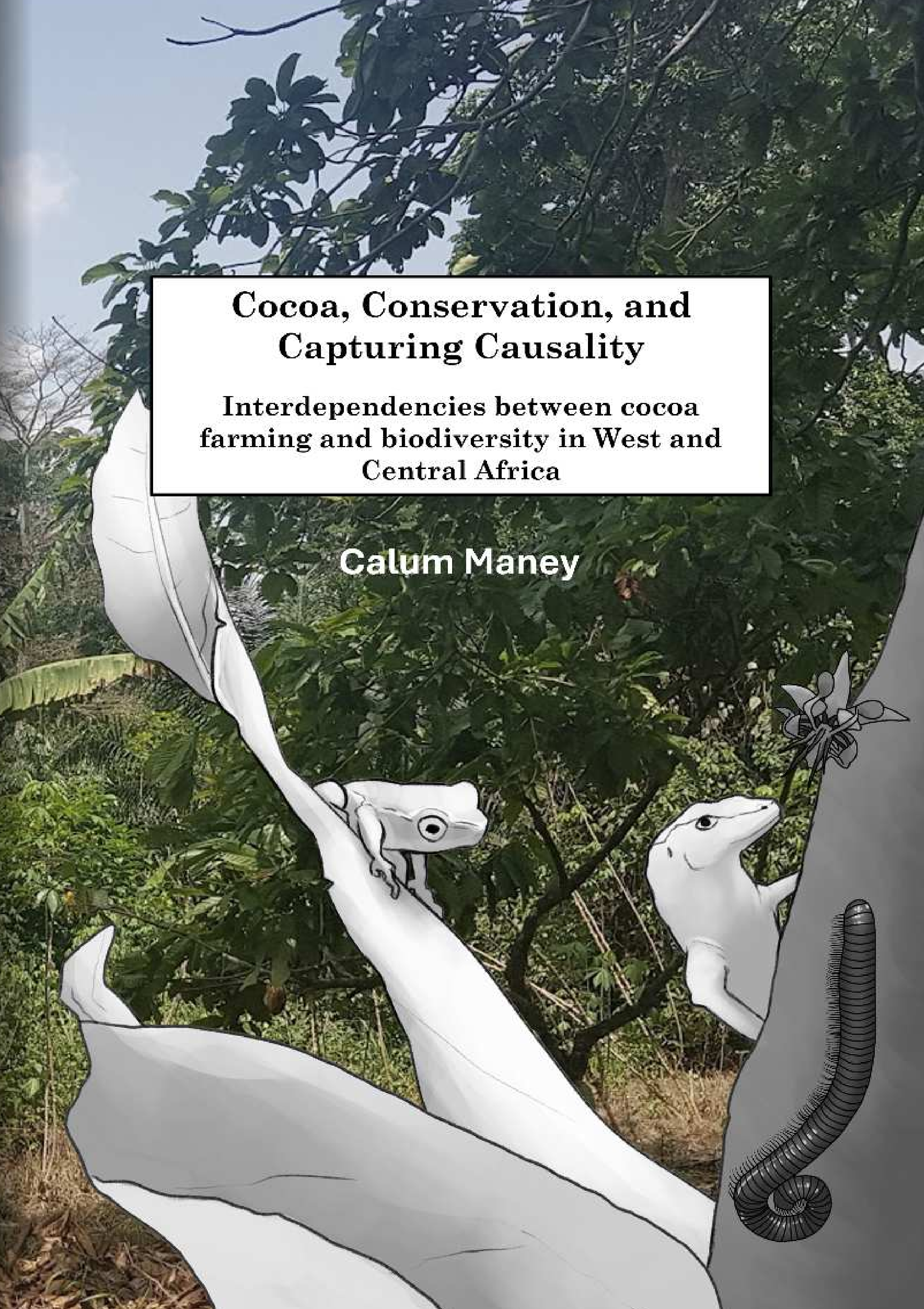
Cocoa, Conservation, and Capturing Causality

Interdependencies between cocoa farming and biodiversity in West and Central Africa

Calum Maney



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Cocoa, Conservation, and Capturing Causality: Interdependencies between cocoa farming and biodiversity in West and Central Africa

Calum Maney

Thesis

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Abstract

Commodity crops such as coffee, cocoa and oil palm are important drivers of biodiversity in tropical forests. Through a review covering a broad set of case studies, I investigated the interdependence of ecosystem services provided by biodiversity and production of commodity crops. The review covered cocoa, coffee, cotton, rubber, soyabean, sugar cane, and tea systems, summarising evidence for and against their impacts and dependencies on biodiversity via pollination, pest control, and soil health services. Cocoa production was found to be particularly vulnerable to biodiversity loss, yet the interactions between cocoa systems and biodiversity are not fully understood. The baseline biodiversity found in cocoa systems, and its variation, is likely to differ across farms, countries, and world regions due to the underlying ecological and socio-economic contexts in which those cocoa systems came about. Context-specific knowledge about the direct and underlying drivers of biodiversity in cocoa systems is also necessary to guide on-farm actions, policy, and the actions of multinational cocoa-buying companies.

This study was a multi-scale investigation of how best to model these interactions to assess the role of cocoa systems in global biodiversity, and to model interventions to benefit biodiversity and ecosystem services. I used top-down methods with globally-distributed, primary field data to build a general picture of biodiversity responses to cocoa production, relative to other land-use types and minimally-disturbed areas. I complemented these methods with bottom-up analyses grounded in field data from ~650 plots on cocoa farms in four West and Central African countries.

I found it possible to attribute the variation in biodiversity between these plots to their land-use history, management and design, and spatial context. Land-use history was particularly important, as it also influenced how biodiversity in cocoa systems responded to the other pressures. I also modelled the underlying causes of these immediate drivers of plant diversity in cocoa systems, and found that contextual factors such as the accessibility of areas to ports (and therefore markets) were very important. While actions by farmers can improve the condition of biodiversity on cocoa farms, the farmers were not always directly responsible for the apparent lack of tree diversity.

Through surveys and trait databases, I found that ecosystem services linked to trees in cocoa systems are highly valued across the study region, though the most valued ecosystem services varied both between countries and sub-nationally. I also found that trees and tree communities with particular traits were more likely to be perceived as providing certain ecosystem services (though this was also true for some disservices). Key examples were fruiting trees providing both food and marketable goods, and larger trees providing soil fertility and productivity benefits to cocoa.

Ultimately, the loss of shade and tree diversity is incompatible with biodiversity goals, with sustainable production of cocoa, and with the provision of ecosystem services to farming communities in West and Central Africa. Cocoa systems provide a promising route through which some elements of biodiversity can be preserved. This requires multi-generational planning and support from the public and private sectors to provide context-specific solutions.

Key words: biodiversity, cocoa agroforestry, ecosystem services, West Africa, Central Africa, land-use change

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Chapter 1. Introduction

This thesis addresses the relationship between commodity cropping systems and biodiversity. An initial review indicated the need for targeted research on cocoa systems, and the subsequent research concerns smallholder cocoa production in West and Central Africa, and focusing on smallholder systems. The analytical approach relies heavily on statistical modelling, with the ambition of using multiple scales of evidence to examine and characterise the impacts of cocoa systems on local biodiversity. It also aims to inform potential responses to these impacts, and interventions related to biodiversity that could benefit nature, cocoa production, and farming communities.

1.1. INTERDEPENDENCIES BETWEEN AGRICULTURE AND NATURE

It is without doubt that the expansion and intensification of global agriculture has, in providing food for the planet's people and supporting the world's exploding economic productivity, destroyed and degraded massive areas of natural habitat (Dasgupta, 2021). Whether or not agriculture is in itself the underlying driver of natural habitat loss, agricultural land use is associated with most land use change on Earth, with an area growing by over one million square kilometres since 1960 (Winkler et al., 2021). Further, global land use change has itself had a greater impact on biodiversity loss than any other driver to date (Newbold, 2018). Simultaneously, agricultural production has always been – and remains – inextricably dependent on biodiversity (IPBES, 2019). Ecosystem services, the processes by which human systems derive benefits from biodiversity, are vital to agricultural productivity and sustainability (Balvanera et al., 2014; Isbell et al., 2017).

Attempts to synthesise, model, and map these interdependencies are numerous. Evidence synthesis and path modelling have shown, at the broadest levels, a positive association between landscape complexity, biodiversity, and ecosystem services, and higher productivity (Dainese et al., 2019). Associations between species known to provide ecosystem services and their habitats can be simplified into spatial models of ecosystem service provision at the global level (Chaplin-Kramer et al., 2022). It has proved more difficult to connect our impact on ecosystem services back to land-use change, closing the “feedback loop”. The knock-on effects of land-use change on the economy (via ecosystem services) have been investigated using global ecosystem service models paired with economic models (J. A. Johnson et al., 2020), but attempts to create fully coupled social-ecological models (where land use impacts on biodiversity lead to feedbacks on land use) rapidly lead to a breakdown of both natural and human systems (Brown et al., 2019). Though this may not be the true nature of interdependencies between agriculture and nature, this typical modelling outcome at least reflects our understanding of the relationship between agriculture and biodiversity.

At the local scale, agricultural systems may undermine their own productivity by expanding into natural areas, reducing ecosystem service to the farm. By becoming more reliant on ‘substitutions’ of lost ecosystem services for manufactured alternatives, agricultural systems could enter such an ‘intensification trap’ (Burian et al., 2024). Further, where there is little economic capacity to continually invest in manufactured alternatives for ecosystem services, farmers without more natural land to exploit may then experience falling yields and diminished livelihoods. These farmers may therefore find themselves with stewardship of degraded land that they have no capacity to restore to health. It stands to reason that if the trade systems driving expansion and intensification of agricultural systems are driving biodiversity loss, which in turn drives a decline in productivity, livelihoods, and well-being, then importers should pay prices that reflect the damage they have caused to biodiversity and ecosystem services and moreover, pay prices that prevent further damage.

1.2. MODELS OF BIODIVERSITY RESPONSES TO LAND SYSTEMS

Different land systems have variable capacity to host ecological communities . As it is impractical to monitor biodiversity directly, especially at large scales, we rely on generalising with models describing biodiversity responses to land use change, which is more readily monitored. Two main approaches are used to model how biodiversity changes in response to changes in land use: species-based models, and community-based models. Species-based models typically use expert knowledge and spatial occurrence data regressed against geospatial data relating to environmental characteristics (including land use), to model the distribution of individual species (Randin et al., 2020). Many of these may be combined to produce an estimate of community level metrics such as species richness (S. L. L. Hill et al., 2019). Alternatively, whole communities can be modelled without disaggregating to individual species. This requires sampling in multiple areas under different land-uses, and modelling features of communities directly, such as their species richness or the total abundance of species in an area. Most individual sampling studies have a focus area and taxon, so many studies are necessary to build a generalised model of community responses to land-use change (Newbold et al., 2016b).

Efforts have been made to harmonize studies of biodiversity across land uses, to derive an overall picture with meta-analyses and synthesis of primary data. For example, the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project has collated 32,000 studies and over three million observations of biodiversity, under a harmonised ontology of land uses, to model global biodiversity responses to land use change in a generalisable way (Hudson et al., 2017). This has enabled spatial estimates of species richness, as well as all-important relative metrics such as community similarity to nearby primary vegetation, and the Biodiversity Intactness Index (BII) – which was the first metric to describe, for the global terrestrial realm, "The extent to which communities of a diverse range of species resemble those found in minimally disturbed habitats".

However, these global dose-response models of community biodiversity have several weaknesses. They are not specific to regions, ecosystems, or the geography of landscapes. Attempts to increase specificity have been made, with focus on different biomes or the island status of ecosystems (De Palma et al., 2021; Ortiz et al., 2021). Current models also do not go beyond the terrestrial realm, though there have been recent advances in collating data on biodiversity responses to land use in freshwaters (Shen et al., 2024), which could complement current terrestrial models. Moreover, there is a key challenge in making modelling results relevant worldwide: current global models are built on data with significant geographic biases. African biodiversity data, in particular, continues to be limited by insufficient and inconsistent funding, instability, and an absence of monitoring programmes (Siddig, 2019). In response to this, expert-driven initiatives such as ‘BII4Africa’ could supplement less-specific global models (Clements et al., 2024). Another potential weakness of this approach is its thematic granularity. To sustain accurate and precise estimates of community biodiversity, land use categories must be condensed into a small number of archetypes. Boiling down global land use into a tractable number of categories is useful, but removes the kind of practice-level details necessary to inform land managers – “forest good, cropland bad” is only interesting at the broadest level of analysis.

To know the effects and impacts of more nuanced changes in land systems on biodiversity, a high volume of data specific to the details of a focal land system will be necessary.

