*	*p*	*AIC*	*Co-eff*	*Error*	*p*	*AIC*	*Co-eff*	*Error*	*p*	*AIC*
Predictors	**Null model**				**Full Pod**				**PMOD 1**				**PMOD 2**			
Pod																
(Intercept)	0.87	0.11	<0.001	780.1	0.943	0.539	0.0807	703.2	1.115	0.396	0.004	699.6	0.86	0.383	0.024	702.5
poll.treat [natural]	-	-	-		-1.643	0.214	<0.001		-1.601	0.202	<0.001		-1.581	0.203	<0.001	
Total flower	-	-	-		0.0009	0.0014	0.54		-	-	-		-	-	-	
canopy.light [Shade]	-	-	-		-854	0.558	0.126		-0.902	0.551	0.102		-0.507	0.53	0.33	
understorey light envt	-	-	-		-0.144	0.069	0.037		-0.16	0.065	0.0146		-0.082	0.055	0.142	
Litter depth	-	-	-		0.0115	0.066	0.86		-	-	-		-	-	-	
Vege.proxy [homogenous]	-	-	-		0.417	0.253	0.098		0.483	0.217	0.0146		-	-	-	
Season [wet]	-	-	-		1.349	0.211	<0.001		1.39	0.199	<0.001		1.389	0.202	<0.001	
Canopy[shade]: understory light_envt	-	-	-		0.186	0.081	0.0216		0.199	0.199	0.012		0.139	0.075	0.065	

Dispersion ratios: Full Pod (0.99), PMOD1 (0.98), PMOD2 (1.07). Vege.proxy refers to the type of vegetation surrounding plantation.

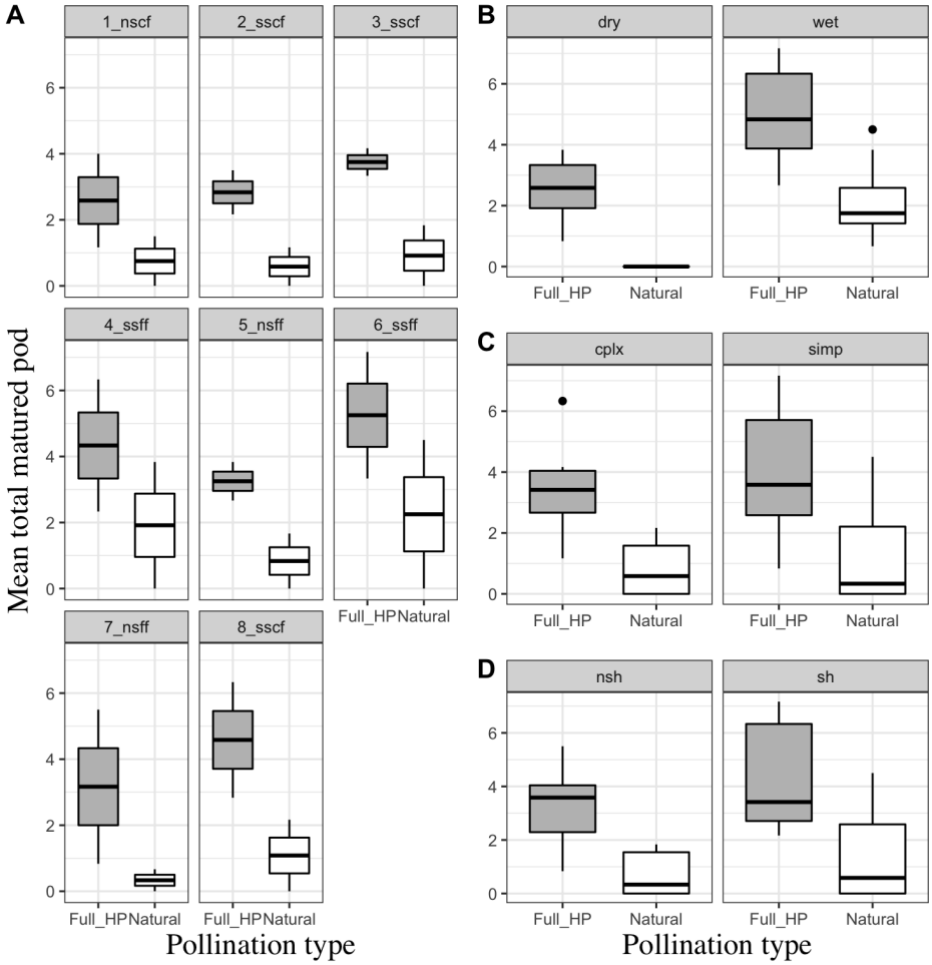

Figure 10: Mean number of matured pods per tree in 100% HP and 0% HP ('natural'): (A) across eight plantations; (B) in wet and dry seasons; (C) with simple and complex vegetation surrounding plots; and (D) with shade (sh) and without shade (nsh) trees.

5.4.4 Pod response to increasing hand pollination across plot, landscape and abiotic factors

The effect of increasing HP rates on pod yield varies at plot level (Fig 11 A). However,

enhanced HP was more pronounced at 80% and 100% HP were consistently different from open pollination (Fig 11 A). The variability of pod output during the wet and dry seasons were more distinct and consistent across pollination rates compared with landscape complexity and canopy light (Fig 11 B, C & D).

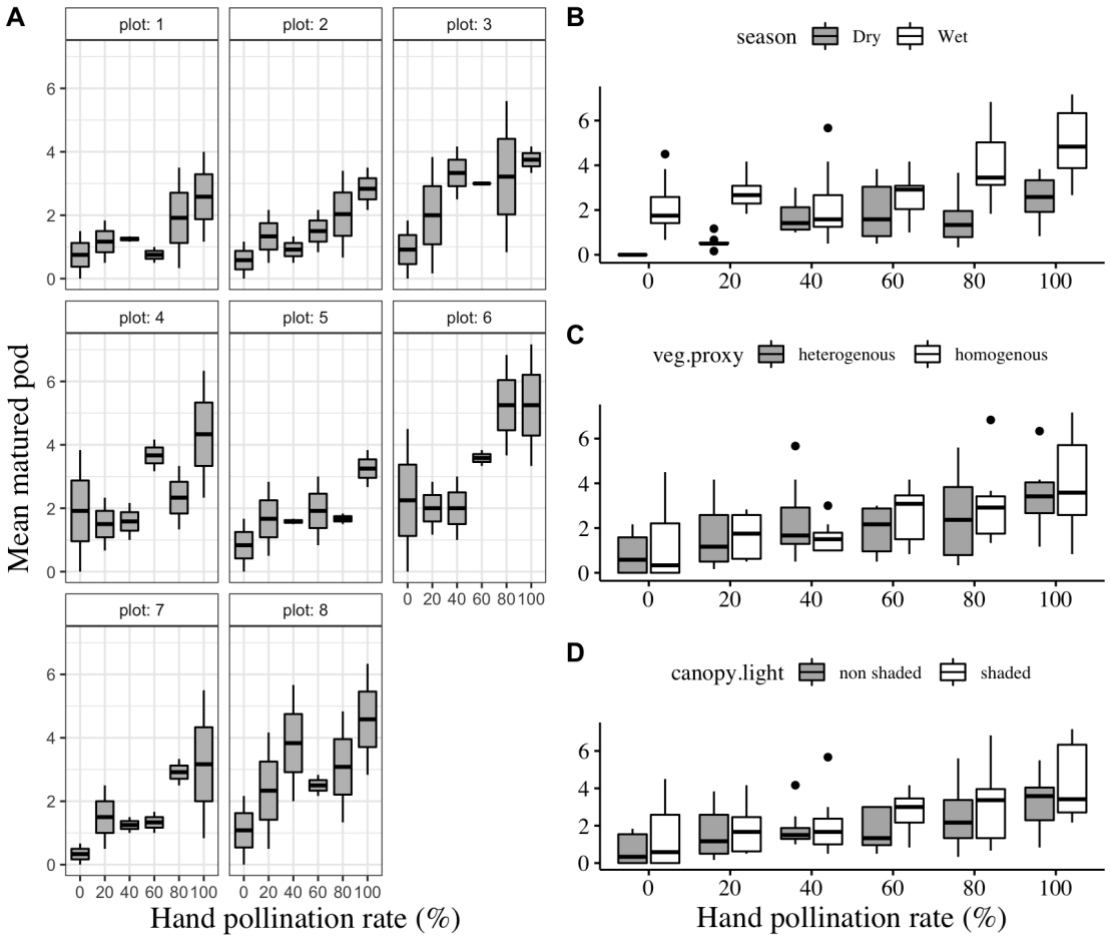

Figure 11: Mean total pod with increasing hand pollination rate: (A) across cocoa plantation sites (B) dry and wet seasons and (C) by the complexity of vegetation surrounding the plots and (D) canopy light of plantations.

5.4.5 Natural pollination levels and yield gap of study site

To estimate pollination levels at the study sites, we compiled hand pollination data from all eight plantations into separate hand pollination and open pollination data and created, for each, a subset data for wet and dry season. The goal here is to plot a linear regression curve of pollination rates (x-axis) against a corresponding pod yield (y-axis). To obtain data for y, we calculated the average total pod yield for each rate of artificial pollination. This is the empirical data we obtained from HP experiments. That is, the average pod yield for 20%, 40%, 60%, 80% and 100% HP for both the dry and wet season. We also calculated the average pod yield for all the open pollination from the 0HP% data (for the wet season and the dry season). Then we calculated average yield for open pollination. From our data, average pod yield for open pollination was 2.2 pods. We used this information and asked, what open pollination rate will produce an average pod yield of 2.2? This should approximately lie between zero and one of the HP rates. So, we construct a full pollination - yield curve with a zero intercept. This is because, we assume that 0%, i.e. absence of pollination will produce zero fruit set. Since we know average open pollination pod yield, $Y_{op} = 2.2$, we plot Y_{op} and the corresponding intercept on the x-axis becomes the model estimate for open pollination rate for the wet season. We repeated the process for the dry season data. From the model estimates, natural pollination at our study sites achieves 43% equivalent pollination rates in the wet season (Fig 12A) and 0% in the dry season (Fig 12B). This corresponds to an estimated yield gap of 56% in the wet season (Fig 12A) and 100% in the dry season (Fig 12B).

The cacao pollination-yield curve (Fig 12 A) shows empirical optimal yield, apparent pollination limitation and by agronomic convention, represent a benchmark for yield

forecasting for the study area. In the dry season, open pollination had no yield, although 100% hand-pollination achieved a 2.5 average pod yield, clearly indicating the dependence of yield on pollination. We found that 1% increase in pollination rates corresponded to 0.03 pod yield.

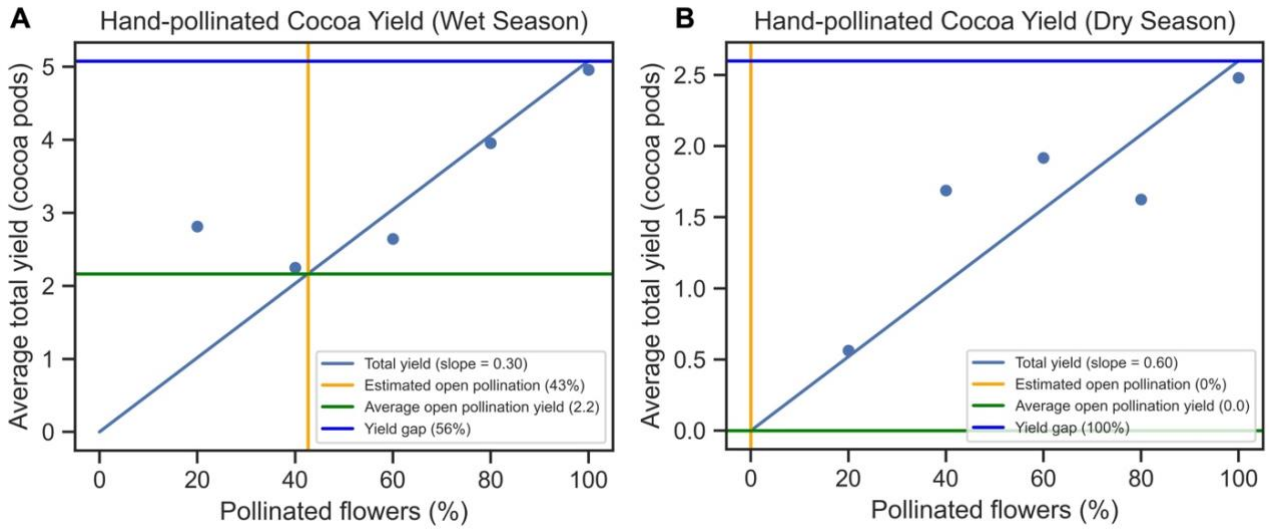

Figure 12: (A) Pollination-yield curve: linear fit of yield response to pollination with a zero intercept, which assumes without pollination there will be no fruit formation. Each data point is the mean yield response to pollination from eight plantations. In the wet season, open pollination levels are at 43% at an estimated yield pollination-limited yield gap of 56%. (B) In the dry season, open pollination is zero with an estimated yield gap of 100%.

5.5 DISCUSSION

To answer whether there is evidence of physiological or pollination limitation in

cacao, we used statistical modelling and deductive approaches from empirical studies. The results show a linear response of increased pod output with increasing hand pollination, suggesting there is little evidence for physiological limitation, although not all pollinated flowers become fruits. These results are in contrast with the findings of Groeneveld et al., (2010b) in studies in Indonesia, where pod yield plateaued at hand pollination values greater than 40%, suggesting a co-limitation scenario, although their conclusion favoured pollination limitation. In contrast to findings on physiological limitation, and in line with studies from Indonesia (Groeneveld et al., 2010b; Toledo-Hernández et al., 2020b), our results provide stronger evidence for pollination limitation in our study sites in Western Ghana. Furthermore, evidence of consistent flower-to-pod conversion with increasing pollination rates (Fig 8) and the significant difference in percent pod gain post-peak production between open pollination and enhanced HP rates (Fig 6) together suggest yield is not limited by tree physiological carrying capacity but pollination deficit.

In a previous study, existing fruits on the cocoa stems were removed before conducting HP experiments (Toledo-Hernández et al., 2020). Contrary to our study, HP experiments were conducted in synchrony with peak-season allocation during the major growing season. If pollination is limiting, the experimental outcome will regardless override ongoing allocation strategies and result in consistent yield response trend (Fig 1A, Fig 5). This aspect of our study further rules out the possibility that cocoa in the study region is physiologically limited or co-limited by pollination. Specifically, in both instances the proportion of flowers that mature into pods will decline as resources become allocated to fruit development. In our study the difference in yield with additional pollination after the trees'

output had nearly reached the limit for natural pollination was found to be statistically significant (Fig 6). The hypothesis that cacao is physiologically limited is often based on high rates of fruit abortion (known for cocoa as Cherelle wilting) as suggested by (Valle et al., 1990). We argue that fruit abortion can be caused by several factors such as infection by pests or diseases (Stephenson, 1981; Bawa and Webb, 1984; Burd, 1998). Nevertheless, it is important to separate fruit abortion due to resource allocation strategies to optimize fruit development from abortion due to pest attack or disease.

On the findings regarding how landscape and abiotic factors relate to cacao pollination limitation on yield, we found that understory light environment was a strong predictor of pod output (Table 4). Although canopy light, in the form of shade trees has been shown to be important for cocoa (Groeneveld et al., 2010a), in our model, canopy light alone did not reliably explain pod output. This is consistent with the findings of Toledo-Hernández et al., (2020). However, we found the interaction of canopy light and understory light environment as a strong predictor of pod yield. We argue that sufficient understory shading may be important for conditioning the habitat environment of pollinator communities (especially the *Ceratopogonidae)* and indirectly impact pollination efficiency and pod yield. Moreso, as cacao is an understorey shade tolerant species, moderate canopy light exposure may be sufficient for photosynthesis needs but nonetheless more important for understorey light conditions ideal for the habitat of pollinator and flower visitors. Although cacao is shade tolerant (Arévalo-Gardini et al., 2021), shade tolerance is often an adaptation to compensate for primary productivity in low light environments rather than a physiological need for low light or shade. Therefore, we suggest that shade management focus on maintaining a balance of low understory light

environment and a more moderate light environment above the canopy. Future studies should investigate the range of light intensity at the plantation understory necessary to balance primary productivity and the habitat requirements of the diverse cacao pollinator populations.

A key observation that has not been previously studied is how the complexity of vegetation surrounding plantation affect pod production. There is strong relationship between natural pollinator habitat area and pollination services (Kremen et al., 2004). Also, increased pollinator visitation rates have been associated with habitat proximity to native forest in coffee farms (Ricketts, 2004). These findings led to the assumption that the proximity of cacao farms to forest may increase flower visitation. However, in recent studies, cacao plantation distance from forest was not important to visitation rates and yield (Toledo-Hernández et al., 2021). Thus, in our study, we considered the complexity of vegetation surrounding the plantations by comparing the effects of simple (homogenous) vegetation with complex vegetation typologies on pollination enhanced yield. Surprisingly, simple, or homogeneous vegetation explained pod production ($P<0.05$, Table 4, PMOD1). Unlike larger size pollinators, the relatively smaller cocoa flowers tend to attract tiny insects which tend to fly at shorter distances and conveniently hide under simple by grass-like or single stratified vegetation covers. For instances, Dipterans such as the Cecidomyiids (a known cacao pollinating taxa), and Chironomids are common pollinators for grasses (Soderstrom and Calderon, 1971; Harris et al., 2003).

On the effect of plantation floor litter, we found no significant effect on pod output. This suggests that perhaps, different litter types or other plantation structures that play a role in the life cycle of pollinators might be more important to cocoa. In a study in Nicaragua, pollinators of cocoa agroforest occurred in 66% of bromeliads on tree trunks which provide

stagnant water in plant tanks for insect larvae (Vandromme et al., 2019).

Finally, from the pollination-yield curve (Fig 12), we estimate that open pollination accounts for 43% yield which suggests a 56% estimated yield gap at the peak of a typical growing season from cacao plantations in Western Ghana. In the dry season, we estimated a 100% pollination yield gap. Open pollination had zero yield effect in the dry season although except from 100%HP which further confirms our conclusion that cacao plantations in the study area is predominantly pollination limited. The null yield from open pollination in the dry season does not imply the absence of natural pollinators as we found similarly high diversity and abundance of flower visitors in both the dry season and the wet season (see paper at chapter 6) and therefore open for further investigation and explanation. While this is the first pollination -limited yield estimate in the study area, the findings more importantly suggest that with proper management that support efficient pollination systems, farmers could potentially benefit from two yearly harvest cycles.

5.6 CONCLUSION

In the study we have shown that *T. cacao* is pollination limited in the study area and discussed landscape and abiotic factors that are important to pollination limited yield. Pollination and seasonality (wet season) were the best predictors of pod yield. Understory light alone and its interaction with canopy light were also important explanatory variables for pod production. However, canopy light alone was not significant. With regards to the vegetation surrounding plantations, homogenous vegetation was associated with higher pod output compared to complex vegetation typology. Natural pollinators achieve 43% of yield leaving a pollination-

limited yield gap deficit of 56%. Dry season yield was non-reliable on natural pollinators and farmers may have to rely completely on hand pollination labour. However, the study suggest that interventions that conserve pollinator diversity and abundance and improve flower visitation rates may not only enrich ecosystems services on plantations but likely benefit economic yield outcomes.

6 FLOWER VISITOR ABUNDANCE, DIVERSITY AND NETWORKS IN *THEOBROMA. CACAO*

Paper two of this thesis established that the cacao plantation study sites in Western Ghana experience pollination limitation. Thus, developing plantation management systems to improve pollination services will be critical to improving cacao yield, and economic and ecological sustainability in Western Ghana. To develop evidence-based, pollinator-focused, management interventions, we need to fill knowledge gaps regarding the biotic agents involved in pollination services. The currently known cacao pollinators belong to the Diptera insect Order. Yet, recent surveys demonstrate that other taxa also visit cacao flowers, may provide pollination services, and in some cases are more frequent visitors than the Dipterans. These new insights open questions about (1) the diversity of taxa visiting cacao flowers, (2) biotic and abiotic factors that affect the taxa visiting the flowers, (3) the ecological relationships between the flower-visiting taxa, and (4) which flower visitors are functional pollinators. This chapter addresses the first three of these questions and from a deductive and empirical conjecture, propose the functional mechanism of a candidate pollinator.

FLOWER VISITOR ABUNDANCE, DIVERSITY, AND NETWORKS IN *THEOBROMA CACAO*

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6.1 Abstract

Pollination is a vital ecosystem service in both wild and cultivated landscapes and underpins some USD 350 billion in annual global agricultural production. *Theobroma cacao* L. is pollination limited. However, cacao pollination ecology remains poorly understood, especially the functional roles of the diverse cacao flower visitors. Understanding the diversity and ecology of cacao flower visitors is essential to developing production systems that optimize pollination and therefore yield. Such systems are also likely to have positive knock-on effects for other ecosystem services. Dipterans have long been associated with cacao pollination

services. However, recent surveys show that other taxa also visit cacao flowers, may provide pollination services, and in some cases are more frequent visitors than the Dipterans. Here, we report on the diversity and abundance of cacao flower visitors from eight cacao plantations in Western Ghana. Of 3,025 flowers sampled, we identified nine insect and two arachnid orders across the dry and wet seasons. Insect visitors of the Thysanoptera (thrips) were the most abundant, followed by the Dipterans (flies, midges). Alpha diversity of flower visitors was best predicted by the vegetation immediately surrounding study plots, followed by canopy shade and season. The abundance of flower visitors was best explained by canopy shade, seasonal moisture, and the vegetation immediately surrounding study plots. Network analysis revealed an arthropod trophic network functioning within individual cacao flowers. In addition, thrips-Dipteran co-occurrence is found to form the primary core of the flower-visitor assemblage and is therefore expected in theory to influence network stability. Furthermore, thrips emerge as the most influential taxa of the cacao flower-visitor network, likely involved directly and or indirectly in cacao pollination.

Keywords: cacao, flower visitor networks, thrips pollination, co-occurrence,

6.2 Introduction

Pollination is a vital ecosystem service in both wild and cultivated landscapes, and underpins some USD 350 billion (Lautenbach et al., 2012) in annual global agricultural production. Unfortunately, unsustainable land use practices have resulted in the decline of pollination services globally (Ghazoul, 2005; Kevan and Viana, 2011). Recent studies suggest it is possible to maintain high biodiversity in human-modified landscapes (Wanger et al., 2020; Malhi et al.,

2022), and that biodiversity in economically active landscapes can enhance economic outcomes (Vansynghel et al., 2022c). These accounts suggest there is the opportunity for a paradigm shift, where ecosystem functions are expected to persist within, and are considered an integral part of, economically active landscapes. To develop evidence-based, pollinator-focused, management guidance, we need to address knowledge gaps about the ecology and diversity of biotic agents involved in pollination services for crops of interest.

Theobroma cacao L. (Malvaceae) is the foundation of the USD 100 billion global chocolate market (Potts et al., 2014), a market forecast to expand to USD 1.33 trillion by 2027 (Statista, 2022). Most cacao varieties exhibit self-incompatibility, in this case, sporophytically controlled non-fusion of gametes that results in fertilization failure (Cope, 1958; Lanaud et al., 2017b). Thus, most cacao varieties are dependent on insect-mediated cross-pollination. Understanding cacao pollination is therefore vital to optimizing yield for this globally important commodity.

The Amazonian origins of cacao and its relatively recent introduction to Africa and Asia suggest the history of co-evolution of local pollinator species might be recent. Although the Ceratopogonidae midges have long been known as cacao flower visitors (Kaufmann, 1975a, 1975b), there is increasing evidence that a diverse range of taxa visit cacao flowers (Toledo-Hernández et al., 2017, 2021b; Chumacero et al., 2018; Vansynghel et al., 2022b). For instance, in Bolivia, parasitoid wasps (Hymenopteran) were the most abundant flower visitors in both wild and cultivated cacao groups (Chumacero et al., 2018). In seasonally dry, semi-arid Northern Peru, aphids (Hemiptera) were the most abundant flower visitors, followed by ants (Hymenoptera). Whereas in moderately humid southern Peru, thrips (Thysanoptera), followed

by various Diptera were the most abundant (Vansynghel et al., 2022a). Vansynghel et al. (2022b) suggest that of the flower visitors reported, the Thysanoptera group rivals the Dipterans as candidate cacao pollinators. Moreover, because cacao originates in South America and is relatively recently introduced to Africa and Asia, we might expect different taxa as flower visitors outside of South America. For example, a survey of flower visitors from Central Sulawesi, Indonesia, showed high abundance of ants (Formicidae), followed by various Diptera (Toledo-Hernández et al., 2021b).

Observation of a species visiting a flower does not prove pollination function (Mound, 2005). However, other methods of confirming pollination function for cacao have proven difficult. For example, studies that have tried to directly identify cacao functional pollinators by quantifying pollen carried on the insects' bodies or by visitor abundance have been unsuccessful, even for Ceratopogonidae and Cecidomyiidae, although they are commonly associated with cacao pollination (Vansynghel et al., 2022a). It is important to note, moreover, that even if a flower visitor is not a direct pollinator, it could indirectly improve pollination efficiency. For example, higher functional group richness in flower visitors has been shown to enhance pollination service through complementarity in radish (Albrecht et al., 2012). Although to date, no study has described a strategy in cacao where pollination is achieved by several flower visitors working in concert, as was shown for radish; the combination of a highly diverse and variable suite of cacao flower visitors, and lack of a direct correlation between flower visitation and effective pollination, suggests that cacao pollination may be a more nuanced and complex process than previously described.

Developing plantation management systems to improve pollination services will be

critical to improving cacao yield, and economic and ecological sustainability. To develop evidence-based, pollinator-focused, management interventions, we need to address knowledge gaps with regards to the biotic agents involved in cacao pollination. Specifically, we do not know which of the taxa are functional pollinators, which may not be direct pollinators but may play other key roles in cacao pollination or ecology, and the ecological requirements of many of these flower visitors. This study begins to address these knowledge gaps by asking the following questions at our study sites in Western Ghana:

1. What are the flower visitors of cacao and their abundance at the study sites?
2. How do abiotic, landscape and site factors affect the diversity and abundance of flower visitors?
3. Are there relationships among the flower visitors?

6.3 Materials and methods

6.3.1 Study site and specimen sampling

Eight cacao plantations located near Tarkwa-Breman in the Prestea-Huni valley district in Western Ghana (Figure 1) were selected for this study. The study region is characterised by a mean annual rainfall of 187mm, average annual temperature of 30°C, and 80% humidity, with hilly, evergreen tropical rainforests. The area is home to three national forest reserves; Bonsa, Ben West and Nkontoben (Prestea/Huni valley district, 2014; Wiafe et al., 2022). The mineral-rich underlying geology means that the region supports high value commodity production, including coffee, cacao and rubber, and contains several active mining operations.

Eight plantation study sites were selected based on two distinct landscape factors: canopy shading and complexity of vegetation surrounding farm plots. A 40 m x 40 m experimental plot was established in each plantation. Shaded plots had a minimum of six large shade trees above the cacao canopy that covered approximately half of the 40 x 40m plot. In unshaded plots the cacao trees were fully exposed to open sun. The two levels of surrounding vegetation complexity were 'homogeneous' and 'heterogenous'. 'Heterogenous' indicates that the vegetation surrounding the cacao plantation was multi-strata and high floral diversity (e.g., secondary forest or wetland). 'Homogenous' vegetation surrounding a plantation indicates there were only one or two species and no vertical stratification (e.g., grass, meadow or agricultural monoculture). Earlier studies have found that proximity to forest did not influence pollinator visitation in cacao farms (Toledo-Hernández et al., 2021b). The rational for this new approach ('homogeneous' vs 'heterogeneous') is that, given that cacao pollinators are expected to be smaller arthropods, the habitat types that support them may be vegetation types that produce many, species-diverse flowers or that contain dense floral habit and refugia spaces, and these characteristics are not specific to forest habitats.