1.3. COCOA PRODUCTION IN WEST AND CENTRAL AFRICA

Cocoa (*Theobroma cacao)* is native to the Amazon, where it was first domesticated and traded by pre-Colombian civilisations as early as three thousand years ago (Paradis, 1979). By the late 1700s, Spanish, French, and Portuguese colonial powers had established cocoa plantations across the Caribbean, Asia and the Pacific, as well as throughout cocoa’s native Central and South America (Lanaud et al., 2003). It was not until the introduction of cocoa to São Tomé by the Portuguese, and the later planting in mainland West Africa in the 1800s, that today’s major cocoa-producing countries first came to grow the crop (Wood and Lass, 2008). Since the mid-20th century, West Africa has produced the majority share of global cocoa production (Food and Agriculture Organization of the United Nations, 2020). The history and current state of cocoa production in West Africa is tied closely to complex histories of population change, migrations, and climate change. There is a clear theme of boom and collapse across much of the region.

In Ghana, cocoa production in relatively complex, shaded systems was strong in the early 20th century, until an epidemic of cocoa swollen shoot virus (CSSVD) killed many trees in the 1930s (Hill, 1961). This precipitated a westward expansion of the cocoa-forest frontier in the country, and meant that the Western Region became (and remains) Ghana’s major cocoa production area (Kolavalli and Vigneri, 2011). Later, in the 1980s, the combination of an aging tree stock with unfavourable economic conditions and resurgent outbreaks of disease caused another production crash (Ruf et al., 2015, p. 201). This led to a regeneration phase for Ghanaian cocoa, utilising more modern hybrid cocoa varieties that were sun-tolerant (Kolavalli and Vigneri, 2011). These cocoa hybrids are typically grown in lower-shade conditions (Ruf and Schroth, 2004). Now, regeneration and replanting schemes continue with a focus on simple agroforestry systems (Wessel and Quist-Wessel, 2015).

Historically in Côte d'Ivoire, cocoa systems were rarely replanted, with farmers favouring the fertile soils and disease-free conditions of newly cleared forest land – conditions described as the 'forest rent' (Ruf et al., 2015). Farmers would subsequently choose to migrate rather than regenerate land due to the temporary nature of such benefits, both through economically-motivated migration and local scale shifting. Here, the early 20th century expansion was facilitated by migrants from the northerly savannah region (Verdeaux and Alpha, 2004), including through colonial-era forced resettlement. The later east-west migration began in the 1970s due to forest land availability and government policy promoting cocoa expansions (Wessel and Quist-Wessel, 2015). Most systems employed little shade/ full sun techniques, capitalising on hybrid cocoa varieties, until the early 2000s (Ruf and Schroth, 2004).

In Nigeria, production declined through the second half of the 20th century, but has expanded since 2000 including with support from the country's 2011 'Cocoa Transformation Action Plan', which aimed to increase national production to 500,000 tonnes by 2015 (Wessel and Quist-Wessel, 2015). However, the targeted sustained growth in yields and production have not been achieved (Food and Agriculture Organization of the United Nations, 2020). Today, many farms are old, and the country therefore faces a similar problem to that faced by Ghana and Côte d'Ivoire in the 1980s.

In Cameroon, cocoa is a younger market. Systems typically remain as complex agroforestry systems, retaining forest trees among the cocoa (Abada Mbolo et al., 2016). However, Cameroon also experiences the highest incidence of Phytophthora pod rot ('black pod' disease) in its highly-shaded cocoa, and yields remain relatively low (Wessel and Quist-Wessel, 2015). In recent years, cocoa in Cameroon has expanded into (degraded) wooded savannas on the northern edges of the forest zone, in response to stronger enforcement of forest protection (Jagoret et al., 2012). This was a response to forest reserve protection preventing farmers from converting further forest to cocoa (Ruf et al., 2015).

Despite the vast export value of cocoa, cocoa farmers on the whole remain relatively poor (Waarts et al., 2019). As many as 90% of cocoa farmers in Côte d'Ivoire and Ghana do not earn a living income, and the majority of cocoa farmers above the poverty line do not rely primarily on cocoa for their income (van Vliet et al., 2021). At the same time, farmers are coming under increased scrutiny, with regulations such as the European Union's anti-deforestation regulation, which aims to ban the import of cocoa (among other commodities) sourced from areas deforested after a benchmark date of 31 December 2020 (The European Parliament And The Council Of The European Union, 2023). This increasing pressure to do more (to earn enough) and to use less (to protect forests) means the long-term sustainability of productive cocoa systems is of key importance to supporting farming communities.

Finally, the impacts of climate change threaten cocoa production. While suitable land for the cultivation of cocoa in Africa is likely to increase slightly under climate change scenarios up to 2060, most of this suitable area is currently-forested. Outside forests, the area suitable for cocoa will be 15% smaller by 2060 (Ariza-Salamanca et al., 2023). Changing climates may have influenced the history of cocoa already, with suggestions that the droughts and consequent wildfires of the early 1980s contributed to the migration of farmers further westward in Côte d'Ivoire – though this is contested (Ruf et al., 2015). Further, the species grown alongside cocoa in agroforestry systems are also expected to undergo range contractions in the next 50 years, threatening the production systems as a whole (Ariza-Salamanca et al., 2023). As of late 2023, the International Cocoa Organization (ICCO) marked record high cocoa prices, noting poor yields caused by high infestation of Phytophthora 'black pod' and critically, unprecedentedly wet weather (ICCO, 2023).

In this context, it is vital to move towards economically sustainable cocoa systems that can provide market and non-market benefits to farmers, systems that are resistant to disease and the future impacts of climate change, without exacerbating impacts on deforestation. Such systems should also contribute to reduce and reverse global trends in biodiversity loss; but that is a much more complicated issue.

1.4. COCOA PRODUCTION AND BIODIVERSITY LOSS

The expansion of cocoa production systems in West and Central Africa has been associated with widespread forest loss, including in high-biodiversity landscapes and even in protected forests (Kalischek et al., 2023; Ruf and Schroth, 2004). This is a complex relationship which is also linked to gradual forest degradation and timber extraction (Orozco-Aguilar et al., 2021). Looking ahead, potential further expansion of cocoa into Central Africa threatens forests in the Congo basin (Kamath et al., 2024).

The expansion of cocoa into forests in West Africa has been linked to the local extirpation of threatened primate species (Bitty et al., 2015). When comparing communities in cocoa to those in primary forests, biodiversity in several taxonomic groups is notably diminished (Bisseleua and Vidal, 2008; Delabie et al., 2007; Jarrett et al., 2021a). That said, there is significant variation, with some cocoa production systems hosting considerably more biodiversity than others (Niether et al., 2020; Tadu et al., 2014). In a study in Bolivia, complex ‘successional’ agroforestry systems were found to gain more understorey plant species over time than simpler agroforests (Marconi et al., 2022). Structural characteristics of cocoa farms have also been found to affect their capacity to host biodiversity. For instance, bat diversity correlates positively with shade cover and tree height (Ferreira et al., 2023a). While there is a growing base of evidence on single taxonomic groups available from around the world, most studies have been done in single landscapes or countries.

Though biodiversity-relevant criteria do appear in sustainability standards, there is currently no widespread biodiversity certification standard for cocoa systems. Despite this, companies producing cocoa products often make commitments related to the cocoa they buy being “regenerative”, which has a biodiversity component, or even explicitly ‘biodiversity positive’ (e.g., ofi, 2023). While these can be linked to interventions at the farm and landscape scale that have been associated with biodiversity, such as forest/tree cover restoration and agroforestry (e.g., Barry Callebaut, 2023), there are no explicit links to measurable biodiversity impacts.

Despite the interest in biodiversity-friendly cocoa, the processes that govern the biodiversity of cocoa systems are complex, and the causal processes that determine different aspects of biodiversity have yet to be fully investigated (Martin and Raveloaritiana, 2022). Imagine the case of understorey plant species. They are impacted by the structural characteristics of the shade canopy, as well as by the supply of species seeding from nearby forests and in the seed banks of farms. Yet vegetation structure of the canopy is also influenced by the presence and nature of landscape forest (Figure 1).

Figure 1. An example graph showing an example of causality in determining biodiversity in cocoa agroforestry systems.

To understand the impact of changes in the landscape of understory biodiversity, one would need to consider the shared influence of landscape forest on both understorey diversity and vegetation structure. This example highlights the reason why many studies regressing single environmental or design characteristics of cocoa farms against biodiversity provide insufficient evidence to guide interventions.

Research has begun to unravel the main causal processes that shape biodiversity in cocoa. For example, landscape forest cover was a stronger predictor of bird diversity than local vegetation in cocoa systems in the Amazon (Cabral et al., 2021), and land-use history has a measurable effect on bird diversity in African cocoa systems (Martin and

Raveloaritiana, 2022). But we lack data and models at scale to be able to make broader conclusions about what can (and cannot) be done on farms to maintain and enhance biodiversity in cocoa systems.

1.5. COCOA AGROFORESTRY SYSTEMS AND BENEFITS FROM BIODIVERSITY

Cocoa is grown in a wide variety of production systems, varying from monocultures, intensified systems with irrigation, and large volumes of agrochemical inputs, to complex agroforestry systems (where one or more shade-tolerant crops are cultivated in combination with trees (Somarriba, 1992) with little to no inputs (Rice and Greenberg, 2000). These systems do not vary on a single axis: not all small farms are complex agroforestry systems, and not all intensified farms use large volumes of agrochemicals (Figure 2).

Figure 2. Example photographs from two cocoa plantations in Ghana, showing an example of a relatively open-canopy, low shade system (top) and a more complex system with shade trees (bottom).

In West Africa, especially Côte d'Ivoire and Ghana, the use of full-sun tolerant hybrid varieties of cocoa was initially successful (Ruf and Schroth, 2004). As of the 2010s, as much as 70% of global cocoa production took place in such low-shade systems (Clough et al., 2009). However, these systems require specific management practices to deal with the increased insect damage, and more agrochemical inputs to sustain productivity. Because most smallholders could not afford these, and did not have access to the technical guidance and labour necessary, many systems prematurely fell in productivity and were abandoned (Kolavalli and Vigneri, 2011).

Cocoa agroforestry systems vary greatly across farms and regions, which leads to a wide range of agricultural and ecological outcomes on farms (Rice and Greenberg, 2000). "Planted shade" systems can range from cocoa plantations shaded by a single species to complex multifunctional systems targeting several ecosystem services. Cocoa systems under natural shade, variously named “rustic cocoa”, “cabrucas” in Brazil, and “forest cocoa”, also vary in structure and design, with some being considerably more intensified (Faria and Baumgarten, 2007; Rice and Greenberg, 2000).

Cocoa agroforestry systems, on average, attain lower cocoa yields than monoculture systems; that said, if the total system yield (including all agricultural products) is accounted for, agroforestry systems have a far higher productivity (Niether et al., 2020). Further, other components of agroforestry systems have diverse use and non-use benefits to farming communities, such as timber for construction and medicinal uses of wild plant species (Sanial et al., 2023). Finally, certain combinations of shade tree could even have a positive effect on yields in cocoa (Asitoakor et al., 2022), though before recommendations can be made more research is needed on these relationships.

There are more potential benefits from the adoption of agroforestry, including those mediated by biodiversity and ecosystem services. Relative to full-sun systems, cocoa agroforestry systems sequester more carbon, contributing to climate change mitigation (Niether et al., 2020). However, there is little evidence that agroforestry systems are significantly better for soil fertility than full-sun systems, which also typically employ fertilisers (W. J. Blaser et al., 2017; Niether et al., 2020). There are also potential trade-offs and drawbacks to implementing more complex agroforestry systems. As well as lower maximum yields than monoculture systems, under dry conditions as may be expected under climate change in some regions, agroforestry systems may be less resilient (Abdulai et al., 2018b). The degree of damage due to diseases in agroforestry systems relative to monocultures depends on the pathogen. While agroforestry practices can mitigate the risk of CSSVD (Andres et al., 2018) and witches’ broom outbreaks, they can exacerbate the risk of Phytophthora ‘black pod’ disease (Niether et al., 2020). Regardless of production system, West and Central African cocoa systems need active and adaptive management to deal with disease outbreaks. Finally, some agroforestry systems may not be as biodiverse as others. Indeed, though some areas on the forest frontier typically retain diverse tree communities, most modern cocoa farmers favour a pragmatic, streamlined approach to agroforestry using just a few species (Ruf, 2011a).

We lack a robust and generalised data-driven understanding of how and why more complex agroforestry systems lead to tangible benefits for farmers, and how the trade-offs between diversity and productivity can be minimised while providing ecosystem services. It is therefore key to understand not just which actions can be taken to enhance biodiversity in cocoa, but how biodiversity leads to different ecosystem services – and which elements of biodiversity are most important to maintain them.

1.6. THIS THESIS

Few agricultural systems today have a more precarious balance of a high dependence on ecosystem services, and low capacity to adapt to changing environmental conditions than smallholder cocoa systems in West and Central Africa. Over the four research chapters in this thesis, I use a combined top-down and bottom-up approach to understand the evidence on the interdependencies between agricultural commodity production and biodiversity in cocoa, its main drivers, and the benefits and trade-offs that exist between biodiversity and cocoa production systems (Figure 3).

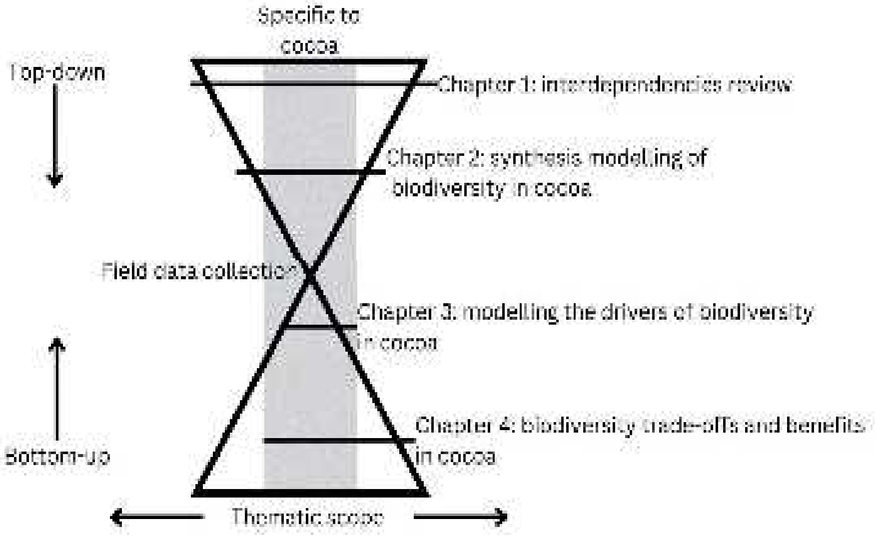

Figure 3. An illustration of the approaches taken by this thesis to investigate the relationships between agricultural commodity production (particularly cocoa) and biodiversity.

Chapter 2 presents a broad review of the interdependencies between agricultural commodity production systems and local biodiversity. This contextualises the evidence available on biodiversity in cocoa, and provides an indication of the likelihood and strength of the relationships between cocoa production and biodiversity, compared with other commodity crops.

Chapter 3 investigates the generalised impacts of cocoa systems on local ecological communities using data from across the globe. Using the PREDICTS database and modelling framework while tailoring the data to focus on areas of cocoa production, I model the 'intactness' of ecological communities in cocoa systems. The aim of this research is to contextualise the biodiversity value of cocoa systems, comparing them to more natural systems (such as primary forest) and to comparable agricultural systems (such as arable cropland and pastures).

While Chapters 2 and 3 are based on review and synthesis of existing data, the next two chapters are built on field data. This combination of 'top-down' and 'bottom-up' approaches yields insights that are practically relevant at the farm level, and allow the findings to be placed in a wider context by comparison with other areas, commodities, and land use systems.

The field data is derived from the CocoaSoils Satellite Trials which are part of an integrated soil fertility management experiment being carried out across four West and Central African countries: Côte d'Ivoire, Ghana, Nigeria, and Cameroon (West to East). The result of this fieldwork is a detailed, georeferenced dataset of around 660 plots on cocoa farms and their plant diversity, combined with *in-situ* assessments of the costs and benefits associated with that biodiversity, detailed site-level land-use history, and landscape-level site characteristics.

Chapter 4 uses this field data resource to investigate the main natural and anthropogenic drivers of plant biodiversity in West and Central African cocoa farms. I create path models based on hypotheses about what factors govern plant biodiversity within cocoa plantations, and test these using data from the Satellite Trials. This links the wider position of cocoa production systems as a land use, as discussed in Chapter 2, to a more detailed view of cocoa system design. This chapter considers specific national contexts, with the aim of understanding causal relationships between anthropogenic drivers and biodiversity. The results are translated into scenario of on-farm interventions to inform “biodiversity-positive” cocoa production.

Chapter 5 presents a more detailed analysis of the benefits and trade-offs associated with biodiversity, built on interviews with farmers and plot-level yield measurements. This not only provides insights into the ecosystem service values of cocoa production systems to farms in West and Central Africa, but also investigates how elements of biodiversity such as vegetation structure, compositional diversity, and functional traits give rise to these benefits. This will enable the design of on-farm interventions that benefit both biodiversity and farmers.

Chapter 6 discusses and synthesises the results of the previous chapters. I use a series of timely and relevant topics to discuss the findings from each chapter in the context of existing research, longstanding debates in ecology and conservation, and emerging trends relevant to cocoa production in the public and private sector. Finally, this chapter closes by suggesting an agenda for future research in this topic, and highlights key messages for decision-makers.

Chapter 2. Is agricultural commodity production at risk from local biodiversity loss?

This chapter is published as “Is agricultural commodity production at risk from local biodiversity loss?” in the Royal Society Biology Letters Journal, at: http://dx.doi.org/10.1098/rsbl.2024.0283

ABSTRACT

Compelling evidence for feedbacks between commodity crop production systems and local ecosystems has led to predictions that biodiversity loss could threaten food security. However, for this to happen agricultural production systems must both impact and depend on the same components of biodiversity. Here, we review the evidence for and against simultaneous impacts and dependencies of eight important commodity crops on biodiversity. We evaluate the risk that pollination, pest control, or biodiversity-mediated soil health maintenance services are at risk from local biodiversity loss. We find that for key species groups such as ants, bees, and birds, the production of commodities including coffee, cocoa, and soyabean is indeed likely to be at risk from local biodiversity loss. However, we also identify several combinations of commodity, ecosystem service, and component of biodiversity that are unlikely to lead to reinforcing feedbacks and lose-lose outcomes for biodiversity and agriculture. Furthermore, there are significant gaps in the evidence both for and against a mutualism between biodiversity and agricultural commodity production, highlighting the need for more evaluation of the importance of specific biodiversity groups to agricultural systems globally.

2.1. Commodity crop production intersects with the threatened biodiversity that underpins ecosystem services

Much of the world’s agricultural land lies within biodiversity-rich areas and is used to produce commodities ‘for export’ at the expense of local biodiversity (Baudron and Giller, 2014; Schwarzmueller and Kastner, 2022). The expansion and intensification of agricultural production have been rapid and are among the most important drivers of global biodiversity loss (Jaureguiberry et al., 2022). At the same time, biodiversity in agricultural landscapes underpins several ecosystem functions, such as wild pollinator activity and the cycling of soil nutrients (Allan et al., 2015; Middleton and Grace, 2004). These functions contribute to the stability of agricultural systems (Cardinale et al., 2012) and their resilience to fluctuations in environmental conditions (Conway, 1987; Frison et al., 2011). Human-mediated impacts on ecosystem services are also increasing: indicators designed to measure pollination, climate, freshwater quality and quantity, the regulation of biological processes, and the provision of food and materials all show considerable declines since 1970 (Díaz et al., 2019).

Observable relationships between agricultural biodiversity and desirable outcomes have led to the idea of a “biodiversity-production mutualism” in agricultural landscapes. This theory suggests that the functions associated with biodiversity contribute to agricultural production (Seppelt et al., 2020). Accordingly, if agricultural expansion and intensification exceed a sustainable limit, ecosystem services will be degraded and crop yields reduced through the loss of functional groups of biodiversity (Aizen et al., 2019; Millard et al., 2023; Synes et al., 2019). For example, increasing demand for commodities that depend on pollination services makes the delivery of pollination services more important to global production landscapes (Aizen et al., 2019). At the same time, increasing land use intensity and the expansion of cropland are associated with falling richness and abundance of insect pollinators (Millard et al., 2021). Systems that impact ecosystem services such as pollination too heavily could become caught in an “intensification trap”, whereby they become increasingly dependent on manufactured inputs to replace lost ecosystem services, reducing the profitability of the system in a lose-lose situation for biodiversity and agriculture (Brown et al., 2019; Burian et al., 2024) (Figure 1).

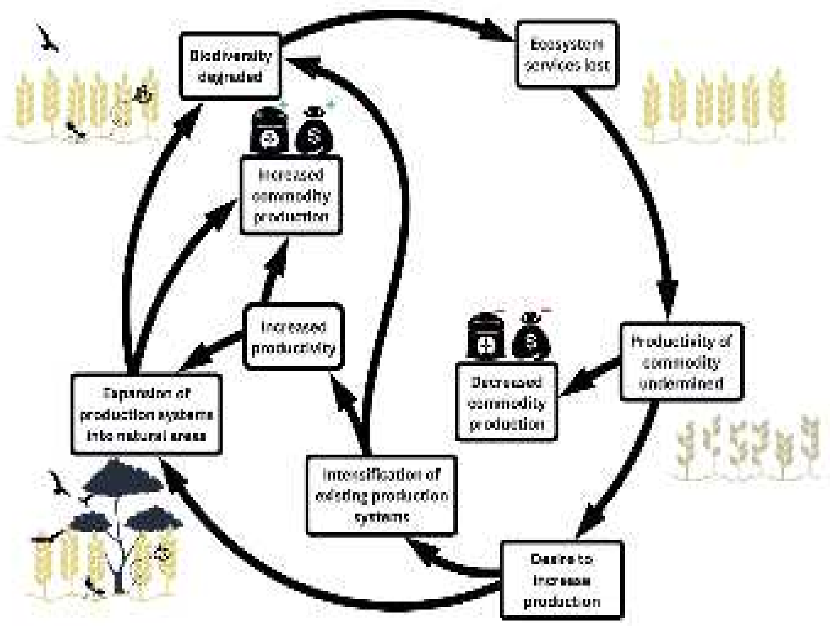

Figure 1. Ecosystem service feedbacks may drive a reinforcing feedback loop with negative outcomes if production is dependent on ecosystem services. Arrows represent hypothesized causal relationships.

At the global scale, simultaneous increases in crop system impacts and dependencies on biodiversity could lead to a future where the production of key commodity crops is jeopardised (Millard et al., 2023). Conversely, the “interdependence” of agriculture and biodiversity means that nature-based solutions could be valuable to support biodiversity and consequently, yields. Utilising nature-based solutions to capitalise on the biodiversity-production mutualism may even reduce the need for continued expansion of agriculture into natural areas (Garibaldi et al., 2021b). Interdependencies are well-known for some species groups such as birds, where context-specific examples of impacts and dependencies are well-described (O’Connor et al., 1986; Whelan et al., 2008). However, the biodiversity-production mutualism is a broad concept, which lacks detailed causal evaluation, and needs contextualisation.

2.2. Projecting the impacts of biodiversity decline on agriculture may overlook context-specificity

Evidence for a biodiversity-production mutualism and the risk of "intensification traps" have fuelled powerful statements about the value of biodiversity to agriculture (Borges et al., 2020; Giannini et al., 2015). This evidence also informs recent global analyses of the risks that declining biodiversity may pose to global agriculture and food security (Aizen et al., 2019; J. Johnson et al., 2020; Millard et al., 2023; Zabel et al., 2019). Global-scale projections of the future of biodiversity and agriculture that incorporate interdependencies between the two often predict large shocks to food systems driven by biodiversity loss (Brown et al., 2019; Millard et al., 2023). At the global level, these findings are important: they highlight a pressing concern that warrants policy responses commensurate with the threat posed to people and nature. However, the biodiversity-agriculture interdependencies underpinning these findings are based on, often broad, theoretical assumptions.(Burian et al., 2024; Garibaldi et al., 2021a). Dependency relationships in particular tend to be simplified at least to crop level; for pollination, this often means using the classification of pollination dependency from Klein et al. (2007) alongside estimates of habitat proximity (e.g. Johnson *et al.*, 2020) or an assumption of linear decreases in yield proportional to crop dependence on pollination (e.g. Millard *et al.*, 2023). Yet, when considering practical options to improve agronomic and ecological outcomes in individual cropping systems, it is important to consider in context the specifics of which biodiversity is important, and the extent to which it is threatened by agriculture (Seufert and Ramankutty, 2017).

The relationship between landscape-level natural habitat, functional group biodiversity, ecosystem service provision, and crop production has been summarised quantitively across many crops and components of biodiversity. Overall patterns indicate evidence of interdependence between agriculture and biodiversity (Dainese et al., 2019). However, analyses to estimate interdependence in individual cropping systems or for specific components of biodiversity are limited by the availability of data, and patterns at the global level may not hold in specific contexts.

Realistically, in any given instance, only a small proportion of species are likely to directly contribute to ecosystem services and yield (Senapathi et al., 2015). These are also often the most abundant species within a given functional group (Winfree et al., 2015), which weakens the overall argument for biodiversity-productivity co-benefits. While there is strong evidence that biodiversity-production mutualisms exist, they are not ubiquitous and need to be established in each case (Duncan et al., 2015; Kleijn et al., 2015). Depending on the specific circumstances, priorities to protect ecosystem service provision and actions to protect biodiversity may not always align (Kleijn et al., 2015; Senapathi et al., 2015). These circumstances can be related to many properties of the production system, including geographic region, farm scale, and cropping system (Cunha et al., 2023; Ricciardi et al., 2021; Tryjanowski et al., 2011). At best, the argument to increase *all* biodiversity within agricultural systems may be inefficient in supporting production. At worst, holding biodiverse agroecosystems as an ideal could risk threatening food security and local livelihoods. Further, farmers can reduce their dependence on natural systems by introducing non-natural substitutes and enhancements. For example, by using bee hives, farmers may reduce the dependence they would otherwise have on nearby forests to provide pollinators (Boreux et al., 2013). Smallholder or 'family' farmers are often particularly dependent on ecosystem services for crop production as they often have fewer resources to invest in external inputs, especially in the tropics (e.g. Waarts *et al.*, 2019). They produce 30% of global food supply (Lowder et al., 2021), highlighting the importance of ensuring tipping points of biodiversity degradation are not crossed.