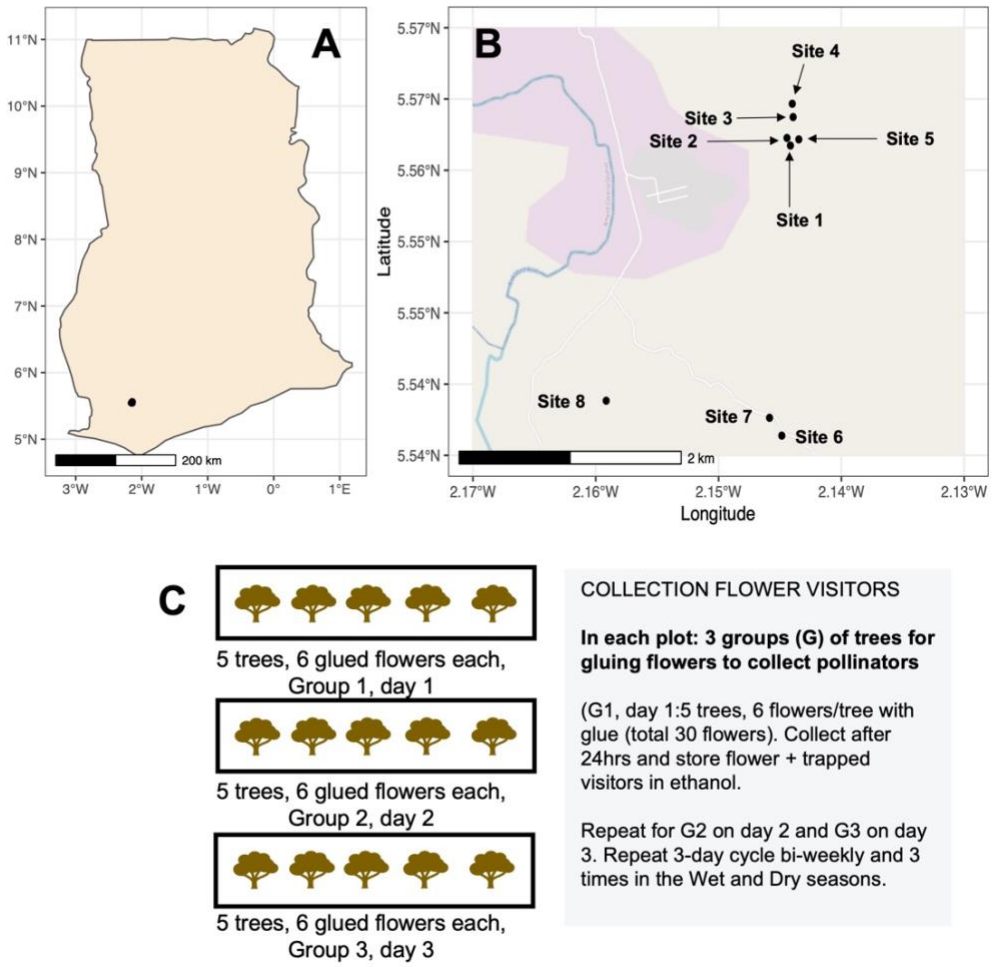

Figure 1: Location of study location in South-western Ghana (Tarkwa-Breman, 5.56173/-2.144153 lat/long) in the Prestea Huni-Valley District (A). Map of experimental sites. The purple regions represents the Tarkwa-Breman community town. Blue line represent a river and white lines represents road networks (B). Summary of flower visitor sampling (C).

Insect sampling took place between August and October during the wet season and January to March during the dry season in Western Ghana. Within each experimental plot, three groups (G1, G2, G3) of five trees were marked. On each tree, a colourless insect trapping glue (Tangle-trap® sticky coating, Tanglefoot) was put on the stamen of six flowers, for a daily total of 30 flowers per plantation. All glued flowers were collected after 24hrs and overtopped

with 98% ethanol in Eppendorf tubes with the aid of a medical syringe. The first group of five trees, G1, was glued on the first day, the second group, G2, on day two, and the third group, G3, on day three. The three-day flower gluing and collection cycle was repeated every two weeks for a total of three cycles and 270 samples per plantation across a 7-week season (wet or dry). A total of 2160 samples were collected for the eight plantations during each season, wet and dry, giving a grand total of 4320 samples collected. Samples were tightly sealed for storage, pending specimen identification.

6.3.2 Specimen identification and imaging

All collected specimen were shipped to Oxford, UK, for identification. First, a specimen was placed in a petri dish and inundated with ethanol. The specimen was morphotyped with the aid of a dissecting scope attached to a halogen light source at the Plant Sciences Department

Herbarium. In consultation with expert arthropod taxonomists[1], and technical manuals, most specimens were identified to the Order level. A higher resolution Leica stereomicroscope with accompanying imaging software from the Oxford University Museum of Natural History was used to confirm detailed features useful for specimen identification and to capture 2-dimentional images of the specimens for analysis.

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[1] Specific acknowledgement and thanks are due to Dr James Hogan, Collections Manager, Hymenoptera and Lepidoptera at the Oxford Museum of Natural History, for his support in insect identification.

6.4 Data analysis

6.4.1 Flower visitor identity and abundance

The list of identified flower visitors was used to calculate abundance per taxa. In this study, collected specimens were identified to the Order level and groups were compared at this level. Hence, 'abundance' here refers to the number of individuals within an Order and 'relative abundance' refers to the proportion of a particular Order to the total of the other Orders present at a given site. Heavy-tailed distributions were Gaussian transformed to normal distributions using the *'LambertW'* R package (Goerg, 2011, 2015, 2022).

6.4.2 Effect of abiotic, landscape and site factors on flower visitor diversity and abundance

6.4.2.1 Alpha diversity

Alpha diversity is defined as a measure of discrete variables that account for the number of individuals of different taxa in a community (Thukral, 2017). The four commonly used alpha diversity indices in Ecology; Shannon-Wiener, Simpson's, Species richness, and Pielou's Evenness, were calculated from a matrix of species abundance data using the *vegan*, version 2.4-6 package (Oksanen et al., 2022) in the R programming software (R Core Team, 2022). The data consisted of total abundance of each taxon identified in the study plots. A numeric score was generated to show the diversity score of the plot.

The Shannon index, also referred to as Shannon-Wiener, is an entropy function, H,

that indicates a set of probabilities that define the chances of occurrence of a finite state space (Shannon, 1948). The index is calculated as:

$$\mathrm{H} = -\mathrm{K}\sum_{i=1}^{s} p_i \, log_b \, p_i \qquad [1]$$

where, K is a positive constant which is unity for ecological application, and p_i is the probability of the state. H is the uncertainty probability for approximating reproducibility of information that has statistical homogeneity property in the field of communication theory (Shannon, 1948). Thus, H is a reliable metric of diversity of taxa across a sampled community whose population is unknown but nevertheless, has similar distribution of residuals as the assumption of homogeneity. In community ecology, H measures diversity of species in a sampled population where p_i, is the proportion of species i , S is the number of species, and b is the base logarithm.

Simpson's index, D_1 estimates the probability that two individuals chosen at random and independently from a population belong to the same group (Simpson, 1949). This is denoted as:

$$D = 1 - \sum_{i=1}^{s} p_i^2 \qquad [2]$$

This diversity gives an indication of the number of species that dominate an assemblage (Magurran, 2021).

Richness S, is the most applied diversity indicator (Magurran, 2004), and represents the

number of individuals or attributes in a defined region (Whittaker, 1972). Lastly, Pielous's Evenness, J, measures how abundance of a taxa is distributed across the community. Thus, evenness approaches zero when the presence of all species is variable and is highest when all species are represented in a sample. J is calculated as:

$$J = H'/\log(S) \quad [3]$$

Where J is evenness, H' is the Shannon Weiner diversity and S is species richness.

All data was graphically presented using the ggplot2 suite in the R programming environment (Wickham, 2016b).

6.4.2.2 Factors affecting diversity of flower visitors

To determine whether abiotic, landscape, or site factors affect the diversity of flower visitors at the study sites, linear mixed effects models were applied. Alpha diversity indices were designated as the dependent variables. Independent variables were vegetation surrounding the plots with two factor levels: homogenous and heterogenous; canopy light with two factor levels: shaded and non-shaded; and seasonality with two factor levels: dry and wet seasons. See section 6.3.1 above for description of surrounding vegetation and canopy light.

All independent variables were denoted fixed effect variables. Each diversity index was modelled separately with plot designated as a random effect variable. Modelling was performed using the *lme4* package with restricted maximum likelihood (Bates et al., 2015). The '*drop*' function in R was used to eliminate the variables with the least effect. The best

model was chosen based on the Akaike Information Criterion (AIC), with the *'aictab'* function from the *AICcmodav* package in R. To determine how diversity varied across the eight study sites, an ANOVA was performed on plot level diversity indices.

6.4.3 Flower visitor networks

Network analysis is a heuristic approach that allows researchers to overcome the computational limitations of establishing clear hypothesis or acceptable causality from complex interaction data (Pereira et al., 2021). In biology, the approach has been used in applications as diverse as identifying drug targets for diseases (Melak and Gakkhar, 2015), analysis of protein function (Vazquez et al., 2003; Deng et al., 2012), investigating ecological complexity (Thébault and Fontaine, 2010; García-Algarra et al., 2017), elucidating ecological community structure (Deng et al., 2012), and predicting and revealing the architecture of ecological interactions such as pollination networks (Thébault and Fontaine, 2010).

Complex systems such as plant-animal interactions can be best described by network topology analysis (Albert-László and Réka, 1999). The data are organized as "nodes" (= actors), and "edges" (= relationships). To identify influential nodes and edges within the network, a combination of network centrality metrics was used. There are approximately 403 centrality indices implementable across multiple computational software packages and platforms (Jalili et al., 2015), which poses a challenge for selecting the right metric for a given study. Currently there is no clear-cut approach for deciding the best centrality metric and researchers use a range of approaches including principal component analysis (Vignery and Laurier, 2020) and correlation of matrices (Rothenberg et al., 1995; Batool and Niazi, 2014).

A culling technique has recently been proposed as a guiding algorithm for selecting a centrality metric but is yet to be broadly accepted into practice (Chebotarev and Gubanov, 2023).

To answer our Question 3, "Are there functional relationships among the flower visitors?", a Flower visitor Network (FN) was built using flower visitor frequency and visitor co-occurrence data. Flower visitor taxa were designated as the network 'nodes' and co-occurrence frequency data were used for 'edges'. The FN structure, properties, component relationships, and the essentiality and functionality of key components were explored using network topology statistics (see below) alongside visualization layout algorithms implemented in the Gephi 0.9.7 model software (Bastian et al., 2009), ForceAtlas2 (Jacomy et al., 2014) which uses a force repulsion for network spatialization, and the Radial Axis layout algorithm (Groeninger, 2011) to study homophily by spatial distribution of nodes.

The following network topology, node and edge characteristics, and centrality metrics were employed to identify functional relationships among the flower visitors:

6.4.3.1 Betweenness centrality

Betweenness centrality, C_{bt}, measures the degree to which a point falls on the shortest path between other nodes and therefore has a potential for control of information flow (Freeman, 1977). C_{bt} captures how much a given node (say f) is in between other nodes and measured by the number of shortest paths between any couple of nodes in the graph that passes the target node (Perez and Germon, 2016). C_{bt} quantifies the capacity of a node as a bridge to connect any node pair in a network. Thus, C_{bt} measures the importance of a node in connecting other network nodes(Bloch et al., 2023). In biological networks such as protein networks, C_{bt} has

been used to show the relevance of a protein in maintaining functionality and coherence of a signalling mechanism (Pereira et al., 2021). Nodes with the highest C_{bt} function like a broker/mediator through whom other nodes in networks must pass to negotiate a service (Wai and Thu, 2015) or the capacity of a node to connect to different graph regions (Jensen et al., 2016). In a flower visitor network, where f denotes flower visitor node, and f_1, f_2,… f_n represent different taxonomic groups of flower visitors, Betweenness Centrality of node is denoted:

$$C_{bt}(f) = \sum_{f_1 \neq f_2 \in f} \frac{\sigma_{f_n(f)}}{\sigma_{f_n}} \quad [4]$$

Here, $\sigma_{f_n(f)}$ is the number of shortest paths that passes through the target node, f and is normalized by σ_{f_n} which is the total number of shortest paths existing between any couple of nodes of the graph. The target node with the highest C_{bt} will mean it appear in many shortest paths.

6.4.3.2 Bridging Centrality

Bridging Centrality C_{br} (Hwang et al., 2008) combines Betweenness Centrality, C_{bt} and Bridging Coefficient, BC (see thesis methods section 3.9) to characterize nodes that act as bridges in networks (Pereira et al., 2021). $C_{br}(f)$ for node representing insect visitor group, f is defined by:

$$C_{br}(f) = BC(f) \times C_{bt}(f) \quad [5]$$

6.4.3.3 K-core decomposition

k-core decomposition (Seidman, 1983) is a topology filtering algorithm used to prune the least connected vertices in a network. The method is used to identify the central core of a network in which all nodes are connected to at least *k* other nodes in the subnetwork thus eliminating all nodes -*k* networks. *K-core* is one of the most widely used methods to detect network structure in network sciences (Kong et al., 2019) and has previously been applied in molecular biology to predict the functional-unknown proteins in protein-protein interactions (Altaf-Ul-Amine et al., 2003), and in ecology to identify key species that preserve richness, and the 'giant component' in mutualistic networks (the connected component of a network that contains a significant proportion of all the nodes in the network) (García-Algarra et al., 2017).

Other centrality metrics considered in the analysis of results in this paper three are described in chapter 3.9 at the Network analysis section.

6.5 Results

Question 1: Flower visitor identity and abundance

Of the 4,320 flowers treated with glue for flower visitor trapping, 3,025 samples (70%) were recovered. Flowers that were detached and displaced from trees by wind, rain or other mechanisms were not recovered. Of the 3,025 samples, 1,373 flowers had flower-visiting arthropods belonging to nine subgroups of Insecta class and two subgroups of the Arachnida class. Eleven specimens could not be identified because they were either damaged or had lost

body parts and therefore difficult to recognize, and thus were labelled, ‘unknown’.

Across both sampling seasons, the Thysanoptera (thrips) were highest in abundance, followed by Diptera (Fig 2). Across study sites, the abundance of thrips and Diptera varied, but was always greater than the other taxa, both in the wet and dry seasons (Figs 3 & 4). For instance, in Plot 6, thrips and dipterans were the most abundant taxa in both the wet and dry seasons, but during the dry season there were approximately seven-fold more thrips individuals sampled than during the wet season (Figs 3 & 4). The low abundance in plot 5 (Fig 3) is the result of missing data. As explained in the general methods (section on missing data imputation), flooding at the site during the wet season made the plot completely inaccessible. Unlike pollination data, imputation here was not feasible but analytically permissive. Note that plot 5 is excluded in biodiversity indices for wet season (Fig 5).

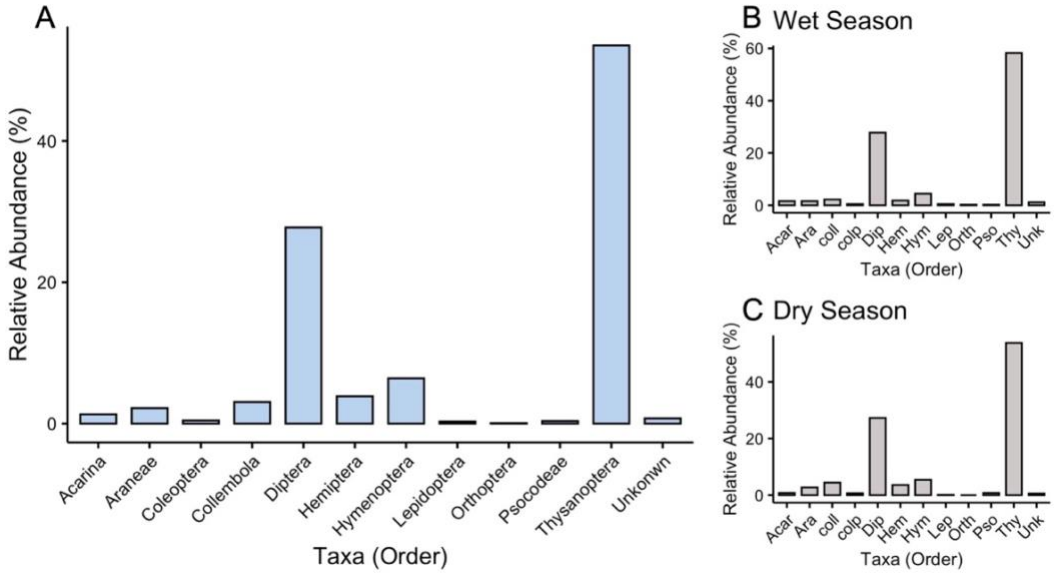

Figure 2: Abundance of flower visitors by Order, Wet and Dry Seasons combined (A). Cacao flower visitor abundance in the wet (B) and dry (C) seasons by Order. All data obtained from eight experimental sites in Tarkwa-Breman, Western region of Ghana.