Crop failure can mean disaster for farmers, so agronomic and ecological research must be thorough and nuanced when evaluating biodiversity as a tool to sustain productivity. If trust and enthusiasm for protecting local biodiversity to prevent food system collapses is to be garnered within agricultural communities, the risk of interdependencies that lead to productivity declines must be established in real-world commodity production systems. Of course, there are many reasons to conserve biodiversity beyond a recognition of its contributions to people – moral, ethical, and biocultural values also guide human interactions with nature (R. Hill et al., 2019). Where such other reasons to conserve a component of biodiversity dominate but are not shared by farming communities, incentives and/or compensation for any trade-offs with farming will need to be found.

2.3. Investigating interdependencies with a case study approach

The goal of this review is to establish, for a range of crops, whether a reinforcing feedback between biodiversity loss and low productivity is likely to exist. We began by combining existing evidence from agronomic and ecological studies. Due to the varied nature of the evidence collected, it was impractical to conduct a quantitative meta-analysis such as has been done for individual services, crops, or biodiversity features globally (Dainese et al., 2019; Tuneu-Corral et al., 2023). Instead, we opt for a case study and narrative approach, focusing on the findings of specific studies, to identify the balance of evidence either supporting or contradicting the two hypotheses. To do this, we reviewed evidence of how biodiversity supports productivity, comparing it to the evidence that those production systems put the same biodiversity at risk. We focus on eight economically and ecologically significant commodity crops, that are predominantly exported and are known to grow in areas of high biodiversity (Ortiz et al., 2021; Schaafsma et al., 2022). Such a selection limits the findings of our review to a specific set of socio-economic and geographic conditions, but should more reliably capture systems where there are material impacts of agriculture of biodiversity, and vice-versa. These were cocoa (*Theobroma cacao* L..), coffee (*Coffea arabica* L., also *C. canephora* P. and others), cotton (*Gossypium hirsutum* L.), oil palm (*Elaeis guineensis* Jacq.), rubber (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.), soyabean (*Glycine max* (L.) Merr.), sugarcane (*Saccharum officinarum* L.) and tea (*Camellia sinensis* (L.) Kuntze).

Our review is targeted at evaluating the evidence for and against two hypotheses, both of which must be true for reinforcing feedbacks between biodiversity loss and low productivity to occur. The first is that, at the local level, the productivity of commodity cropping systems depends upon specific components of biodiversity. The second is that these same components of biodiversity are impacted negatively by the expansion and intensification of specific cropping systems. Following literature searches using the "Web of Science" tool (https://www.webofscience.com/) and constructed search terms (Table S1), we identified the components of biodiversity implicated in delivering ecosystem services. For each component, we reviewed the evidence that cropping systems benefit from biodiversity, focusing on studies which measured both a component of biodiversity and a measure of productivity. We then reviewed the evidence on the impacts of the cropping system impacting each component. This limited our review to components of biodiversity that are already known or assumed to be useful to production systems.

Our initial searches identified a total of 159 scientific papers containing findings about the impacts and dependencies of commodity production systems on biodiversity. This limited number of findings was surprising, though perhaps less so when the specific requirements for evidence on “dependency” are considered. There are only a small proportion of published articles concerning biodiversity and ecosystem services that directly relate the diversity of a component of biodiversity, through the provision of an ecosystem service, to productivity in crops. For instance, the CropPol database, the largest open database on biodiversity-crop pollinator interactions, covers 202 studies over 32 crops - a much larger range than the scope of this study (Allen-Perkins et al., 2022). Thus, we were satisfied a genuine data gap has been identified. Our review covered nine components of biodiversity, some of which were nested, such as “ants” within “insects”. Our follow-up searches for impacts and dependencies of production systems on the components of biodiversity uncovered 46 further sources, including for derivative and prior research linked to sources in the original search, and those in languages other than English. In total, our review covered eight commodity crops, three ecosystem service categories, and nine main components of biodiversity. The total number of ‘findings’ was 151 for dependencies of crop systems on biodiversity, and 163 for impacts of crop systems on biodiversity We summarised these in both a narrative format (Table S2) and figures (Figure 2, Figure 3).

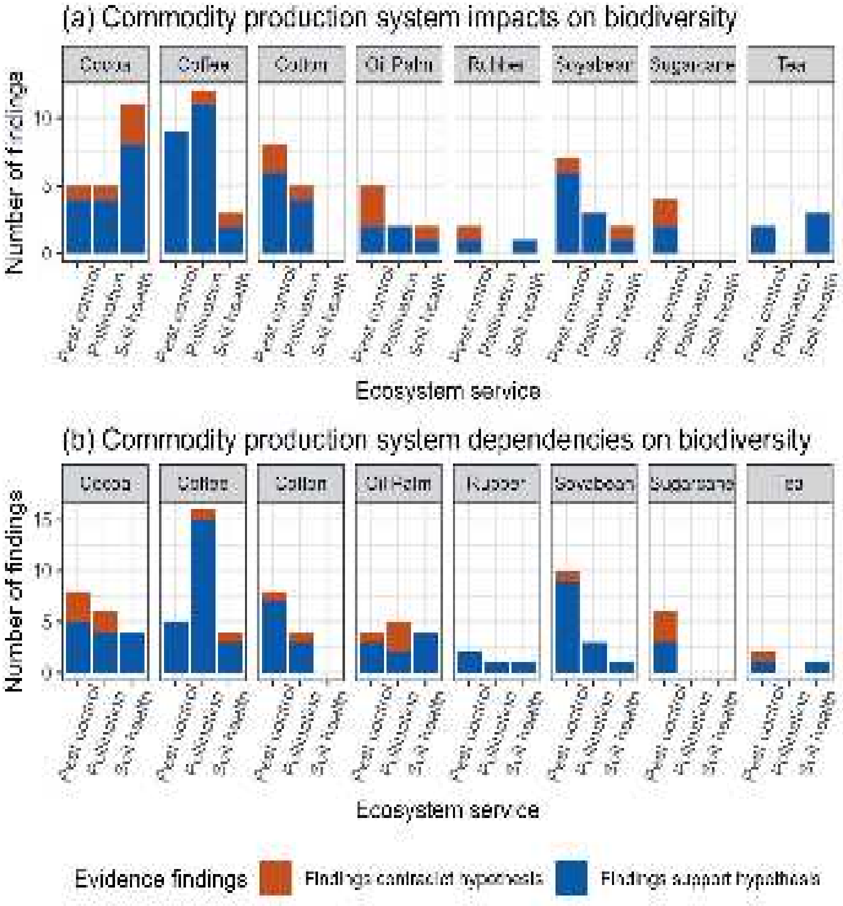

Figure 2. The distribution of evidence collected in the review, arranged by crop and ecosystem service. Plot (a) represents the evidence collected on the hypothesis of dependence, and plot (b) represents the evidence collected on the hypothesis of impacts. Fill colour represents the balance between evidence broadly supporting hypotheses, where red (the top colour) represents the number of findings not supporting the hypothesis or with only context-specific support for it.

To illustrate how these findings translate into the likelihood of observing effects of interdependencies in the eight target cropping systems, we identified findings from the context-specific evidence base simply as supporting (Y), mixed (Y and N), or contradictory (N) to the dependency impact hypotheses. We then summarised the evidence base in a simple Bayesian framework (McElreath, 2020), with a prior assumption that finding evidence to support or contradict the two hypotheses was equally likely:

$$Y_{dependence} \sim Binomial(n_{dependence}, p_{dependence})$$

$$p_{dependence} \sim Uniform(0,1)$$

$$Y_{impact} \sim Binomial(n_{impact}, p_{impact})$$

$$p_{impact} \sim Uniform(0,1)$$

$$R = Y_{dependence} \cdot Y_{impact}$$

‘n’ represents the number of findings related to each of the two hypotheses that were identified for each combination of crop, service, and component of biodiversity; the Y variables represent the number of those studies supporting the hypotheses, and overall risk, R, represents the probability that two pieces of evidence, one concerning each hypothesis, will reflect impacts and dependencies of a cropping system on a component of biodiversity.

2.4. The evidence base for impacts and dependencies is distributed differently among biodiversity groups

As reflected in the combined evidence for impacts and dependencies of agricultural systems on wild biodiversity (Dainese et al., 2019), the findings of this review show consistent evidence both for agriculture degrading the diversity of potentially beneficial species groups, and for the measurable benefits of those species groups to productivity. However, the evidence base for impacts and dependencies is distributed differently among biodiversity groups. When results are separated by their relevant component of biodiversity, evidence concerning some species groups is weaker, or may even indicate a lack of dependence or impact (Figure 3, Figure S2).

Rather than reiterating the findings of each study contributing to the results of this review (Figure 3, Table S2), here we discuss illustrative case studies, apparent data gaps, and departures from the overall trend that interdependencies between agriculture and biodiversity are present in the reviewed commodity production systems. The evidence base substantiates pollination service interdependencies across most implication components of biodiversity. This reinforces the value of broadly-applied models of this ecosystem service, that typically focus on bee species (Chaplin-Kramer et al., 2019). While the evidence for interdependence in the case of other pollinator groups was more mixed, it was still mostly supported. The evidence for interdependencies was strongest in coffee and cotton, though benefits have been found to depend on important interactions between pollinators and other insects.

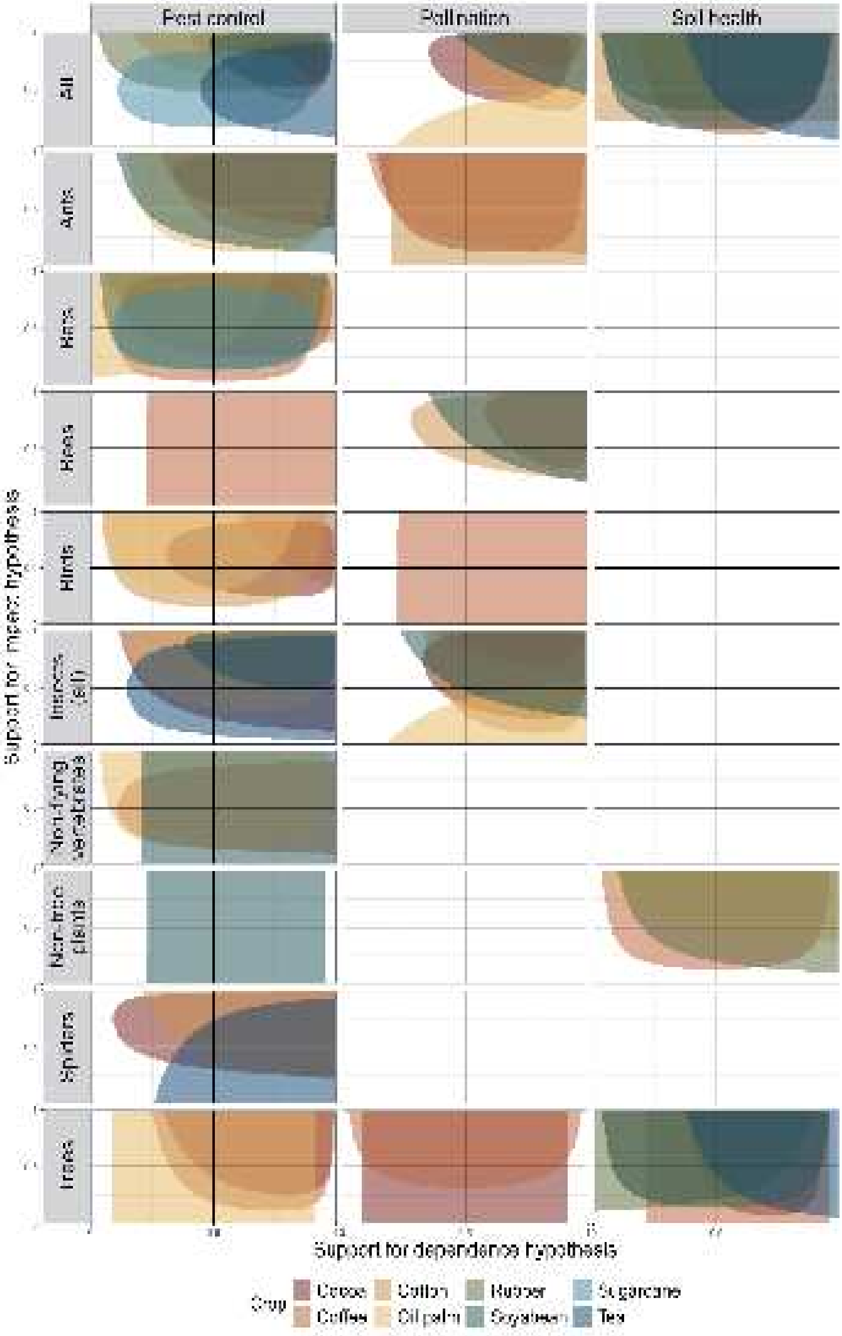

Figure 3. The evidence bases for ecological impacts and agronomic dependencies of commodity crop production systems on biodiversity. Shaded areas mostly in the top-right quadrant belong to combinations of crop, ecosystem service, and biodiversity component, where evidence is likely to support the hypothesis that interdependencies, feedback loops, and "intensification traps"

could emerge due to crop-induced biodiversity change. The shaded regions represent the 95% percentile mass of the joint posterior distribution of findings' support for the impact and dependence hypotheses in the reviewed evidence. This therefore represents the likely outcome of seeking both evidence for dependence and evidence for impacts of a given cropping system via one of three ecosystem services. A complete breakdown of the results by crop is also available for clarity (Figure S2).

Oil palm systems present a well-known departure from typical pollination interdependencies. Oil palm pollination depends on the oil palm weevil *Rhynchophorus ferrugineus*. This species lives within the palm itself and is not known to be affected by the habitat degradation typically associated with oil palm production. Yet, periods of heavy rainfall and nematode infections have been associated with pollinator declines and low yield in oil palm (Woittiez et al., 2017). More research is warranted on interdependencies linked to pollination in some of our crops. For example, cocoa is highly dependent on pollination (Klein et al., 2007), cocoa yields are low in most production systems, especially in West Africa and hand-pollination is known to increase yields (Bos et al., 2007; Groeneveld et al., 2010; Toledo-Hernández et al., 2020). The abundance of *Diptera* in cocoa plantations increased with increasing shade and shade complexity in one study (Toledo-Hernández et al., 2021). Yet, other practices with narrower biodiversity co-benefits, such as adding rotting banana pseudostems to farms, can also benefit pollination (Vanhove et al., 2020). The evidence suggests that enhanced pollination services would benefit cocoa production, but the key target pollinator species and the best ways to promote them remain uncertain.

There are key discrepancies in some findings related to biodiversity dependencies, for instance, in soyabean pollination. One recent article argues that current systems ignore the importance of this service to the crop, and its potential to help maintain global soyabean production whilst sparing land for biodiversity (Garibaldi et al., 2021b). Indeed, different studies find that insect pollinators may contribute to soyabean productivity (Blettler et al., 2018; Cunningham-Minnick et al., 2019; de O. Milfont et al., 2013; Levenson et al., 2022; Santone et al., 2022), and the design and management of soyabean production systems mediates the diversity of insect pollinators (Huais et al., 2020; Levenson et al., 2022; Schulte et al., 2017). This suggests that soyabean production systems may experience feedback loops related to pollination interdependency. Yet, soyabean is a self-fertilising crop; how this can be reconciled with the observed contributions of pollinators to soyabean yields is debated (Cunha et al., 2023). Secondary mechanisms, such as the revival of relegated flowers when pollen is delivered to them, have been suggested as an explanation (Blettler et al., 2018), though further research is needed to make a stronger case for biodiversity within the production system from the perspective of soyabean growers. Overall, nature-based solutions to pollination-limitation, such as on-farm habitat provision (Forbes and Northfield, 2017; Merle et al., 2022) are likely to become more important as pollinator-dependent commodity crops expand and intensify worldwide (Aizen et al., 2019). Indeed, some coffee and cotton supply chains already integrate knowledge of this interdependence in their policies and strategies. For example, Texas, the largest cotton producing state in the USA, has a pollinator conservation plan targeting butterflies (Texas Parks Department, 2016). Nestlé's "bees for coffee" project (Nestlé, 2021) seeks to protect pollinators to benefit their "regenerative agriculture" plans.

For pest control, known to be a more varied and context-specific ecosystem service than pollination (Alexandridis et al., 2021), the evidence showed a more variable risk of interdependencies. Departures from generalised expectations of both impacts and dependencies on biodiversity were found for bats, birds, non-flying vertebrates, and spiders across multiple cropping systems. Most of the studies on the benefits of flying predators did not consider birds and bats separately (Ferreira et al., 2023b; Maas et al., 2013). In the few studies that did separate effects, benefits from bats were lower (Gras et al., 2016; Karp and Daily, 2014), suggesting that birds may have driven most of the service provision in the mixed studies. Studies on invertebrates generally supported both the dependence and impact hypotheses (Costamagna et al., 2008; Jezeer et al., 2019), though some groups such as spiders were not studied in all systems. A recent review of the economic benefits of pest suppression by bats found that no exclosure experiment to measure the pest control benefits of bats in cotton had been carried out (Tuneu-Corral et al., 2023). This may be particularly pertinent in Southeast Asia and the Amazon, which are both global centres of cotton production and bat diversity (Alves et al., 2018; Food and Agriculture Organization of the United Nations, 2020). We did not find any study linking natural enemy diversity to rubber or sugarcane production. Yet, these commodity crops can have significant negative impacts on the diversity of the species groups implicated as natural enemies in other crop production systems (Araújo et al., 2022; Chowdhury et al., 2021; Ramos et al., 2022), so research into their role in these systems is warranted. Conversely, while spiders were identified as a potential group around which a feedback could develop in tea, the negative impacts of tea plantations on spider diversity were found to be limited (Liu et al., 2015; Rubio et al., 2019). Non-flying mammals were not typically implicated as beneficial natural enemies (e.g., Gray and Lewis, 2014), and though there was evidence for pythons as predators of the common rodent pests in oil palm, python diversity has not been linked to yield (Shine and Madsen, 1997). Finally, in agroforestry systems such as those used in cocoa and coffee production, we identified evidence for knock-on benefits to pest control from trees, though more evidence supporting specific species, benefits, and potential trade-offs is needed to fully understand interdependencies in these systems (Daghela Bisseleua et al., 2013; Rezende et al., 2021).

Regarding biodiversity-mediated soil health services, evidence for production benefits was sparser than for other services, though generally positive towards both hypotheses. Evidence largely revolved around plant species associated with cocoa, coffee, and tea production systems. Trees supporting soil health made up most of the evidence (Saha et al., 2010; Sauvadet et al., 2020; Schmidt et al., 2022), though the structure, placement, and identity of trees might be more important than tree diversity itself (W.J. Blaser et al., 2017; Wartenberg et al., 2017). In systems such as cocoa there are also important trade-offs with tree densities, as shade removal allows for higher cocoa planting densities, and too much shade may enhance the spread of common fungal diseases (Niether et al., 2020). For tea, studies so far have found positive results for single-species agroforestry using alder and gingko trees (Mortimer et al., 2015; Tian et al., 2013). As tea plantations are often considered detrimental to biodiversity at the site and landscape scale (Chowdhury et al., 2021), further research into more complex mixes, and the impacts they have on biodiversity, is warranted. Identifying the best range and diversity of species to include in agroforestry systems allows for fine-tuning ecosystem service provision and the maximisation of benefits (Cerda et al., 2020).

Evidence for biodiversity-mediated benefits to the production of sugarcane and soyabean via soil health services was limited; some evidence on benefits from non-tree plants was found, but this was relatively sparse. Increases in soil organic carbon have been associated with incorporating woody vegetation into soyabean systems (Salceda et al., 2022), but no direct connection to productivity was observed. Continuous sugarcane replanting harms both soil biodiversity and production (Pang et al., 2021), so studies into any dependence on biodiversity in sugarcane systems have the potential to reveal interdependencies.

2.4.1. The case of soil microbial diversity

During our search, we identified several studies that implied a role for soil microbial diversity in supporting the focal crop production systems. Most of these studies involve fertility treatments or other soil interventions where microbial diversity is also a response variable (Jiang et al., 2019; Rao et al., 2021; Zhang et al., 2017; Zhou et al., 2020). Studies based on interventions that increase both fertility and microbial diversity or activity cannot establish causality between them and, therefore, do not provide reliable evidence.

2.5. Takeaways and lessons for practice and policy

Broadly, the evidence examined in this study supports the notion that negative consequences can emerge through the impacts of agricultural commodity production on specific groups of local biodiversity, as reflected in recent syntheses (Dainese et al., 2019; IPBES, 2019). Still, interdependencies between nature and agriculture are unique to crop, service, and biodiversity component combinations. Even within similar combinations of crop, service, and component of biodiversity, different patterns emerge. For example, while both wild bees and butterflies were implicated in delivering pollination services in coffee, the evidence base was much stronger for bees. Geographic patterns in crop impacts and dependencies further complicate relationships (e.g. Cunha *et al.*, 2023). Studies investigating only broad functional groups make an inadequate case for protecting groups at a finer taxonomic level that do not provide tangible benefits. Maintaining landscape-level habitat and overall ecosystem health in agricultural matrices overall seems likely to provide benefits to biodiversity with feedbacks benefitting the agroecosystem (Dainese et al., 2019; Garibaldi et al., 2021a). However, it is important for the content of both public policy and private-sector initiatives to reflect a context-specific and nuanced understanding of biodiversity-agriculture interdependencies.

Across the evidence in this review, the most consistent driver of reinforcing feedbacks and lose-lose situations for agriculture and biodiversity was related to insects, which were consistently found to both support production and be impacted by changes to farms and farming landscapes – including pesticide use (Asiimwe et al., 2014; Goldenberg et al., 2022). Tree diversity was also linked to a variety of on-farm benefits as well as knock-on biodiversity and ecosystem service benefits (De Beenhouwer et al., 2013; Niether et al., 2020).

Not all beneficial species are of conservation concern. Many of the useful plants identified by studies in this review are specific species, and not necessarily wild, natural, or native to the regions where their benefits have been measured. This was the case for many cover crops, as well as for some trees (Chen et al., 2019; Mortimer et al., 2015; Tian et al., 2013).

When land-use change or land-use intensification impact biodiversity, there are ‘winners’ and ‘losers’ among groups of species: some are strongly impacted, while others thrive in modified environments (Newbold et al., 2018). In some cases, the species responsible for providing benefits to cropping systems may actually be the “winners”, reducing the risk of biodiversity-mediated feedbacks on agricultural production even as impacts on biodiversity at large grow (Senapathi et al., 2015).

Charismatic, unconventional service providers may benefit commodity production systems, as shown by a scattered but significant amount of evidence. These species, including marsupials in soyabean (De Camargo et al., 2022), owls in oil palm (Zainal Abidin et al., 2022), and reptiles in cocoa and coffee (Monagan et al., 2017; Wanger et al., 2009), are not usually accounted for in large-scale analyses of biodiversity-mediated ecosystem services. However, human-wildlife conflict remains a pertinent barrier to the suitability of some of these species for promotion as nature-based solutions (Baudron et al., 2022). While charismatic species associated with pest control services may come from groups typically associated with conservation gains (Braczkowski et al., 2023), decision-makers need to consider potential local-scale trade-offs, such as danger to people, livestock, crops (Baudron et al., 2022) and property (Mackenzie and Ahabyona, 2012).

The development of effective solutions and generating trust in them requires avoiding oversimplifications. The chain of causality between interventions, biodiversity responses, ecosystem functions, ecosystem service provision, and production outcomes should always be established through context-specific studies. Though interdependencies are likely in many cropping systems, it is important to avoid making projections of agricultural outcomes related directly to biodiversity loss, where evidence is currently limited or not indicative of interdependencies for the relevant species and crop combinations. Continuing to evaluate and publish evidence when biodiversity is found not to support agriculture, or found to thrive in an intensified environment, is crucial to developing and refining reliable interventions. Furthermore, this will help to establish where alternative options to enhancing ecosystem services are most appropriate for different farming systems. Smallholders in particular should have the right to 'substitute' for nature when their livelihoods are dependent on optimal decision-making (Boreux et al., 2013).

Many of the studies included in this review were carried out in systems where some kind of nature-based solution or biodiversity-friendly practice was already implemented. This does not match the reality of many commodity crop production systems, which can be extensive and intensified (Waha et al., 2020). Biodiversity baselines are therefore needed for many species groups and cropping systems, especially in intensive agriculture. If we are to understand the extent and importance of feedbacks in commodity production systems, we must also survey biodiversity and ecosystem services in more intensive systems and degraded landscapes to assess the extent to which biodiversity and ecosystems are also degraded. The "green deserts" of large-scale, intensified agricultural commodity production systems have an as-yet unknown potential for feedbacks between their biodiversity and productivity for most of the crops in this study. Further, there was geographic bias in the studies in this review. When the locations where evidence was found were compared to the overall growing regions of the crops, some areas had evidence focused on impacts or dependence only; other regions represented evidence gaps (Figure S1).