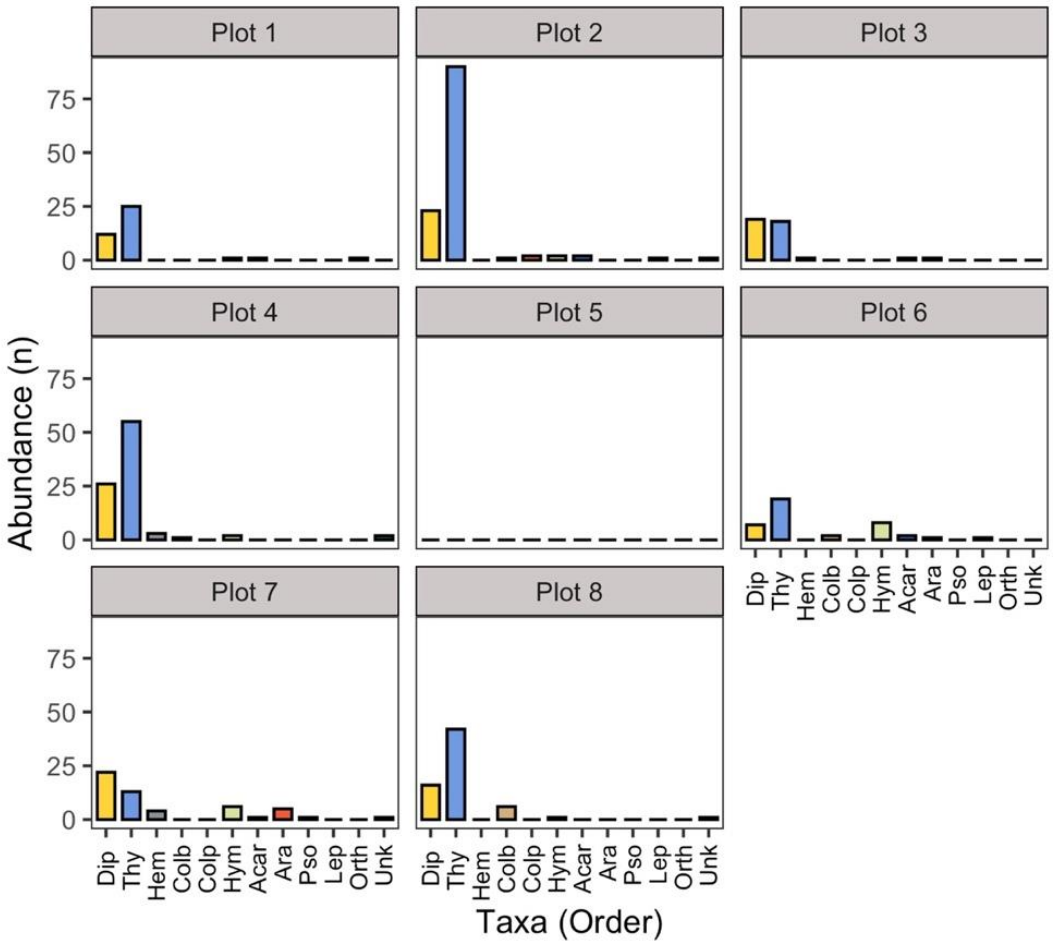

Figure 3: Cacao flower visitors in the wet season by Order from eight experimental sites in Tarkwa-Breman, Western region of Ghana.

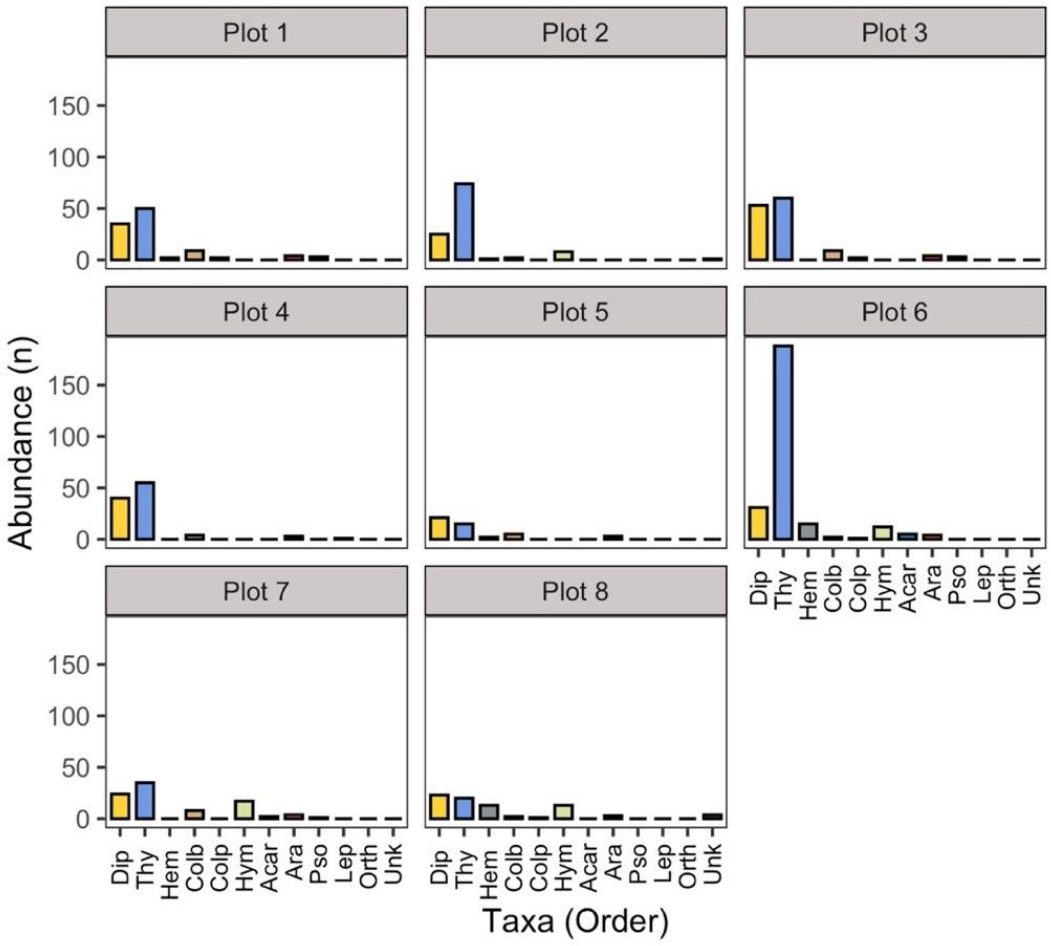

Figure 4: Flower visitor abundance during the dry season by Order from eight experimental sites in Tarkwa-Breman, Western region of Ghana.

Question 2: Effect of abiotic, landscape and plot on flower visitor diversity

Across the eight study sites and the wet and dry seasons, alpha diversity did not statistically differ (Table 1, Fig 5). The best mixed effect model for taxa abundance included surrounding vegetation, canopy shade, and wet season (an indication of moist conditions) (Table 2). The best model for species richness included both canopy shade and surrounding

vegetation (Table 2). The models for Shannon, Simpson and Evenness diversity indices were only explained by the vegetation surrounding the plots (Table 2). Thus, the type of vegetation immediately surrounding the farm was important across all biodiversity indicators considered.

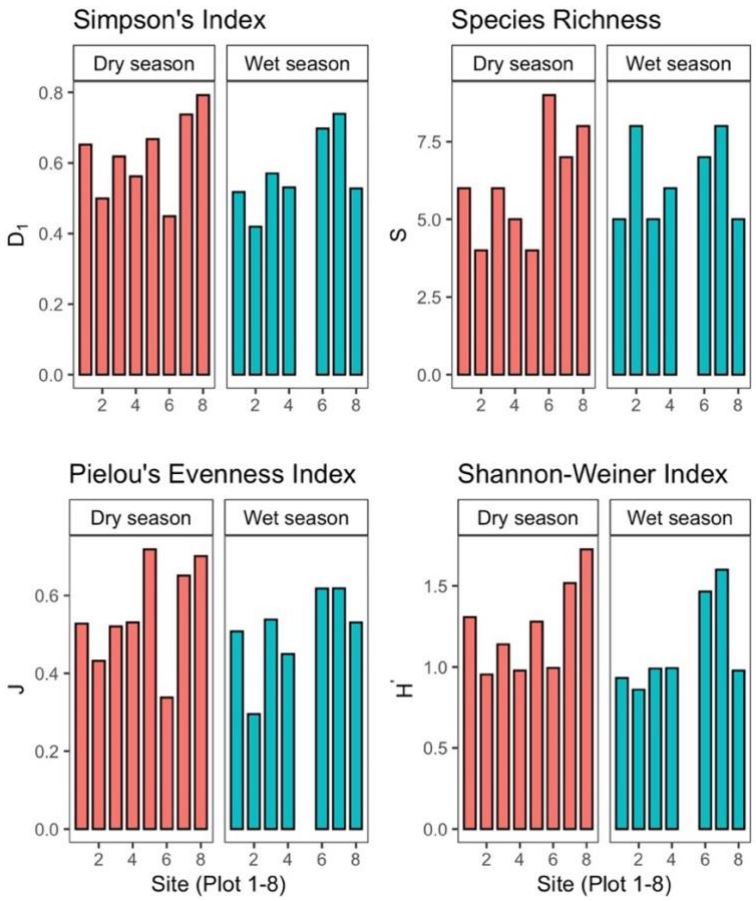

Figure 5: Biodiversity indices at sites for wet and dry season. Each bar indicates calculated diversity score per site from species abundance data. Diversity indices for sites are not statistically different between the wet and dry seasons. Missing bar in the wet season plot indicate missing plot data.

Table 2. ANOVA differences in alpha diversity indices across eight plantation sites at 95%CI.

Index	Var	DF	Sum Sq.	Mean Sq.	F value	Pr (>F)
Shannon, H'	Site	7	1.074	1.535	1.105	0.441
	Season	1	0.213	0.2134	1.665	0.238
Simpson's, D_1	Site	7	0.1712	0.02446	1.742	0.227
	Season	1	0.0007	0.00071	0.45	0.839
Richness, S	Site	7	38.8	5.543	1.893	0.195
	Season	1	1.16	1.160	0.365	0.565
Pielou's Evenness, J	Site	7	0.13652	0.0195	2.025	0.186
	Season	1	0.00149	0.001488	0.135	0.725

Table 3. Anova and AIC output of full and optimal Linear Mixed Effects Models. Abundance and alpha diversity indices are dependent variables. Surrounding plot vegetation, canopy light and season are explanatory variables.

Full Model					**Optimal model**			
	Co-eff	t-value	Pr(>|t|)	AIC	Co-eff	t-value	Pr(>|t|)	AIC
Abundance								
A-Surrounding vegetation (homogenous)	-20.962	-0.592	0.57127	141.87	-12.557	-0.579	0.58748	141.87

B-Canopy light (shade)	18.728	0.638	0.55815		43.744	2.018	0.09960.	
C-Season (wet)	-40.458	-1.446	0.19825		-57.068	-2.948	0.02148*	
A: B	50.031	1.205	0.29455					
A: C	-33.220	-0.840	0.43326					
Richness, S								
A-Surrounding vegetation (homogenous)	0.1251	0.057	0.9564	70.3	0.186	0.146	0.888	70.28
B- Canopy light (shade)	0.9872	0.501	0.6430		-	-		
C-Season(wet)	-0.2557	-0.189	0.8562		-	-		
A: B	0.6869	0.246	0.8176					

A: C	-0.5657	-0.296	0.7773					
Shannon, H'								
A-Surrounding vegetation (homogenous)	-0.03089	-0.076	0.942	30.91	0.0265	0.125	0.904302	25.76
B-Canopy light (shade)	0.08266	0.229	0.830		-	-	-	
C-Season (wet)	-0.37416	-1.435	0.201		-	-	-	
A: B	-0.17155	-0.336	0.754		-	-	-	
A: C	0.28633	0.777	0.467		-	-	-	
Simpsons, D_1								

A-Surrounding vegetation (homogenous)	0.02757	0.297	0.7761	2.87	0.08721	1.139	0.298	-4.751
B-Canopy light (shade)	-0.06182	-0.754	0.4927		-	-	-	
C-Season(wet)	-0.14166	-2.296	0.0615.		-	-	-	
A: B	-0.13741	-1.186	0.3014				-	
A: C	0.25668	2.941	0.0259*		-	-	-	
Evenness, J								
A-Surrounding vegetation (homogenous)	0.09325	0.843	0.432517	2.39	0.06189	0.822	0.444513	-6.63

B-Canopy light (shade)	-0.03375	-0.347	0.747206	-	-	-
C-Season(wet)	-0.07759	-1.103	0.317823	-	-	-
A: B	-0.15834	-1.116	0.325672	-	-	-
A: C	0.11852	1.124	0.307070	-	-	-

Question 3: Relationships among the flower visitors

In the flower-visitor network (FN), both thrips and Diptera distinctively ranked higher with respect to degree (Fig 6A), authorities (Fig 6B), and by network eigenvalue centrality (Fig 6C), meaning thrips and Diptera are the most influential and well-connected nodes in the entire cacao arthropod network. Moreover, thrips and Diptera constituted the largest distinct network Hubs and connectivity amongst the arthropod taxa (Fig 7A, B). Furthermore, thrips and Diptera had the highest co-occurrence frequency indicated by the colour intensity of connecting node edges (Fig 7). However, thrips emerge as the single most influential taxonomic group in the arthropod network with highest Betweenness Centrality (Fig 7C), which measures the number of times a node lies on the shortest path between nodes and controls the flow of information or resources (Freeman, 1977).