Policies are now in place attempting to limit the damage done to natural ecosystems by commodity production systems. The EU restoration law has specific elements addressing pollinators and farmland birds, among other important biodiversity components associated with ecosystem services in agriculture (The European Parliament And The Council Of The European Union, 2024). The EU anti-deforestation regulation (The European Parliament And The Council Of The European Union, 2023) also attempts to address the demand-driven impacts of globally traded commodities. This regulation covers, among other crops, cocoa, coffee, oil palm, soyabean, and rubber, for which we found evidence for reinforcing feedbacks driven by on-farm changes. If countries importing agricultural commodities wish to stop their trading activities from driving further deforestation, collapses in production driven by feedbacks must also be avoided. Furthermore, countries importing large quantities of agricultural commodities from biodiversity-rich areas need to strike a balance between protecting and restoring their own local biodiversity and protecting biodiversity in the overseas landscapes where commodities are produced (Bateman and Balmford, 2023).

Future trends in global trade will undoubtedly drive further expansion and intensification of key agricultural commodity production systems. Understanding the intricate and context-specific relationships between land use intensity, specific components of biodiversity, ecosystem services, and productivity is crucial to determining the hard limits of such intensification and expansion. Developed rigorously, and implemented well in decision-making, this understanding may be able to circumvent a scenario of biodiversity loss, service failure, and unsustainable production.

Chapter 3. Modelling biodiversity responses to land use in areas of cocoa cultivation.

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ABSTRACT

Interest in economically and ecologically sustainable cocoa has grown in recent years. Cocoa-based agroforestry systems are promoted as a potential win-win option for long-term yields, multiple benefits, and the preservation of biodiversity. Yet, even though recent studies have shown such agroforests can support biodiversity, their value relative to natural areas and open-land systems is not fully known. We estimated the biodiversity intactness (BII) of different land uses associated with cocoa-driven land-use change using mixed-effects models. We distinguished between agroforests established under natural shade and those grown from open land, and compared these to intensively grown cropland (including cocoa monoculture), and primary and secondary forest. We found that species richness in cocoa-based agroforestry systems, under both natural and planted shade, was lower than in primary forests but higher than in open-land systems. However, we found that land-use history influenced the biodiversity intactness of agroforests: whilst open-land-derived cocoa-based agroforestry systems and forest-derived cocoa-based agroforestry systems share similar species richness, open-land-derived cocoa-based agroforestry systems have lower community similarity to primary forest than forest-derived cocoa-based agroforestry systems. The results highlight that high levels of BII can be sustained by retaining the natural shade in existing agroforestry systems, but also that incentivising planted shade agroforestry can enhance biodiversity intactness in degraded areas whilst delivering co-benefits. Importantly, the results highlight that cocoa planning seeking to achieve biodiversity benefits should consider the direction of land use and biodiversity transitions.

3.1. INTRODUCTION

Cocoa (*Theobroma cacao*) is native to the Amazon, but is now grown across the tropics, notably in tropical South American countries, West and Central Africa, India, and Southeast Asia. Between 1961 and 2016, the production and area of land harvested for cocoa doubled (Food and Agriculture Organization of the United Nations, 2020). The majority of new cocoa farms are established by smallholder farmers on recently-cleared forest in an attempt to secure fertile soils, stable environments, and disease resistance (Ruf and Schroth, 2004). With an annual growth rate of over 3% in West Africa (Norris et al., 2010), the conversion of tropical forest to cocoa agriculture, alongside other perennial crops, poses a known risk to forest species. It is important to understand the effects such conversions may have on local biodiversity and ecosystem services, and if paths exist to mitigate these effects and preserve these values.

Different studies have found that cocoa plantations, relative to primary vegetation, host fewer forest species (Bobo et al., 2006), restricted-range species (Oke and Chokor, 2009), and species that play key roles in the functioning of ecosystems, such as dung beetles (Davis and Philips, 2005) and termites (Eggleton et al., 2002). However, there is also evidence that cocoa farms can support high proportions of forest species (Holbech, 2009; Waltert et al., 2005) and species that support ecosystem functioning (Tadu et al., 2014), suggesting that the range of biodiversity outcomes across sites where cocoa is produced is large. It is therefore useful to consider the effects of different practices in cocoa production systems.

Agroforestry systems, where one or more shade-tolerant crops are cultivated in combination with trees (Somarriba, 1992), are thought to provide and support more ecosystem services and higher levels of biodiversity relative to open-land alternatives, including perennial monocultures such as cocoa. Various studies have found that growing cocoa in the shade of natural forest trees provides a habitat for greater biodiversity (Abada Mbolo et al., 2016), and benefits farmers and crops via ecosystem services such as pollination and pest and disease control (Tscharntke et al., 2011a). For example, some (windborne) viral and fungal diseases, such as witches' broom, may be diminished in traditional agroforestry systems compared to monocultures (Andres et al., 2018; Rice and Greenberg, 2000). Carbon storage in cocoa-based agroforestry systems is significantly higher than in monoculture cocoa (Nijmeijer et al., 2019; Schneidewind et al., 2019; Schroth et al., 2016) and agroforestry systems can provide a cooler and more sheltered microclimate (Niether et al., 2020). Additionally, there is evidence that nutrient cycling in agroforestry systems can be comparable to natural systems (Nijmeijer et al. 2019; though see also Blaser et al., 2017). The land-use history and management of cocoa-based agroforestry systems may also affect outcomes for biodiversity and ecosystem services (Bisseleua and Vidal, 2008; Martin et al., 2020). More complex agroforestry systems can support higher levels of some measures of biodiversity (De Beenhouwer et al., 2015), and agroforestry systems under natural shade derived from forests are likely to host higher numbers and densities of certain species – sometimes comparable to that of nearby forests – than open-land derived systems (Sambuichi et al., 2012).

The scale and intensity of cocoa cultivation has risen over past decades to meet growing global demand, including through new more productive hybrids that perform well without the need for shade (Ruf, 2011b). The removal of shade from cocoa plantations can increase yields, and therefore farmer income (Clough et al., 2011; Niether et al., 2020), especially in the short term, as shade trees compete with cocoa trees for resources (Blaser et al., 2018; Sanchez, 1995). This drive for intensification has generally led to a reduction in shade levels and shade tree species diversity in cocoa growing areas (Vaast and Somarriba, 2014). Globally, up to 70% of cocoa is grown under light or no-shade conditions, especially in Indonesia and West Africa (Clough et al., 2009), a trend also seen in other perennial cropping systems (Feintrenie et al., 2010). Moreover, there is a perception that the low light, humid environments created by high shade levels facilitates fungal diseases such as black pod rot (Clough et al., 2009). Yet, there is also evidence that reduced shade increases physiological stress to cocoa trees, their susceptibility to certain pests and diseases, and the amounts of fertilizer and insecticides required to maintain high production levels (Clough et al., 2009). In addition, smallholder cocoa farmers are overwhelmingly poor (Waarts et al., 2019) and unable to invest in the required external inputs. As a result, adoption rates of full-sun cocoa have been low, and no-shade systems are now generally considered inappropriate for smallholder farmers.

Intensification, including by removing shade to increase cocoa production, is also seen as a way to avoid the further conversion of forests, as such intensified systems can be achieved in existing plantations, degraded land or other non-forested lands (Ruf, 2011b). On the other hand, well-managed shaded cocoa-based agroforestry systems may support more sustainable yields over time (Johns, 1999; Nijmeijer et al., 2019) and similarly reduce the need for further forest conversion. Additionally, the total system yield of cocoa-based agroforestry systems may be higher, as they can provide secondary crops besides cocoa (Blaser et al., 2018; Waldron et al., 2012), support income diversification (Niether et al., 2020), and provide a higher return on labour relative to more intensive, monoculture strategies (Armengot et al., 2016). Such advantages can reduce the need for further conversion, though increased profitability can also drive further forest conversion, which means forest protection policies need to be in place.

Despite some trends towards reduced or no-shade systems, large cocoa companies increasingly promote the integration of shade trees in existing cocoa plantations as part of their environmental and social sustainability strategies, as do governments and NGOs in the cocoa sector (Mondelēz International, 2021; Nestlé, 2020; Republic of Côte d'Ivoire, 2018; Republic of Ghana, 2018). Agroforestry is increasingly seen as a win-win solution to meeting an increasing demand for commodities such as cocoa, coffee, and vanilla, all while protecting local biodiversity and supporting ecosystem services. In light of these initiatives, it is important to understand the impacts on local biodiversity of different practices in cocoa production systems and the implications of promoting transitions such as toward agroforestry.

Individual studies into the biodiversity impacts of cocoa-driven land-use change are often limited to just one area, with one set of baseline conditions, and usually focus on one or a few taxa. The range of outcomes among these studies highlight the need for analyses utilising a broad spectrum of data and investigating the effects of variation within cocoa cultivation methods on a wide range of taxa across many locations. However, quantitative analyses of the effects of cocoa agroforestry on biodiversity have so far been limited by the volume of comparable data and the quality of reporting (Norgrove and Beck, 2016).

In this study, we reinterpret and analyse primary data from a wide range of sites and locations in a quantitative analysis of the effects of land-use change in different types of cocoa agroforestry systems, accounting for agroforest land-use history. We model the effects of land-use change linked to cocoa cultivation on whole-community biodiversity intactness. We collated original biodiversity field data from 36 studies (1295 sites) from the cocoa-producing regions of the world. We estimated species richness and community composition, relative to primary forests, in areas with different land uses to produce estimates of biodiversity intactness in areas with varying land uses related to cocoa agriculture. We used the results of mixed-effects models to make inferences about the potential consequences of a) continuing to replace primary forest with cocoa agroforests, b) maintaining current agroforests under natural shade, and c) using planted-shade cocoa agroforestry to rehabilitate open land.

3.2. METHODS

3.2.1. Data collection

Biodiversity data was taken from the PREDICTS (Predicting the Responses of Ecological Diversity in Changing Terrestrial Systems) database (Hudson et al., 2017), and supplemented by targeted literature review (Appendix A). The PREDICTS database brings together data from studies where local biodiversity was sampled from a range of land uses, including different crop types, land-use intensities, and differing means of agricultural production.

Specifically, the database consists of a hierarchical structure of data sources, studies (sampling campaigns within data sources), geographic blocks of sites (as identified by data entrants based on maps and sample locations), and study sites. Each study site has an assigned land use following a standardised classification table (Newbold et al. 2016a).

We identified 31 studies from the existing PREDICTS database as suitable for our analysis. We included any study that included one or more sites described as containing cocoa, contrasting with at least one other land use; these studies generally compared either cocoa cultivation types or cocoa cultivation with other crops or land-use types. We supplemented these studies with four new data sources, accounting for five new studies (Da Silva Moço et al., 2009a; Haro-Carrion et al., 2009; Kone et al., 2012; Rolim et al., 2017a), resulting in 36 studies covering 1295 sites (Table 1). 673 sites were situated in African countries, 330 sites in Indonesia and Papua New Guinea, and 292 in South and Central American countries. Our dataset included 3807 unique taxa (most identified to species level) from across the 36 studies (Table S1).

3.2.2. Data coding

All sites within the PREDICTS database are assigned a category according to the land use present during sampling, as recorded by the field researchers at the time of sampling. The PREDICTS categories (Hudson et al., 2017) include: primary forest, young secondary vegetation (< 10 years old in tropical areas), intermediate secondary vegetation (between 10 and 30 years old in tropical areas), and mature secondary vegetation (>=30 years old in tropical areas), cropland, pasture, plantation forest, and urban. We subdivided the plantation forest into forest-derived cocoa agroforest (defined as cocoa under natural shade from thinned forest or remnant forest trees), open-land-derived cocoa agroforest (where shade trees have been planted), non-cocoa plantation, and “open-land systems”, which included cocoa monocultures, croplands and pasture systems. The information necessary to make these classifications for many sites was already available in the ancillary information held in the PREDICTS database; for other sites it was necessary to refer back to the original study (often a published research article) or to reach out to the authors for more information. Overall, our study included 1295 sites from 36 studies and 23 unique data sources (Appendix A), and included a spread of land uses in primary and secondary vegetation, cocoa-based agroforestry systems, and open-land systems (Table 1). These categories were selected to explore recent suggestions that the land-use history of cocoa agroforests may be one of the principal determinants of their biodiversity value and ecosystem service provision (Martin et al., 2020; Tadu et al., 2014).

Table 1. The distribution of land-use categories in this analysis, with category definitions and their spread at a site- and study-level.

Habitat	**Land use**	**Description**	**Studies**	**Sites**
Primary forest	Primary forest	Natural tropical forest.	36	392
Secondary vegetation	Young secondary vegetation	Secondary forest > 10 years old.	3	72
	Intermediate secondary vegetation	Secondary forest 10 to 30 years old.	8	174
	Mature secondary vegetation	Secondary forest >= 30 years old.	3	7
Cocoa agroforest	Forest-derived cocoa agroforest	Cocoa agroforest grown under natural shade	16	87
	Open-land-derived cocoa agroforest	Cocoa agroforest grown from open-land systems, with “planted” shade	18	377
Open-land systems	Cropland, pasture, monoculture cocoa	Monoculture or polyculture open land (no shade).	8	186
Total			**36**	**1295**

3.2.3. Statistical modelling

We make a space-for-time substitution to model the effects of cocoa production, using studies that compare nearby areas under differing management regimes. A space-for-time substitution compares otherwise-similar sites which have been subject to a defined set of differing conditions, and assumes that a temporal conversion of a site from one condition to another would cause similar changes in response variables to the differences between the differently-treated contemporary sites.

The hierarchical structure of the PREDICTS database, where each study has its own taxonomic focus, geographic area, sampling technique, and sampling effort, means that a large amount of variation in biodiversity response variables can be assigned to differences unrelated to pressure variables. For example, it allows assessing if biodiversity measurements are more strongly determined by the specific study or by the within-study land use. Mixed-effects models can help to elucidate patterns in the response variables that emerge within this hierarchical structure due to factors, such as land use. This method is established and has been used in analyses of local biodiversity intactness (Newbold et al., 2016a). When modelling species richness, we used a model with Poisson errors and a log link; when modelling compositional similarity, we applied a logit transformation to the variable, which gave it a suitable distribution to use a model with Gaussian errors. We used the identity of the study as a random effect to control for variation in taxonomic focus, geographic location, sampling methods, and sampling effort. In our species richness modelling, we tested for the inclusion of the geographic block of sites within a study as a random effect to control for the spatial design of sampling within some studies – though this did not lead to improved goodness of fit as measured by AIC (Table S2). We also tested if the inclusion of an ancillary data layer describing human population density in 2015 (CIESIN, 2017) would improve the species richness model; again, this did not lead to improved goodness of fit and so was excluded from the final model (Table S2). In our compositional similarity modelling, we included the geographic distance between the pair of comparison sites as a predictor in the models as it would be expected that nearby sites would share more similar communities – this emerged as significant and was necessary to control for in our projections of the effects of land use.

We performed all analyses in R version 3.6.2, (R Core Team, 2019) using the lme4 package (Bates et al., 2003) to generate all mixed-effects models of biodiversity responses to land-use(see detail in Appendix A). Models were selected using the Akaike Information Criterion (Table S2). In the interests of analytical robustness, we combined the intermediate and mature secondary vegetation categories because the number of sites with each of these land uses was low.

We developed mixed-effects models for community species richness and an asymmetric measure of community composition relative to primary forest sites (the Asymmetric Jaccard Index). To allow for natural variation in spatial turnover between primary forest sites, we rescaled community composition so that it was equal to 1 for primary forest sites, giving a scale of 0 (completely dissimilar) to 1 (completely similar) in our data. Robustness of the model fit was tested using cross-validation using the influence.ME R package (Rense Nieuwenhuis, Ben Pelzer, Manfred te Grotenhuis, 2009). The richness-based Biodiversity Intactness Index (henceforth BII) is the product of the rescaled coefficients of the models of community species richness and community compositional similarity (Newbold et al., 2016a, 2016b). Thus, BII represents the diversity of a system relative to primary forest: 1 means that it is identical to primary forest, and it decreases down to 0, based on having fewer species or species that are not found in primary forest.

$$BII = \frac{Species\ richness_{LandUse}}{Species\ richness_{Primary}} \cdot \frac{Community\ similarity_{Primary-LandUse}}{Community\ similarity_{Primary-Primary}}$$

Equation 1. The formula for the richness-based Biodiversity Intactness Index used in this study.

3.3. RESULTS

Land conversion results in a decline in species richness (Figure 1a). The land use with the least impact is mature/intermediate secondary forest, whilst the land use with the highest impact is open-land systems. Cocoa-based agroforestry systems maintain a higher species richness than open-land systems, comparable to young secondary forest, but lower richness than in intermediate/mature secondary forest. Species richness impacts do not differ significantly between agroforests derived from forest and from open land (Figure 1a).

The modelled impacts of different land uses on community composition relative to primary forest also differ (Figure 1b). Again, the land-use type with the highest negative impact on community composition is open-land systems. However, here the results for open-land and forest derived agroforests differ: the composition of species in forest-derived agroforests is as similar to primary forests as mature/intermediate secondary forests, whereas open-land-derived cocoa-based agroforestry systems' community similarity to primary forest is between open-land systems and young secondary vegetation.

Though all land uses tested had a lower BII than that found in local primary sites, further differences were observed between the disturbed land uses (Figure 1c). Open-land-derived cocoa-based agroforestry systems and young secondary vegetation have a BII higher than that of open-land systems, but lower than forest-derived cocoa-based agroforestry systems and mature secondary vegetation. The biodiversity intactness of forest-derived cocoa-based agroforestry systems is comparable to both young and mature/intermediate secondary forests.

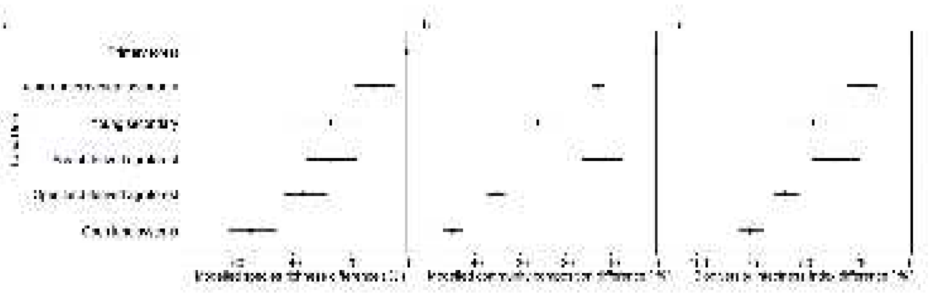


Figure 1. Data and modelling results. (a) modelled species richness difference of each land-use as a percentage-difference from primary forests. (b) modelled community composition difference (asymmetric Jaccard index) between each of the land-uses and primary forest, expressed as the % of species in each land-use that were also found in primary sites. (c) overall modelled effects of land-use change on biodiversity intactness.

3.4. DISCUSSION

3.4.1. Biodiversity in cocoa-based agroforestry systems is lower than in primary forests.

Biodiversity intactness in even the least impactful (forest-derived) cocoa-based agroforestry systems is on average 22% lower BII than in primary forests. The conversion of natural forests to agroforests involves, at a minimum, the removal of understory and thinning of forest canopies (Asare, 2005), and therefore the habitat of some forest species, leading to an overall decrease in the intactness of local biodiversity where this land-use change occurs.

3.4.2. Biodiversity intactness in cocoa-based agroforestry systems is higher than in open-land systems.

Our results show that biodiversity intactness is, on average, 14% higher in cocoa-based agroforestry systems than in open-land systems (Figure 1c). These findings support previous studies that have suggested that the higher complexity of agroforest vegetation, along with the more diverse range of available niches and thermal regulation that forest shade provides, are able to support a wider range of species than open-land farming systems (Niether et al., 2020).

3.4.3. Forest-derived cocoa-based agroforestry systems support higher intactness than open-land-derived cocoa-based agroforestry systems.

Biodiversity intactness in forest-derived cocoa-based agroforestry systems is comparable to intactness in secondary forests, and it is higher than in open-land-derived cocoa-based agroforestry systems. This is potentially due to the retention of natural forest trees and the niches they provide (Abada Mbolo et al., 2016). The two components of our BII – species richness and community composition – react differently to these two systems (Figure 1a and 1b). The species richness in the two land uses is not significantly different; our estimates suggest that host 10-15% fewer species than primary forests at a given site. However, the composition of communities drives the main difference in BII between these two types of cocoa agroforest. Forest-derived cocoa-based agroforestry systems host a community with a higher proportion of forest species than open-land-derived cocoa-based agroforestry system. Agroforestry systems with native shade trees may provide a structural environment more similar to primary forest than systems with planted shade trees. The trees in open-land-derived cocoa-based agroforestry systems likely do not provide this complex structure, leading to a greater divergence from natural communities and a greater number of non-native species too. Forest-derived cocoa-based agroforestry systems may also provide better connectivity, allowing for the movement of forest species between remnant patches of primary forest in a wider matrix than open-land-derived cocoa-based agroforestry systems. This way, forest-derived cocoa-based agroforestry system may improve the beta-diversity of the landscape. However, another reason for the difference in community composition may arise from the matrix itself that surrounds each of these land uses: despite the fact that the distance between agroforests and primary forest is accounted for in our modelling, forest-derived cocoa-based agroforestry systems may be more likely to occur within a mostly-natural matrix, whereas open-land-derived cocoa-based agroforestry systems may be more likely to occur within a mostly-degraded landscape, affecting the kinds of species that appear when each type of site is surveyed.

These results build on previous findings that whilst high-biodiversity cocoa-based agroforestry systems are possible, many, notably those that are derived from open land, have more similar characteristics to open-land systems than they do natural forest (Norgrove and Beck, 2016; Tondoh et al., 2015). There is considerable variability in measurements of biodiversity in cocoa agroforests, as evidenced by conflicting conclusions from across the literature; these can be at least partially explained by the difference between naturally shaded and open-land-derived systems. Our results support the conclusions of Tadu et al. (2014) that the habitat type that cocoa agroforests are established from determines the richness and composition of species that can thrive there. However, it is important to note that the biodiversity condition of agroforests may improve over time if the systems are allowed to mature and undergo some level of succession (Nijmeijer et al., 2019). The mean age of open-land-derived agroforests in our study was ~10 years younger than the average age of forest-derived systems, which may have led to some bias in our comparisons. Time-series of biodiversity surveys in before-after control-impact experiments could help understand and control for such effects.

3.4.4. Forest- and open-land-derived cocoa-based agroforestry systems represent different transitions for biodiversity intactness.

Open-land-derived cocoa-based agroforestry systems have a lower BII than forest-derived cocoa-based agroforestry systems, but it is important to consider the context and directionality of these two land-use changes. Forest-derived cocoa-based agroforestry systems are necessarily established on land that was previously primary forest at some point in the past. Whilst forest-derived cocoa-based agroforestry systems have a relatively high BII, they still have a BII 22% lower than primary forest. Conversely, an open-land-derived cocoa-based agroforestry system could be established on what was previously open, or even degraded, land – though this is not necessarily the case as a primary forest could also be cleared, and then planted on. A transition from an open-land system such as abandoned cleared forest, cropland, pasture or cocoa monoculture, to a cocoa-based agroforestry system, could lead to an estimated increase in biodiversity intactness of 14%. Finally, further degradation of forest-derived cocoa-based agroforestry systems to open-land systems, as is often seen (Sonwa et al., 2007), could lead to an estimated 19% further decrease in BII. Thus, conserving the shaded state of forest-derived cocoa-based agroforestry systems would prevent substantial losses in biodiversity intactness. Whilst not as beneficial for biodiversity as large-scale forest restoration, extensive landscape scale tree cover achieved from a mixture of forest restoration, cocoa-based agroforestry implementation and primary forest protection could prove a practical mitigation strategy for the long-term biodiversity impacts of cocoa-linked deforestation.

3.4.5. Study limitations and further research needs.

In this study, we were unable to discover enough data on biodiversity in cocoa monocultures to include them as a separate land-use category in our models. A recent review of 52 articles comparing cocoa-based agroforestry systems' performance with that of monoculture systems found that only 10% of these addressed any element of biodiversity (Niether et al., 2020). Some data is available, for example a study in Côte d'Ivoire which found that plant species richness in monoculture cocoa was much lower than forests, at levels similar to our "open-land systems" category (Tondoh et al., 2015), but more studies on the impacts of cocoa monocultures on biodiversity are needed to get a fuller picture of the relative biodiversity costs and benefits of different cultivation methods. Further, this study relies on a space-for-time substitution to make inferences about the consequences of land-use change in areas of cocoa production. Yet, before-after-control-impact comparisons have shown that, in the context of tropical deforestation, studies substituting space for time may underestimate biodiversity impacts (França et al., 2016). Long-term controlled assessments of the biodiversity outcomes of cocoa monoculture and agroforestry, as well as assessments of biodiversity change after planting shade on established cocoa monocultures, would provide a more accurate and precise understanding of the impacts of these land-use transitions.

In terms of impact and policy, incorporating modelled biodiversity impacts into maps of land use in regions of cocoa production could provide a better picture of the overall impacts of land-use change on biodiversity in those regions. Further, incorporation of these models into projections of land-use change under different policy scenarios could help to understand how a mixture of forest protection, maintenance of natural shade in cocoa-based agroforestry systems, and establishment of more open-land-derived cocoa-based agroforestry systems on degraded land could mitigate related biodiversity loss at the national scale. At the moment this is limited by a dearth of spatial data on cocoa growing areas and systems, though ongoing developments in remote sensing and classification techniques will hopefully provide new opportunities. Connecting models of biodiversity impacts to those covering yield and other ecosystem services, including measurements of continuous factors such as percent shade cover, will be necessary to better understand trade-offs and synergies in cocoa-related decision-making. Finally, using these models alongside landscape-scale metrics of connectivity and fragmentation could show how cocoa agroforestry might contribute to different national goals for ecosystems and biodiversity.