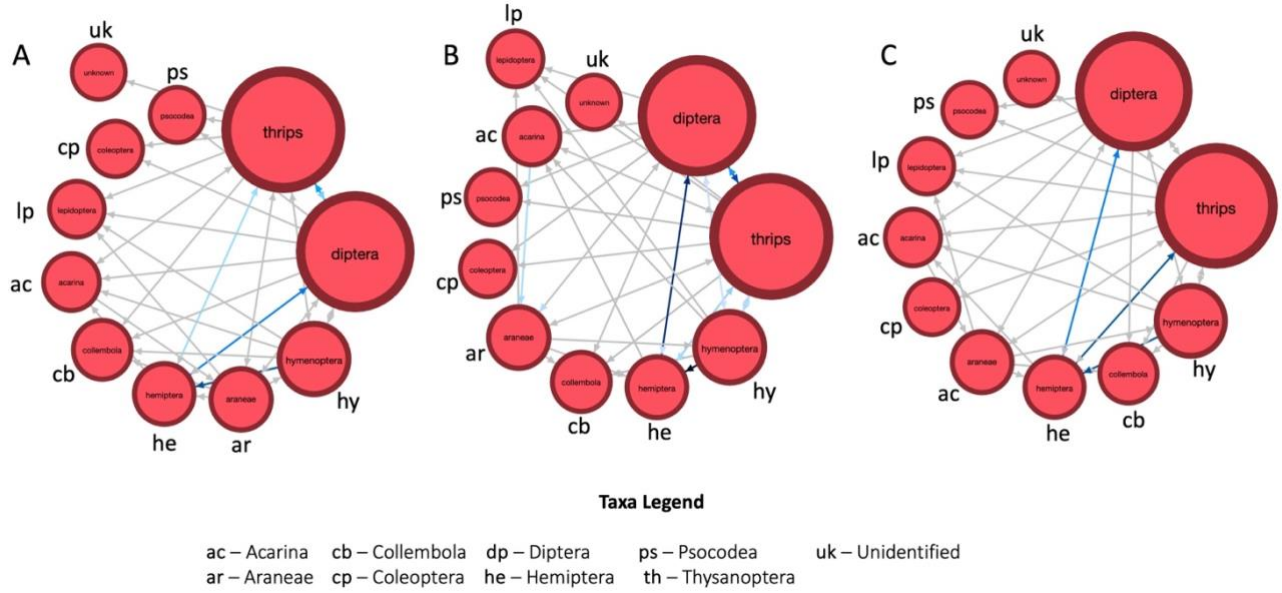

Figure 6: Radial Axis Layout of Flower-visitor network. Circles are nodes and arrows are edges. Networks are grouped and ordered by the network attributes: Degree (A), Authority (B), and Eigenvector Centrality (C). Edges indicate the total number of arthropod visitors per flower, where grey = 2-3 visitors, light blue = 4-6 visitors, sea blue = 7-9 visitors and deep blue = 10-17 visitors.

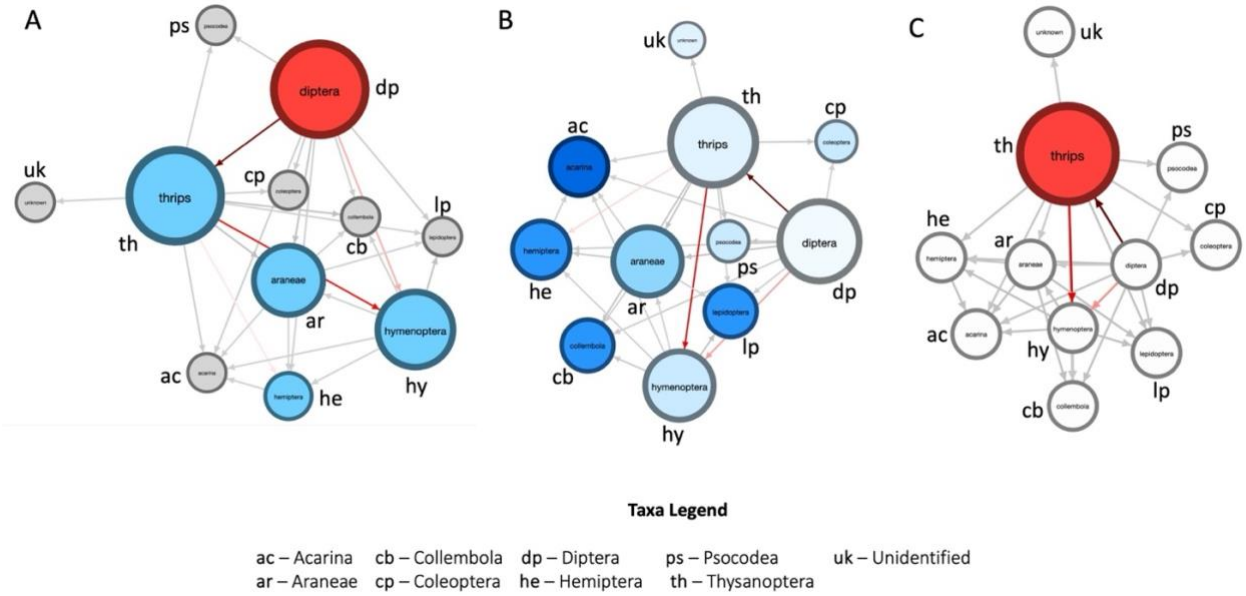

Figure 7: A ForceAtlas 2 layout of co-occurring arthropod network. Circles are nodes and each node represent a taxonomic Order. Arrows are edges which indicates the frequency with which the connected taxa were found to co-occur within individual sampled flowers. (A) Node size weighted by Hub score, node colour indicates Closeness Centrality (0=grey, 1=blue, 0.91=red), and edges indicate co-occurrence frequency (grey= 1-7; increasing red scale = 11, 16, 27 and 123). (B) Node size by weighted Degree, node colour indicates network Authority, and edges indicate co-occurrence frequency (grey= 1-7, increasing red scale = 11, 16, 27 and 123). (C) Node size indicates Betweenness Centrality, node colour indicates Bridging Centrality, C_{br} (red = C_{br}, white = no C_{br}), and edges indicate co-occurrence frequency (grey= 1-6, increasing red scale = 15, 25 and 121).

To elucidate the structural complexity of FN, we decompose FN into all plausible sub-network units using the *k*-core decomposition algorithm. Here, the cacao study system reveals nine arthropod subnetwork structures in which thrips and Diptera emerge as the constitutional primary core of the cacao arthropod network at a decomposition constant, $k = 44$ (Fig 8H). The second ranked network structure is a Hymenoptera-Diptera-Thrips network (Fig 8G) followed by a 5-taxa network which introduces the Hemiptera and Araneae groups, commonly known

for predation (Fig 8F). However, unlike the Araneae, the Hemiptera node connects strongly by edge degree, authority, and eigenvector centrality with the thrips, Diptera and Hymenoptera (Fig 7).

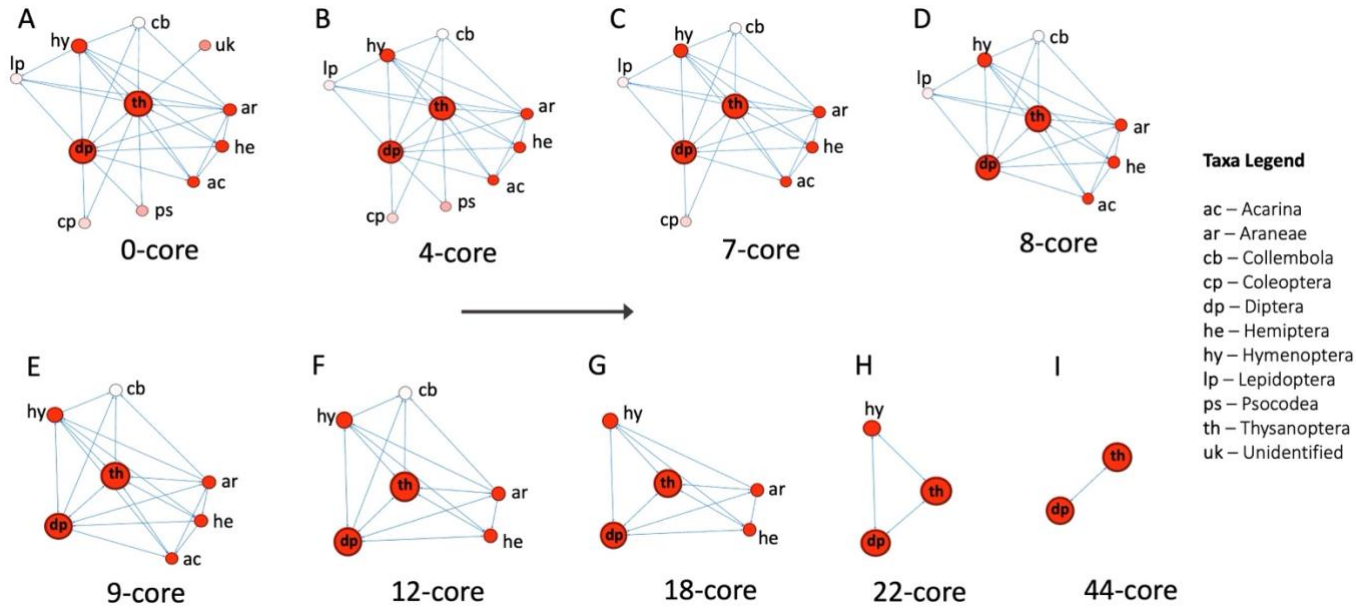

Figure 8: Decomposition of arthropod network by increasing k-core constant. Node size is ranked by node degree (total connections). Nodes are colour partitioned by Strength of Connectedness. The *0*-core (A) is the baseline network structure. (B) to (G) are network cores that can exist in the cacao study systems. (H) Diptera-Thrips network forms the primary network core of the cacao study system. Diptera = dp, Thrips = th, Hymenoptera = hy, Araneae = ar, Acarina = ac, Hemiptera = he, Unknown = uk, Psocodea = ps, Coleoptera = cp, Collembola = cb and Lepidoptera = lp.

6.6 Discussion

Question 1: Flower visitor identity, abundance and biodiversity driving factors.

Across the eight sites surveyed, flower visitors that belong to 11 arthropod taxonomic orders were identified. Of these, thrips and Diptera accounted for approximately 60% and 25% of flower visitors respectively. The trend in relative abundance of thrips and Diptera was consistent across the wet and dry seasons, although there were a few exceptions at specific sites where Diptera were slightly more abundant than thrips (dry season plot 3, Fig 4; wet season plots 5 and 7, Fig 5).

An earlier study in Ghana near the Bobiri forest reserve (appx. 205km from current study area) reported only Diptera and Hymenoptera as cacao flower visitors (Adjaloo and Oduro, 2013). While this could suggest a shift in cacao flower visitor biodiversity in Ghana, a recent survey in Peru found that cacao flower visitor diversity and abundance can vary between locations in the same region (Vansynghel et al., 2022b). Differences in cacao flower visitor abundance and diversity between sites have also been reported in Bolivia (Chumacero et al., 2018) and Indonesia (Toledo-Hernández et al., 2021b). However similar to our results, thrips were found to be the abundant flower visitor in Southern Peru, although this was not the case in Northern Peru (Vansynghel et al., 2022b).

In their review, Toledo-Hernández et al. (2017) suggested that cacao flower visitors yet to be identified may play a key role in cacao pollination. As a result, management interventions that solely promotes pollination services by a selected sub-set of recognized pollinators may jeopardise the potential benefit of having all functionally relevant flower visitors present. Henceforth, identification of cacao flower visitors is an important first step for improving both understanding of cacao reproductive ecology, and implication of on cacao pollination management.

Question 2: Factors affecting flower visitor diversity.

Flower visitor abundance was explained by the type of vegetation that surrounded farms, canopy shade and season, with a positive correlation with the wet season. The diversity of flower visitors did not vary significantly across the study sites and did not differ across the wet and dry seasons. However, flower visitor species richness was best explained by canopy shade and surrounding vegetation, whereas the Shannon, Evenness and Simpson diversity indices were explained by only surrounding vegetation, and specifically had a positive correlation with homogeneous.

It has been suggested that the taxonomic diversity and abundance of cacao flower visitors is likely to be driven by local abiotic factors such as light environment as well as seasonality, rather than biotic factors (Vansynghel et al., 2022a). As an example, in Bolivia, site location and variation in local climate explained flower visitor diversity and abundance, but there was no difference in diversity between wild and cultivated cacao tree varieties (Chumacero et al., 2018). In this study, light environment (canopy shade) and seasonal moisture explained flower visitor abundance, but abiotic factors did not explain alpha diversity indicators except species richness, for which canopy shade was important. Contrary, the homogenous vegetation type surrounding cacao farms was an important explanatory variable across all alpha diversity models.

Cacao flowers are small (~1cm) and expected to attract pollinators inconspicuously small enough to maneuvered through the petal hood. These small pollinators are unlikely to travel long distances and so may require breeding and foraging sites within proximity. The homogenous or ‘simple’ vegetation cover types surrounding study sites included open grassy

patches that contain a diversity of crops and agricultural weeds, and so these sites may provide better habitat for cacao flower visitors than the relatively bare understory of closed canopy forest. The ground covering meadows and weedy understory farm grasses appeared to have flowers within the size range of cacao flowers and might serve as alternative foraging source of nectar and or pollen. Other studies have found that wildflower resources in crop fields improve crop flower visitation (Blaauw and Isaacs, 2014; Ganser et al., 2018; Ratto et al., 2021), and that these non-crop flowers provide alternative food resources outside the crop flowering season (Carvalheiro et al., 2010). These may be the same relationships that explain why there was a positive relationship between 'simple' surrounding vegetation and cacao flower visitor abundance and diversity in our study.

This study investigated the influence of surrounding vegetation types on cacao flower visitation rates, rather than specifically investigating the impact of proximity of native forest. This is because previous studies that investigated the importance of forest proximity to cacao flower visitation found no relationship with cacao yields (Toledo-Hernández et al., 2021b; Vansynghel et al., 2022a). The same pattern has been found for durian and mango, and their fly and bat pollinators (Sritongchuay et al., 2016). Carvalheiro et al., (2010) also reported that proximity to natural habitat and biodiversity of flower visitors had a negative effect on pollination services for mango. In contrast to these observations, forest proximity has been found to determine flower visitation by bees in species including coffee, Rubiaceae (González-Chaves et al., 2020) Rambutan and Sapindaceae (Sritongchuay et al., 2016). Hence, there is evidence that appropriate management interventions for crop pollination will vary, depending on the crop and pollinators of interest. Morel et al., (2019) reported a negative linear

relationship between yield and the distance of cocoa tree from litter pile on cacao farm floor suggesting that proximity of litter to cocoa tree increases yield. In this thesis, the mean litter depth of plantation floor was used as proxy for farm litter and found not to be a strong predictor of cacao yield (see table 4, section 5.4.3). Previous studies suggests that litter layer depth and quantity of decaying vegetative material (Frimpong et al., 2011) and the distance to native vegetation (Young, 1986; Clough et al., 2011) impact pollinator community composition and total pollinator abundance in cacao plantations (Woodcock et al., 2019). This might be explained by relative life history distinction in behavioral activities between breeding and foraging sites. Farms surrounded by the homogenous vegetation type, such as grassy meadows that select for microarthropod flower visitors will likely attract adult cacao flower visitors as alternative or competing foraging site. Litter may serve in addition to breeding, resting site. On plantation plot #5, I observed a colony of very long appendaged mosquitoes hanging beneath an intact green cocoa leaf. However, with respect to pollination services, the homogenous vegetation may provide pollen and nectar rewards to sustain microarthropod population during on and off flower bloom season in cacao plantations in ways farm floor litters cannot accomplish. Furthermore, homogenous surroundings might explain why cacao flower visitors were similarly abundant and diverse during peak flowering in the wet and regardless of the very low flowering in the dry season.

Question 3: Relationships among flower visitors.

Here, we describe the first flower visitor network for cacao, and decompose the network structure to reveal its functional core. In the arthropod network, thrips and Diptera emerge as the essential and influential taxa groups within the network. While thrips and Diptera are the structural core of the arthropod network, the co-occurrence network suggests that thrips may play an influential role in Dipteran function as well as being the bridging taxa that connect all cacao flower visitors. This is shown in consistent high degree of co-occurrence in edges directed from Diptera to Thrips (Fig 7). Early studies of thrips visitation on cacao found that biotic and abiotic factors in relation with cacao leaf thrips (*Selenothrips rubrocinctus*) abundance in the wet season was explained by leaf nitrogen availability and environmentally induced delay in protein synthesis (Fennah, 1955, 1965). Although cacao leaf thrips are parasitic herbivores, several species of thrips are flower visitors, obligate pollen feeders and host selective (Kirk, 1985). Biles (1941) reported the first evidence of direct cacao pollination by thrips but also noted their flight behaviour inhibited their effectiveness as pollinators.

The Araneae and Hemiptera taxa, both predators, appear in the third-degree network core (Fig 8F). Of the established enemies of thrips in the tropics; anthocorids, mirids, lygaeids and reduviids, all Hemipterans, three species of mirids (genera: *Miridae*) are reported as obligate predators that prey exclusively on thrips (Myers, 1935; Callan, 1975). Kaufmann (1973) gave the first account of the involvement of spiders (Araneae) in the pollination behaviour Cecidomyiid midges and recording one or two spiders per about 150 nesting midges. These studies provide compelling evidence that Araneae and Hemiptera taxa play a predatory function. As such, the abundance of Araneae and Hemiptera and their presence in the third-degree network core, suggests there is an arthropod trophic network functioning within

individual cacao flowers. Some of the representative taxa such as thrips and collembola in the cacao network typify early Devonian terrestrial arthropod colonizing taxa (Kevan et al., 1975). Thus, our network provides essential insight that adds to currently limited data on arthropod-plant connections.

Although thrip pollination has been debated (Mound, 2005), evidence from early Cretaceous fossils suggests that thrips not only were involved in gymnosperm pollination 105 million years ago but may be the earliest insect plant pollinators (Peñalver et al., 2012). Moreover, Charles Darwin, in his seminal pollination studies, described thrips moving between flowers carrying pollen:

> *"I have seen more than once a minute Thrips, with pollen adhering to its body, fly from one flower to another of the same kind; and one was observed by me crawling about within a convolvulus with four grains of pollen adhering to its head, which were deposited on the stigma."(Darwin, 1876).*

In this study we do not provide direct evidence of thrip pollination of cacao. However, the sheer abundance of thrips as flower visitors across the eight study sites suggests that even if thrips are not direct pollinators, they are likely to influence pollination at least indirectly through their positive or negative interactions with other key flower visitors found in the network analysis, specifically the Dipterans, Araneae, and Hemiptera. In addition, the thrips are the only group for which we found evidence of long-term residence within the cacao flowers. During morpho surveys, large groups of thrips at different stages of maturation were found within individual flowers suggesting a life-cycle link in which cacao flowers may serve as habitat, breeding, nesting, or mating site at least at a stage in their life history (Fig 9 B).

Contrary, all other species appeared likely as foraging visitors.

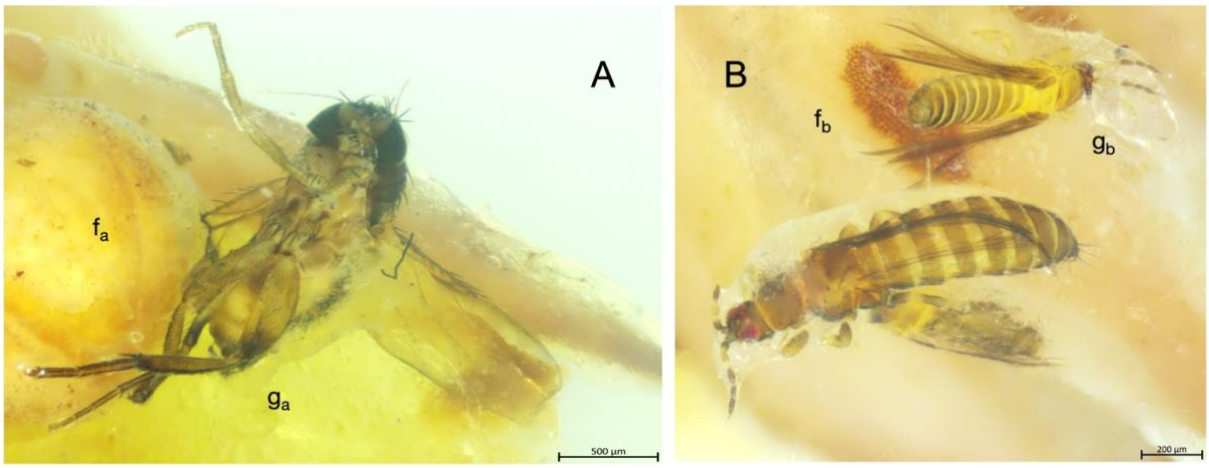

Figure 9: Stereo micrograph of the two most abundant taxa groups, (A) ventral view of a midge (Order: Diptera, Fam: Phoridae, Curtis 1833) and (B) three thrips, dorsal view (Order: Thysanoptera) at different life cycle stages. Specimens are trapped in Tangle glue, g_x and attached to flower tissue, f_x.

6.6.1 Thrips pollination in cacao

We note that cacao flowers are only open for 24 hours, and thrips have a life cycle of ~12-18 days. However, thrips deposit eggs into flower buds (Ananthakrishnan, 1993) so that thrip maturation may largely take place before the flowers open. This suggests that mature female thrips may not be active pollinators as oviposition occur in premature flowers without pollen. Nevertheless, young adults in search of new floral resources and mature males in search of mates are likely to be involved in thrips pollination. Furthermore, thrips-flower association with pollination is established to depend on host (flower) succession, resulting in continued

resource availability, which sustains thrips population build-up and leads to pollen dispersal (Ananthakrishnan, 1993). Cacao exhibits continuous flowering throughout the year, providing favorable growth conditions and ensuring pollen availability year-round. Therefore, cacao appears to be a suitable candidate host for the thrips life cycle. In our study sites, vegetation including cacao are evergreen due to rainfall during the wet season and heavy diurnal fog during the dry season. The consistent high abundance of thrips populations during the wet and dry seasons (Fig 2 B & C) strongly supports this conjecture. Lastly, thrips are considered obligate pollinators unlike bees and butterflies as they transfer pollen grains only in one species (Ananthakrishnan, 1993) most likely because their life cycle is tied to the flower host.

To contribute to the century old debate on whether cacao flower thrips visitors are involved in pollination, we have provided empirical evidence using centrality measurement, that thrips are the bridge node (Fig 7C) essential to network functionality and coherence maintenance, structural regulation and control information flow in the cacao networks. Moreover, thrips appear to form a mutualistic symbiotic relation with Diptera as likely co-pollinators and supported by additional literature on thrips involvement in pollination services.

We propose that cacao thrip pollination is a consequence of life history stage attained primarily by male thrips during mating but also likely contributed through foraging by both male and females. Female thrips deposit eggs in flower buds which serves as source nourishment juvenile thrips who matures alongside flower development. As flower opens, thrips disperse in search of new foraging sites from neighboring trees and or for mating carrying pollen.

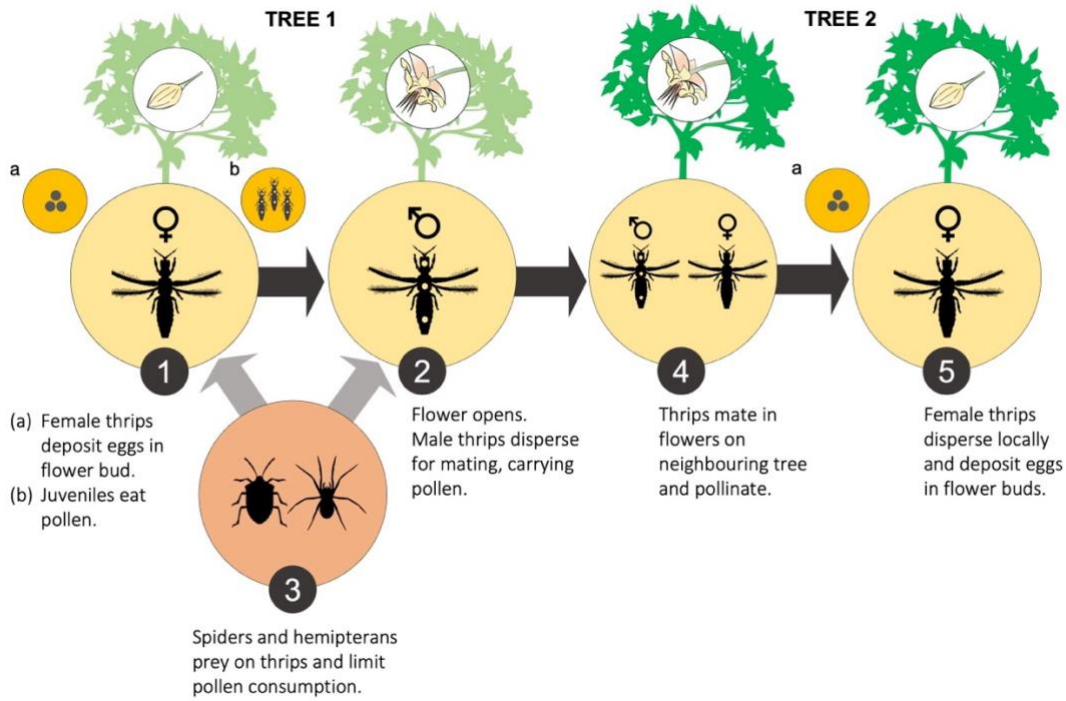

Figure 10: Illustration of ideal thrips pollination in cacao with respect to their life cycle and flower visitor network.

These observations suggest that unlike for other flower visitors, the cacao flower provides habitat that is central to thrips life history, in which they interact with other arthropod visitors as 'resident' hosts. Early Cretaceous evidence of sub-sociality behaviour in thrips supports the likely social behaviour of cacao thrips (Kevan et al., 1975). In our survey, in some cases, several thrips' nymphs were present on the same flower. Despite the low level of natural pollination in cacao and Dipterans consistently implicated in all cacao flower visitor surveys, thrips, since its original discovery are reported in limited surveys and suggest that cacao thrips pollination might be an opportunistic adaption that typifies Anthropocene co-evolution in human modified systems. Future studies on comparative pollen loads of cacao flower thrips

and Dipteran may bring clarity on which of the two are the most efficient pollinators and further improve our understanding on the nature of thrips-Diptera relationships. It is also important to note that because thrips pollination depends on continuous cacao flowering which depends on moisture availability, this relationship may be particularly vulnerable under a changing climate.

No study to date has fully explored the functional interactions and biological significance of the major actors in the cacao flower visitor network. However, the apparent importance of thrips in cacao pollination opens new questions about the complex pollination ecology and diversity of arthropod interactions in cacao ecosystems. Scale-free networks are characterized by highly connected nodes with high error tolerance, making them robust (Albert et al., 2000). However, such networks are highly vulnerable when the key nodes (network core and bridge nodes) that are vital in maintaining the network connectivity are removed (Albert et al., 2000). In the cacao flower-visitor network, thrips are bridge nodes, and thrips-Diptera cooccurring duality serves as the highly connected nodes and network structural core. Henceforth, cacao plantations may benefit from a systems management approach that does not isolate only key species of known economic importance but rather maintains the integrity of diversity arthropod networks and micro-habitats to protect all plausibly known and unknown ecological functionality.

6.7 Conclusion

In this study, we surveyed flower visitors of cacao in plantations in Western Ghana to evaluate the diversity and abundance of cacao flower visitors and their functional relationships.

The arthropod network consisted of insects and arachnids. Thysanoptera group had the highest abundance followed by the Dipterans commonly associated with cacao pollination service. The vegetation type surrounding plantations is important to the arthropod diversity and abundance.

The study reveals a thrip mediated arthropod network complex and a high degree of thrips-Dipteran co-occurrence that form the core building block of the cacao flower-visitor network, suggesting a possible functional symbiosis or co-operative in cacao pollination. We further propose that cacao thrips pollination involved in thrip life history cycle independent of Diptera but possibly facilitate some Dipteran pollination activity in cacao flower. Further, we show an arthropod trophic network functionality within individual cacao flowers in which the Araneae and Hemiptera taxa likely act as predators to moderate populations of the flower visitors. Thrips mediation of the network implies that thrips are pivotal to the ecosystem services provided by the cacao flower visitor assemblage.

7 GENERAL DISCUSSION

Cacao cultivation has served civilizations over thousand years and today, its growing industry remains at the heart of economic prosperity for the diverse dependent and beneficiary stakeholders such as millions of cacao farmers, the economies of the producer countries, the global soft commodities exchange and futures market, and the confectionery and cosmetics industries that rely on it for raw materials. Moreso, cacao production underscores several related socio-economic and environmental challenges particularly at the production level. Despite the development in the cacao industry over the century, the underlying biological complexity of cacao cultivation surprisingly remains poorly understood. Expanding the knowledge base of cacao will be critical for addressing the cross-linked environmental, social, and economic challenges.

Increasing the productivity on current cacao farmlands hold promise to curb the environmental cost of expanding cacao production into natural landscapes. On this premise, this thesis explores opportunities that may likely improve the yield outcomes on cacao farms. The thesis attempts to address on-the farm productivity of cacao by first, evaluating the current state on yield gaps, the key factors that affect yield outcomes, and proposes a direction of focus that could narrow existing yield gaps. Then the thesis navigates deeper to explore the underlying questions that need to be addressed to allow the identified intervention avenues to materialize in practice. This is achieved in three independent, but related papers which together

show that pollination, an essential biological process that precedes successful fruit development, is important to addressing current yield gap challenges in cacao.

The first paper of this thesis introduced the concept of yield, evidence of yield gaps, proposed cacao is physiological, or pollination limited and suggested practical interventions to close the yield gap. The second paper tested which, between pollination and tree physiology, limits cacao yields most, and constructed an empirical yield curve based on the factor optimality model to estimate yield gap in the study area. Having established the yield gap of the study region, the third paper lastly explored questions about the driving influencers of the most constraining yield limiting factor, pollination, to direct the future of research focus.

In the subsequent paragraphs, I briefly discuss the results and implications of the three thesis papers.

Achieving conservation-livelihood win-win by addressing cacao yield gap is based on the background that the socio-economic challenges of smallholder farmers that drives the need to expand farmlands into forested landscapes is the main driver of cacao related deforestation in growing areas. “Shifting cultivation” is an old landuse practice in Ghana whereby subsistent settlers would relocate to cultivate new fertile lands while leaving their relatively less productive farmlands to fallow (leaving land uncultivated for a period). Establishing new cultivation sites would include clearing forests. Thus, agricultural expansion into forest lands is not a new “unsustainable” practice per se. Rather, it might seem there are relatively fewer forests available to “sustain” the practice today. This clarification and context are extremely important to avoid misdiagnosis of the “problem”, leading to “solutions” that fail in practice. Shifting cultivation is embedded in the traditions and culture of the Sahel regions of West

Africa. The Ghanaian policy framework on concessional logging, called “Manual of Progress” by the Forestry Commission assigns a 50-year logging operation over a period of 200 years. The philosophy of this policy framework is routed in the ancient “shifting cultivation” practice whereby a 150 year-rotation sufficiently allow well stocked secondary forests to be readily available for the next 50-year logging. Like cocoa production, sustainable logging was a failure not because the policy was wrong. A 150-year fallow was a significant safe margin to guarantee market ready timber supply. In contrast, temperate forest management in North America would require only a couple of decades but benefit from significant investment in the productivity, ensuring privately managed forest lands are profitable and supply sufficient timber for markets including wood and paper supply. The missing variables in the cacao scenario, compared to the sustainable logging analogy could be the externalities related to evolving local and international demand-supply markets and global climate threats. Limited long-term investment towards sustained cacao productivity may be the main threat to cacao sustainability.

Paper one argued that increasing the productivity of current agricultural lands to increase the yield outcomes will alleviate the need to expand into agricultural lands. However, this does not factor-in conditional scenarios where increased farmer profitability resulting from increased farm productivity motivates further conversion of forests for more profits. While that possibility cannot be rejected, it is only a speculative hypothesis yet to be proven. Again, the sustained profitability of private timberlands in North America as analogy proves that increasing yields (productivity) on existing farms can mitigate forest conversion for plantation expansion. For now, the motivation, low productive farms which drives current forest conversion is valid and justifies the proposed focus of the paper to increase cacao production

on existing farmlands. The paper summarizes reported factors that affect cacao yields and found that increasing pollination service offers an opportunity potentially close the yield gap.

Practical interventions for yield constraints associated with tree physiology (e.g., Cherelle wilt), genetics (e.g., self-incompatibly) and low efficient pollination is currently lacking but could narrow existing yield gaps if developed. Toledo-Hernández et al., (2020) showed the cost effectiveness of manual hand pollination as intervention for low efficient pollination. However, the underlying problem of natural pollination remain unsolved due to limited understanding of cacao pollination ecology. Increasing the pollination efficiency of natural pollinators can be a cost-effective strategy. Regarding pollination ecology, in relation with yield, Vansynghel et al., (2022) gave a compelling account on the complexity of cacao yield dependence on a variety of interacting biotic agents. Not only was yield affected by biotic and abiotic factors, but also, farm level characteristics and management decisions. Unlike factors such as precipitation or temperature or pollinators, farm level interventions are difficult to generalize and to implement broadly, due to the subjectivity of management approach and the peculiarity of local farm conditions, characteristics or local culture.

To investigate variability in farm-level management, we used a case study in our study area with survey response from the plantation manager of the study area to show that management of cacao farms within cultural proximity is subjective and can impact yield outcomes. For instance, regardless of the common access to farm management inputs, management practices such as pruning for shade management, or preferred agrochemical brand and the timing of application were subjective to individual farmer choice and could result in different productivity outcomes although farms are exposed to the same biotic and abiotic

agents. Such variation in management practices could likely accentuate other underlying yield factors which when taken for granted could significantly impact cacao production.

Overall, the paper suggests a few plausible directives towards increasing the understanding of pollination and physiological limited yields and to consider the importance of farm management factors in order to narrow yield gap. For instance, as fruit abortion is likely a conditional mechanism, the paper suggests bio-stimulation, a technique whereby an exogenous input is treated to a living plant to optimize metabolic or physiological process that results in increased yield. The paper further highlights the nuanced nature of physiological limitation by showing that the size of tree (dbh) which relates with its ability to acquire carbon resources do not correlate with pod production. However, by narrowing yield gap through the potential avenues shown in the paper, cacao farmers in Ghana can increase their revenues share to improve their livelihood while conserving remaining uncultivated landscape to safe-guard biodiversity. The paper is suitable to communicate yield limiting constraints of cacao to both technical and non-technical stakeholders and hopefully, stimulate open dialogue that may research interest and policy direction- on pollination biology and sustainable production.

Paper one is limited in a few ways. Firstly, the development of later papers (two and three) is informed from the conclusions of paper one, which is based on the literature at the time of inquiry. However, the body of knowledge and development on the subject has not change and pollination and physiologically limited yield gaps still are to be resolved and attracting growing research interest. Secondly, I acknowledge that all the literature I accessed from google scholar or web of science repositories were written in English. This might be a concern given that most active cacao producing regions are in the global South and may have

considerable wealth of information that may not be digitized or catalogued in the existing English language and databases. Nevertheless, this does not change the framing of the questions as aligned with the realities of cacao production challenges in Ghana, where I have spent considerable time living near cacao farms. Thirdly, studies that reported actual yield data or conducted empirical test on the yield effects on specified factors are limited. Conventional systematic review approach proved less practical. Thus, I searched papers through a combination of cross-referencing and iterative search to identify papers that reported values on yield. This might be due to the challenge in conducting "controlled" experiments on field grown cacao which cannot easily be cultivated under controlled environment at full maturity as would be typical for annual crops. Nevertheless, the representative studies are satisfactory for at least achieving the goal of the paper in recommending the needed areas for yield gap interventions.

Paper two of the thesis presents a hypothesis-driven, deductive analysis to resolve pollination and physiological limitation of cacao in the study region. The paper tests which is more limiting, pollination or physiological factors, using field data from hand pollination experiments in eight plantations. Based on a set of a-priori hypothetical axioms, the experimental data from the study region favoured pollination limitation. The paper explored landscape and abiotic factors that affect pollination-limited yield. Pollination treatment, moisture, plantation understory light, vegetation surrounding farm and the interaction of canopy shade and understory light environment were all important predictors of pod output in the study area. Furthermore, the paper constructs a pollination-limiting yield curve, a linear regression curve from using hand pollination data to estimate the current level of yield achieved

by open pollination, which is 43% for the wet season. From this, we estimated pollination-limited yield gap of 56% in the peak season (wet season). During off-peak season (dry season), open pollination achieved 0% yield, at a 100% yield gap deficit. This is the first yield estimate based on pollination limitation. Clearly, decreased yield during the dry season may be ascribed to a factor other than pollination. However, for pollination to occur, the tree must produce flowers. Continuous flowering in cacao depends on sufficient moisture resources. In practice, crop yield limitation is determined at optimal plant growth conditions, in this case, the wet season. Moreover, where open pollination resulted in 0% yield, artificial pollination still increased yield, adding further support for pollination limitation.

Paper two of this thesis provides compelling evidence that focusing on improving the efficiency of pollination services will not only increase yield outcomes during the growing season but demonstrates that cacao farmers can benefit from the peak season and off-peak seasons throughout the year. The paper confirms that cacao yield in the growing area is pollination limited. This study implies that farms are achieving less than half their potential yields, meaning under efficient pollination scenario, farmers can obtain twice current revenues. The extra labour needed to sustain efficient pollination may imply that farmers will be busy managing farms all year round for doubled yield and therefore may have minimal incentive to further expand farmlands into forested areas. The paper further contributes to sustainable food systems management and suggest, as the case in cacao systems that ecologically based interventions that improve the operational efficiency of natural pollinators (biotic ecosystems function) can have direct positive economic consequences.

Having shown pollination-limited yield in the study area, the follow up questions then

evolves around the underlying drivers of pollination limitations. Who are the pollinators? What do we know about the pollinators? How can knowledge of pollinators and factors that influence their biological functioning help us to improve the efficiency of cacao pollination services?

To address these questions, paper three of this thesis attempts to contribute to some of the knowledge gaps in cacao pollination ecology. The paper applies exploratory empirical data, statistical inferencing, network topology and deductive inference to evaluate the diversity and abundance of cacao flower visitors, their functional relations, and the factors that influence their diversity and abundance. The study found that cacao flowers are visited by a wide range of microarthropods that represents 11 taxonomic orders, including two arachnids and nine insect orders.

The paper revealed that cacao flower visitor assemblage is a complex functional dichotomy of arthropod trophic network structure, in which Dipterans and Thysanoptera (thrips) groups has the highest co-occurrence and constitute the functional core of the network structure. The core of the network structure has implications on network stability against external perturbations. For instance, in the case of cacao systems, this means that the demise of Dipterans and thrips may indirectly collapse the flower visitor network and the ecological function that support the cacao ecosystem. The study further suggests that thrips are the functional mediators of the cacao network. From our data and compelling findings from network analysis, the study conjecture that thrips are functional cacao pollinators and facilitates the functional services of Dipterans in cacao systems at the study area. The paper further describes the probable mechanism of thrips pollination which is integral to their life history. Thrips association with cacao was first reported in Trinidad over a century but their function

as cacao pollinators were disputed. Our findings for the first time over a century show the functional role of thrips and describes thrip pollination. Unlike other flower visitors, the life-history link to pollination might suggest a probable case of co-evolution. The study results provoke further studies to improve our understanding on the relative efficiency of thrips and Dipterans. Unlike the Dipterans who are legitimate flower visitors, thrips form a permanent association with host flowers throughout their life cycle. Thus, the increased colonization of cacao flower thrips may implicate pollination efficiency. However, more work is needed to fully understand the efficiency of thrips pollination in cacao.

The study limitation is the difficulty of finding traceable evidence of pollen genetically linked to another tree. This is difficult as specimen must be attached to flower to prove it is a flower visitor. As cacao flower is very small and attracts relatively small arthropods, our approach has been to trap visit that are typically inconspicuous. The trapping glue compromises the opportunity to study pollen intact captured specimen and difficult to tell whether pollen, suspended in the specimen solution comes directly from the flower or from the captured arthropod's body.

This thesis has established for the first time that:

- Cacao yield in Western Ghana is pollination limited.
- The efficiency of natural pollination rate in the study area is 43%.
- Homogenous type of vegetation surrounding cacao planation increases the abundance and diversity of flower visitors.
- The interaction of understory light environment and canopy are important for cacao

pollinator and yield.

- Pollination in cacao is attained by a thrips-Diptera co-operation.
- Cacao flower visitor network is a multi-functional complex involving different symbiotic guilds likely with direct and indirect functionality associated with pollination.
- Cacao thrips pollination is integral to thrips life history.

8 BROADER IMPLICATIONS AND RECOMMENDATIONS

This thesis provides empirical support that there is yield gap in cacao production, shows pollination limitation as a priority avenue to narrow cacao yield gap and estimate the current natural pollination levels attainable at study sites. The study further identifies the functional structure of flower visitor network, the driving factors of their abundance and diversity, and shows that cacao pollination is attained mainly by a symbiotic co-occurring insect species of Diptera and Thysanoptera taxonomic order. The thesis describes for the first time since observed in 114 years, the mechanism of thrips pollination in cacao. The study broadly implies that increasing pollination efficient can narrow existing cacao yield deficit at study sites. Unlike previously known, the study further shows that cacao pollination is the result of complex interactions among microarthropods that may function independently as in the case of thrips through their life cycle (i.e obligate cacao pollinators by life history) and co-occurring as thrips-dipteran as probable facilitators for Dipteran pollination or directly and indirectly as mediating part of arthropod network assemblage with intersecting functions involving mutualist and predators. The complexity of flower visitor interactions in the tiny cacao flower highlights the critical importance of implementing ecological intensification solutions in cacao systems. Lastly, the study introduces two variables that have not considered previously in the cacao ecological studies: complexity of surrounding vegetation and understory light environment. The thesis shows that the interaction of understory light and canopy light (a

commonly used variable for shade management) explained yield than canopy light alone. Furthermore, homogenous vegetation surrounding plantation explained pod yield than plantation floor litter.

More work needs to be carried out at different locations to evaluate the functional complexity and structure of flower visitor networks from different locations to identify variations or possible consistent patterns critical towards expanding our understanding of ecological network theories and applications in modern food systems. The study opens up questions for future work to elucidate the process of pollen transfer and traits that determine the level of efficiency or limitation by thrips and Diptera. The study further suggests a new way of managing cacao farms by providing a buffer of grassy meadows or source of vegetation that blooms wildflowers similar in size with cacao flowers to serve as alternative foraging sites while maintaining farm litter such as pod piles as breeding sites. This may likely sustain the flower visitor population and diversity during flowering off-peak, allowing foraging continuity while potentially maximizing the chances of natural pollination services.

Pragmatic implementation of this study depends on well-defined stakeholder roles. Although the cacao value-chain is globalized, different markets control different stages of the value chain. For instance, the cultivation, fermentation and drying of cacao beans largely occurs in West Africa, Southern America and South -East Asia while cocoa liquor, cocoa butter and the confectioneries are largely occur in the European Union and Northern America. This work directly implicates the producer end-chain. Unfortunately, they have low market valuation and thus receive significantly lesser proportion of cacao market value, are likely to have less functional institutions and mostly predominantly low-income economies and

therefore likely less resourced to translate knowledge and innovation to higher cacao production and strategic economic opportunities. In the sections below, I discuss why regardless of research advances and discoveries in cacao research, the unanimous stakeholder involvement is much more critical for sustaining the sector and recommend possible next steps to advance sustainable cacao production.

8.1 Cacao industry, policy, and stakeholder outlook

Cacao is the most valuable soft commodity whose production has been sustained over the century largely by smallholder farmers from the global south. Despite, the commercial growth of cacao end-use across the confectionery, pharmaceutical, beverage and cosmetic industries, cacao cultivation to date, rely on traditional farming practices and has yet to experience the transformative power of technological innovations that can significantly revolutionized production outcomes compared to advances made in commodities like wheat or grapevine. Not only is cacao one of the main contributors to deforestation in major growing areas in West Africa, but the cacao sector is also a source of socio-economic and market controversies. Cacao is the first traded commodity in recent times to disrupt the global financial market because of the effect of climate shocks on production. Also, cacao, like crude oil is produced in few countries, yet serves a larger global consumer market, and inter-weaves all economies and cultures. Despite the scale of global interest, the biggest challenges of the modern cacao industry tend to be skewed towards the producer end of the value-chain and the short and long-term risks are not fairly distributed proportionately by market stake, as expected, business as usual. According to the shareholder theory (also known as Friedman's doctrine),

the social responsibility of business is to increase profits and maximize the returns of shareholders (Castelo, 2013). Contrary, the stakeholder theory is concerned with balancing shareholder's financial interest against other stakeholders including employees, customers, suppliers, and the community collectively, even if sometimes, at the loss of shareholders' returns (Jeff Smith, 2003). While stakeholder theory suggests a lesser emphasis on shareholder interests, Jeff Smith (2003) argues, that stakeholder theory equally account for shareholder interests by ensuring the long-term sustainability by added duty assigned to individuals and constituent beneficiaries or risk bearers that voluntarily or involuntarily contributes to the wealth creating capacity and activities of the entity. While the shareholder theory largely tend to benefit the global technology or financing sectors, the stakeholder holder theory is strategically beneficial to cases such as the global cacao value-chain, whereby the long-term profitability and prosperity of cocoa processing companies depends invariably on the sustained production by farmers and their respective producer economies. Thus, the biggest beneficiaries and losers of a failed cacao industry by market capitalization will be the stakeholders with the largest profit share across the value-chain (currently, the EU and Northern America). This is why processors (sectors that buy beans or process cocoa into various end-use) must commit a reasonable proportion of their collective revenue share towards investments and incentives that will sustain their long-term interests in cacao production. This may include fair market adjusted pricing that pays for the actual business cost of cacao production. To date, the Ghana government provide subsidies that covers some of the farmers' management cost in the form of free fertilizers, seedlings, and pesticides. Such agronomic management initiatives may depend on the political priorities and the will of the government of the day and therefore

unsustainable. This makes the cacao production non-lucrative especially, to the increasingly educated younger labour force needed to replace the current older generation of farmers and their aged farms. Unlike most smallholder farmers who are less formally educated, the younger generation of Ghana today, have access to free education up to pre-tertiary level. Education may increase labour quality, nonetheless in the cacao production sector, likely leading to two possible outcomes. Firstly, well informed agronomic practices will increase productivity, leading to increased supply and market price fall but a temporal win for the cocoa processing end of value-chain. Secondly, lower prices will lead to farmers looking for alternative and more lucrative labour opportunities which alongside climate shocks projections, will decrease global cocoa supply, increase market demand and eventually, cause commodity price hikes at the detriment of increased chocolate manufacturing/cocoa processing cost and long-term market supply uncertainties. On this account, I recommend that industry stakeholder consider engagement in serious business policy negotiations that guarantee long-term financial win-win as stipulated by the stakeholder theory. It will be prudent business to invest to save and guarantee sustained revenues bound to grow over the next decade than to lose century-long market legacy.

Producer markets on the other hand must embark on local strategic policies that increase their share of total market revenues by expanding local competitive market needs beyond raw material production while exploring new market products beyond the confectioneries for instance, from non-bean cacao products such as the pod husk. Cacao pod husk is a raw material for several profitable industrial products including pectins (Vriesmann et al., 2011; Barrios-Rodríguez et al., 2022) and bioactive compounds (Campos-Vega et al.,

2018). For instance, more cacao bean exports have become more critical to the stability of Ghana's current fragile economy more than ever. The post-COVID-19 pandemic double digit inflation (24%, 2024) continues to rise due to currency depreciation, resulting in higher cost of imported goods and unfavourable interest rates (Trading Economics, 2024b). As Ghana's main agricultural export earner, increasing cacao production alone can significantly impact currency stabilization, increase purchasing power, and reduce the high inflationary living cost crisis in Ghana. By mid 2022, Ghana ranked second on global property price index (PPI) at a price per income ratio value of 66, for comparison, ahead of Beijing, London, and Hong Kong (NUMBEO, 2022). PPI is a proxy index of living conditions where higher values reflect affluence. However, in the case of Accra, high PPP means high cost of living than big cities like London and New York at the expense of significantly lower labour income. At this PPP values, Ghana's minimum labour wage is GHS 18.15 or ~USD 1.25 or GBP 0.98 (based on May, 2024 forex rate) or for context, can hardly afford a decent coffee or a cup of tea let alone, a bar of chocolate for those who are the support base for chocolate production.

Addressing cacao yield gap and sustaining increased productivity is not only a farmer's dilemma, but a necessity for the health of Ghana's economy to guarantee the overall livelihood need its population aspires. At the current yield-gap and production deficit, a ten-fold productivity at a corresponding market growth means nearly $18 billion accessible capital for investments in social infrastructures such as improved quality of education, health care and expansion of the services sector that could trigger a cascade of tax revenues and improve the overall economic performance, poverty reduction and quality of life without the pervasive over reliance on sovereign foreign debt capital. Moreso, the processors by the same projection gains

added market share up to a trillion USD based on stakeholder theory if they invest more aggressively in the producer economies. By investment, I do not mean economic aids and handouts to government which have historically been counterproductive.

Besides the disparity in fair stakeholder risk sharing, climate change remains a common enemy of the value chain. Recently, climate-induced production losses in the year 2024, caused exponential hikes in cocoa index price (Nasdaq, 2024). At 250% price increase, cocoa outperformed Bitcoin and gold, becoming the most valuable global market commodity and attracting buzz terms like, “Choco-pocalypse”(Nasdaq, 2024a). Although increase market prices should lead to increased nominal revenue and share price, this was not the case in the cacao value chain. At the peak of the market shock, producer countries like Ghana and its farmers were the biggest losers. They lost both to production losses due to El Niño event and diseases infections. Although chocolate manufacturers, unlike farmers can easily pass the business cost of temporal price increment in raw material along to retail customers in the short-term, corporations still risk long-term supply shortages especially when farmer have no economic incentives to motivate longer interest in cacao farming. It is important to understand that unlike seasonal crops like soybean or grains, the business of perennial farming is a long-term commitment, thus market uncertainties can signal permanent exit. In the case of cocoa, a small viral infection will require immediate decimation of all neighbouring trees to ‘contain’ spread. As smallholder farms are mostly uninsured, a farmer would hardly wait another half decade to get back to business.

Cacao production is significantly undervalued, contrary to its realistic market value and therefore threatens the sustainability of future production. Cacao cultivation requires

multiple skills and stages including an annual cycle of agronomic management, harvesting, fermentation and tended sun drying. These are unique crafts that demand several labour hours and are key to guaranteeing quality beans, which gives cocoa it's delicate luxury notes of flavours. Compared to other agricultural commodities or the extractive industries, and given the relatively higher market value of cocoa, and the global market size, farmers are significantly undervalued and nearly exploited in the context of pragmatic business sense. I argue that if not smallholder farming, a typical agricultural corporation may need to invest separately in operational labour cost (by hiring permanent or seasonal workers) for farm management, labour for harvesting, fermentation and drying (human labour or added energy cost, if machine operations). The real value need not be speculative but by the sheer application of the opportunity cost. The opportunity of cost of the industry without the motivated career farmers will be in the order or tens of USD billions. For, instance, cacao harvesting has been a subject of controversy due to the involvement of child labour. Figure 1A, Chapter 2 of this thesis shows a photo in which I am voluntarily working on the second phase of communal harvest which involves the removal of fresh beans from crashed pods using matchet/cutlass. This involves regular daily hours for several weeks depending on the size of farm and the size of household. This is unpaid labour for the farmer household and their supporting neighbours or community members. At the peak of the cocoa child labour debate, if was assumed that "farmers" subjugated their children to harsh labour, instead of staying in school yet, far from reality. To be able to sell the year-long managed cacao fruit and support their households, they must first harvest, ferment and sun-dry to zero moisture content. If the cocoa processors paid the due business cost, farmers could hire extra labour just as high-income economies have special visa

designation to attract seasonal agricultural labour during the harvest season. In the cocoa sector, the realistic cost translates into profits for the high-end of the value chain where CEOs make USD millions in annual salaries. Ghana is signatory to the International Labour Organization but yet to ratify the Protocol of 2014 to the Forced Labour Convention, 1930 (No. 29). As a globalized industry, and regardless of the weak negotiating strategy and geopolitical power imbalance, the stakeholder theory stipulates that the long-term sustainability and interests of the higher end value-chain depends on the prosperity at the producer-end value-chain. Although I do not have data on the manhours per workforce per tonne of beans from pods, I argue from over two-decade experience working with farmers, and as an agricultural investment consultant and executive board of a US incorporated Private Equity, that the cocoa production sector is at the mercy of inevitable crisis. In 2022, I pitched investment in Ghana's cocoa to portfolio managers of the Harvard University endowment with mandate to diversify investments in sustainable agriculture. Regardless of the sustainability driven intentions and the genuine goodwill to support the smallholder farmer economy, the investment in production was no deal breaker simply because the production value was ridiculously under-priced despite the incredible performance of the global cocoa commodity index.

Another long-term risk of a downgraded labour valuation that should concern the chocolate industry is that increasing level of education in Ghana might mean soon, high school will be the lowest level of education of the labour force. For instance, considering the educational level of a generation 'z' (those born between 1997 to 2012) labour demography and the explosive opportunities of today's digital economy which is modelled to adjust for global pricing, the annual revenue per hectare of cultivating cacao farm can easily be obtained

in a week or less through content creation on the web or social media platform and from the comfort of your room without the intensive labour under the scorching unforgiven sun. As multinational corporations are paying on international pricing, conventional business models such as the cacao may struggle to replace the current older generation of cheap labour, unless it is made sufficiently reasonable or adopt robots– a less likely alternative for a developing country that barely provide sufficient electricity for its population. There is a high chance that chocolate will become a true luxury in the foreseeable future or as companies strategize to survive the market. Moreover, the Ghana COCOBOD may consider re-examining the sustainability of the current fixed farmer pricing versus a free market approach, while the larger cacao industry should recognize that livelihood of the farmer is determined solely by income earnings just as industry players such as an executive or formulating biochemist, and that real value should be determined by fair valuation that accounts for production cost or in economic terms, the opportunity cost of farmer absence. Both cocoa producers and processors should consider evaluating the cost-benefit of fair pricing and safeguard losing future generation of cacao farmers.

Another threat to cacao sustainability due to unmet livelihood needs is implicated in the growing menace of illegal small-scale mining operations on cacao farms in Ghana. Despite the environmental damage of illegal gold mining and the risk of police arrest, some farmers are willing to sacrifice their cacao plantations in exchange for higher income from gold mining as a preferred alternative livelihood income source. Figure 1 below shows an operational illegal mining crackdown that I witnessed on my way to visit one of my experimental sites. The incident occurred a few kilometres from plot #8 at Tarkwa Breman. Despite the operation, the

miners returned to their illegal operations in the following week. Here again, income is the main driver and to the perpetrator, is worth the risk.

Figure 1: Photo of confiscated illegal small-scale mining ('Galamsey') excavator adjacent a cacao plantation (A). Military tax force personnel inspecting a cacao plantation for illegal mining operations (B). Photos were taken from my truck while waiting for excavator to load unto the carriage vehicle.

Lastly, the woes of climate threats and the associated market risks are further relegated to the least economic power brokers. The collective low production valuation means low production cost for cocoa processors and higher profits. If chocolate sales guarantee meaningful livelihoods for shareholders, then fair pricing should improve firstly, farmer livelihoods and then stronger economic fundamentals for cacao-dependent economies. Alternatively, a shift to investments in large corporate cacao production such as in apple or peaches in California or Washington State in the future may perhaps guarantee the cocoa commodity futures but at a likely high cost to chocolate manufacturers, as agricultural production corporations as emerging in the Republic of China, unlike smallholder farmers, can always afford to hedge

produce to create artificial scarcity and force higher price margins for profits.

8.2 Future research and support

The biological uniqueness of cacao offers several opportunities to expand knowledge across basic and applied research areas and overlapping disciplines. Below, I summarize recommended areas that can attract interest in further research development.

- **Ecology:** reproductive ecology of cacao is at its infancy, although work on cacao pollination biology began over a century ago. Particularly, more work is needed to elucidate the behaviour of biotic pollinators and the functional complexity of cacao flower visitor networks and their ecosystem benefits. The consumption of cocoa is speculated to date back to the Aztec civilization, yet little is known about the evolutionary mechanism that mediate the symbiotic relationship of cacao flower morphogenesis and pollinator selection. The diversity of flower visitors across geographic regions suggest that temporal adaptations process is recent and likely opportunistic, but I won't rule out co-evolution. Moreso, there is need to understand how flower-pollinator symbiosis in cacao may have been shaped over time by selection pressures including climate change and human modified landscapes. Lastly, more work on pollinators should focus on developing methodological techniques that can capture the process of pollination with evidence of pollen flow between trees.
- **Physiology:** Cherelle wilt, which occurs after successful fertilization of compatible gametes is a considerable source of fruit loss and remain poorly

understood. This thesis provide evidence that cacao yield is not limited by tree size (see case study in paper 1 of thesis) and suggest that cacao can have a potentially wider range of physiological capacity for increased fruit production. However, more work is needed to understand the mechanism and controls in resource allocation and partitioning.

- **Genetics:** early breakthroughs in cacao genetics, especially in the area of self-incompatibility peaked by the middle of the 20th century. Research and development declined in coincidence with the end of the colonization era across the West Indies and West African producing countries which were then the global research centres for cacao research. More research work on the molecular genetics of cacao selfing, and application of gene-editing may be critical towards increasing the selection of highly selective genotypes but with low selfing susceptibility. This thesis emphasized on pollinator-based yield limitation. There are interesting questions regarding pollen-based limitation of cacao yields that are yet to be explored within the genetics disciplines.
- **Economics:** cacao's influence on the global market and profitability has increased remarkably in recently times. Major research needs include economics of labour, fixed versus competitive free market pricing and valuation. To determine price equilibrium at diminishing marginal return threshold, there is need for significant research on the economics of labour, price valuation and the maximum yield per hectare.
- **Humanities:** expanding anthropological nuances of the inter-linked complexity

of smallholder farming business model, cultural norms and how it influences community and national policy can be a critical bottom-up foundation to improve our understanding of the complexity of labour, the notion and determination of livelihood value, exploitation and corporate ethics and policy-regulatory implementation and enforcements in cross-border business practices.

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