3.4.6. Implications for decision-making.

Our results have different relevance according to different contexts of historical and ongoing (cocoa-driven) deforestation trends, prevailing cocoa systems and policy objectives in individual cocoa growing countries. In countries such as Ghana and Côte d'Ivoire, with extensive historical and ongoing deforestation due to cocoa and other factors (Brobbey et al., 2020), forest protection, restoration and the increase of tree cover in cocoa landscapes are a major focus of government and private sector sustainability initiatives (e.g. Republic of Côte d'Ivoire, 2018; Republic of Ghana, 2018). For instance, under the Cocoa and Forests initiative in Côte d'Ivoire (Republic of Côte d'Ivoire, 2018), cocoa agroforestry is to be used as a restoration tool in highly degraded forest reserves. For these countries our results show that open-land-derived cocoa-based agroforestry systems (or supported natural regrowth where possible) can support progressive increase in biodiversity intactness in cocoa landscapes and can also lead to an increase in other ecosystem services. On the other hand, there are countries, such as Liberia and Cameroon, with large areas of remaining forest that are highly suitable for cocoa and, in light of historical trends, therefore potentially at risk of conversion (Sassen et al., 2022). Agroforestry systems are more prevalent here than in Ghana and Côte d'Ivoire and their maintenance should be supported to avoid a gradual loss in biodiversity values. Where national policies do not have legal provisions that preclude the conversion of forests outside protected areas or other areas of high conservation value, diverse forest-derived cocoa-based agroforestry systems should be supported.

Whether farmers plant or maintain forest trees in their cocoa farms depends on many factors, including perceptions about effects on productivity and diseases, preferences for tree species and also tree and land tenure (Mbolo et al 2016). Efforts are underway to make tree and land tenure arrangements more conducive to retaining trees on farmland (e.g. Republic of Ghana, 2020). High shading can affect cocoa productivity, though most studies find that shade is unlikely to compromise annual productivity at levels up to around 40% (Blaser et al., 2018), or even 60% (Zuidema et al., 2005). Moreover, agroforestry systems can help improve net farmer income through diversification of products from the cocoa farm (Sonwa et al., 2014; Tscharntke et al., 2011). They may also increase resilience (Norgrove and Beck, 2016), and provide a higher total system yield than an intensive full-sun cocoa monoculture when these other products are accounted for (Niether et al., 2020). Tailoring shade species to local peoples' needs and desires, maximising context specific benefits from agroforestry (Gyau et al., 2015), as well as management of shade species succession, can help capitalise on the potential of shade trees to provide multiple products and services over time (Braga et al., 2019). Finally, yields in cocoa agroforests may be more stable over time – this is evidenced anecdotally in the long persistence and productivity of many of Brazil's "cabruca" cocoa plantations in natural shade; some are still active more than 80 years after the take-off of the globalised cocoa industry in Brazil (Johns, 1999). Evidence on the production costs and profitability of agroforestry is mixed (Niether et al., 2020; Ruf, 2011), though it is established that the initial investment in agroforestry can be high when trees need to be planted in open-land systems (Clough et al., 2009; Martin et al., 2020; Ruf, 2011b). Farmers therefore need support to make such transitions, including through training, appropriate inputs, market access for diversified products, and finance. In and near high-biodiversity areas, highly shaded and diverse agroforestry systems are especially desirable to maintain landscape integrity. Rewarding farmers for biodiversity and other ecosystem services' conservation through payment for ecosystem services schemes such as carbon finance, or other innovative finance mechanisms, will likely be required in such areas (Waldron et al., 2012).

3.5. CONCLUSIONS

Cocoa-based agroforestry systems are an intermediate-complexity system hosting biodiversity greater than that of open-land systems. In planning for better outcomes for biodiversity in cocoa landscapes, it is important to consider the direction of the biodiversity transition. Though forest-derived cocoa-based agroforestry systems host biodiversity of most similar form and substance to natural forest, they are necessarily degradative, and biodiversity benefits are predicated to an extent on retaining natural species (not exploiting them for a benefit). Planted shade systems represent a clear benefit to biodiversity above comparable open-land systems, and can support biodiversity restoration objectives in agricultural landscapes. In support of ongoing cocoa sustainability efforts, both types of agroforest can play a role in improving and maintaining biodiversity in cocoa landscapes. The re-agro-forestation of highly degraded forests and open-land systems with functional, valuable, and useful tree and understory crops may provide further favourable outcomes for farmers, including food security amid volatile cocoa prices. In forested areas where agroforestry systems prevail or where expansion is inevitable, the maintenance and promotion of naturally shaded forest-derived cocoa-based agroforestry systems may provide low-biodiversity-impact options that can still be made economically interesting to farmers. However, the continued destruction and degradation of natural habitats for cocoa agriculture, even alongside restoration planting, may not be enough to prevent further widespread biodiversity loss linked to cocoa. Our results emphasise the importance of protecting remaining natural forest land and promoting the maintenance of existing natural shade systems alongside increased system productivity from cocoa-based agroforestry systems.

Chapter 4. Determining the drivers of plant diversity in cocoa production systems in West and Central Africa.

This chapter will be submitted to the *Journal of Applied Ecology* as “Maney, C., Douma, J.C., Hill, S.L.L., Giller, K.E., and Sassen, M. (2025) Determining the drivers of plant diversity in cocoa production systems in West and Central Africa.”

ABSTRACT

The expansion and intensification of cocoa production systems into the lowland humid forests of West and Central Africa is a major threat to biodiversity. Cocoa companies have recently pledged to transition to “regenerative” biodiversity-friendly agriculture. While knowledge of the biodiversity across the wide range of cocoa production systems in this region is growing, many gaps remain in our understanding of the drivers of biodiversity change, their strength and how biodiversity may respond to regenerative interventions. Potential drivers include farm design and management, landscape effects, and the land-use history of farms. Though these have all been investigated previously, their relative strengths have not been assessed. Here, we used data collected on 168 cocoa farms in four countries (Côte d’Ivoire, Ghana, Nigeria, and Cameroon, West to East), where we paired ecological surveys of trees and understorey plants to information on farm design/management, land-use history, and landscape context. We construct and test causal models to disaggregate the immediate and underlying drivers of tree and understorey plant diversity on the farms, focusing on the differences among countries, and which interventions are most likely to have a positive impact on plant diversity in cocoa farms. We characterise the typical ecological context of cocoa farms across West Africa, describing regional patterns in landscape composition, land-use history, and on-farm shade cover. We find significant effects of landscape, design and management, and land-use history on plant diversity in cocoa farms, and further conclude that the drivers of plant biodiversity vary depending on the history of the farm. Finally, we test scenarios based on possible targets and interventions related to biodiversity in cocoa. Tree planting and regeneration schemes could enhance on-farm plant biodiversity in cocoa agroforestry systems, but current targets from national and corporate strategies leave room for significant further biodiversity loss on-farm. The balance between preventing further deforestation and diminishing on-farm biodiversity in a land system that already covers millions of hectares in West and Central Africa should be carefully considered when implementing demand-side policies to protect biodiversity.

4.1. INTRODUCTION

4.1.1. Deforestation and degradation linked to cocoa production has impacted biodiversity

Cocoa (*Theobroma cacao* L.), native to the Amazon, is now grown throughout the humid tropics (Food and Agriculture Organization of the United Nations, 2020). The ecosystems where cocoa is cultivated are typically biodiverse, and cocoa-related land-use change is linked to biodiversity loss (Maney et al., 2022). Therefore, the historic and continued expansion of cocoa production is a matter of global conservation concern.

Cocoa production is concentrated in the “cocoa belt” of West and Central Africa, which produces 70% of the world’s cocoa (Wessel and Quist-Wessel, 2015). This region is also a biodiversity hotspot (Myers et al., 2000) which has experienced considerable deforestation in the past hundred years (Fairhead and Leach, 2003), much of which has been associated with cocoa (Ruf et al., 2015). Remaining natural habitats are under threat from the continued expansion of cocoa farming: at the landscape level, cocoa farming is still associated with 37% of forest loss in protected areas in Côte d’Ivoire, and 13% in Ghana (Kalischek et al., 2023).

The relationship between cocoa, deforestation, and biodiversity is more complex than simple expansion of area and degradation of natural habitats. Cocoa is grown at a wide variety of intensities, from monoculture plantations to highly complex agroforestry systems (Niether et al., 2020). Cocoa is also established on land with a wide history of use. Planted-shade agroforests are often established on relatively biodiversity-impoverished land such as croplands, whereas forest-derived agroforests are established under and within existing forests (Martin et al., 2020). The introduction of sun-tolerant, hybrid cocoa, and perceptions that shade promotes the fungal ‘black pod’ disease, have led to the increasing dominance of low-shade and monoculture systems in much of West Africa’s cocoa growing region (Ruf and Schroth, 2004).

4.1.2. It is important to understand the drivers of biodiversity change in West and Central African cocoa systems

Biodiversity in cocoa systems is determined by a mixture of intrinsic properties and anthropogenic drivers. An intrinsic property can be defined as a characteristic of a system that is independent of past or present human activities on-farm or in the landscape. For the purposes of this study we consider rainfall patterns an intrinsic property, though there is strong evidence that human-driven climate change is already altering rainfall patterns in the region (Nkrumah et al., 2019). An 'anthropogenic driver' refers to a system characteristic that is a consequence of past or present human activity in the region, whether on-farm or in the surrounding landscape. An example is shade cover, a characteristic of the land-use system that is actively managed by farmers (Abdulai et al., 2018a).

There are several reasons why it is important to disentangle the effects of anthropogenic drivers of on-farm plant diversity in cocoa farms. From a conservation perspective, cocoa is a threat to biodiversity, though significant diversity remains within cocoa plantations and interventions could protect and further enhance this biodiversity. Complex cocoa systems shaded by native tree species could act as refugia for threatened species within heavily-degraded landscapes, meaning cocoa systems could have a role in reducing the extinction risk of endangered species (Sanderson et al., 2022). Cocoa agroforests could also contribute to landscape connectivity, enhancing the integrity of the landscape matrix by providing corridors between remnant forest patches, and providing habitat for animal species (Asare et al., 2014). The extensive network of buyers and traders engaged in cocoa supply chains have broad interest and a widespread understanding of the importance of limiting negative impacts of cocoa on biodiversity. This is translated into the adoption of voluntary certification standards, company policies on "biodiversity-positive" or "regenerative" practices to meet such standards or their own targets (Barry Callebaut, 2023; Mondelēz International, 2021), or into responses to international trade legislation governing deforestation-free supply chains of commodities (The European Parliament And The Council Of The European Union, 2023). Finally, biodiversity in cocoa production systems is important for farmers and farming communities. Farmers across West and Central Africa have broadly positive perspectives on agroforestry systems, with most evidence reflecting an association of agroforestry systems with benefits such as shade for cocoa plants, fruit provision, and saleable goods (Atangana et al., 2021). However, some farmers also associate higher-diversity, high-shade systems with higher humidity and greater incidence of disease. Overall, there is strong evidence that more complex agroforestry systems provide more ecosystem services, greater total system yields (the total yields of all food products in the cocoa system, including cocoa), and greater yield stability (Niether et al., 2020; Sauvadet et al., 2020).

Biodiversity in cocoa plantations has been extensively studied in Latin America, with studies focused on reptiles (Heinen, 1992), mammals (Estrada et al., 1993; Faria et al., 2006; Zárate et al., 2014), invertebrates (Da Silva Moço et al., 2009b; Majer et al., 1994), birds (Faria et al., 2006; Greenberg et al., 1997), and plants (Andersson and Gradstein, 2005; Braga et al., 2019). There have been fewer studies in West and Central Africa, mostly focusing on invertebrates (Eggleton et al., 2002; Room, 1971; Tadu et al., 2014) and plants (Sonwa et al., 2014).

Plant diversity is an interesting target for interventions to enhance biodiversity in cocoa. Plant biodiversity is directly manageable by cocoa farmers and company interventions (Wade et al., 2010), and tree diversity is commonly associated with provisioning ecosystem services on cocoa farms (Niether et al., 2020). Further, plant biodiversity can have knock-on benefits for other species groups, for instance, by providing lower storey habitat for forest birds (Holbech, 2009).

4.1.3. The state of knowledge of biodiversity and its drivers within cocoa systems in West and Central Africa

Although all cocoa systems appear to be less biodiverse than comparable nearby forests, the extent to which they are biologically impoverished differs greatly (Maney et al., 2022). Relative to more complex agroforestry systems, cocoa monocultures are associated with less biodiversity of many groups, including ants, birds, frogs, termites, and midges (Niether et al., 2020). The large variation in the biodiversity of cocoa systems warrants further investigation to understand the drivers. This will give insight into how farms and their surrounding landscapes could be managed to reduce the negative impacts of cocoa production on biodiversity. The relative importance of single anthropogenic drivers of biodiversity has been investigated. For example, a study in Brazilian cocoa farms identified landscape composition as a more important driver of bird biodiversity than local vegetation. Yet, studies of biodiversity in cocoa seldom include more than one or two drivers (Martin and Raveloaritiana, 2022), and, where multiple drivers are considered, the studies are often restricted to one landscape or country (Cabral et al., 2021). A robust model that describes the links between the intrinsic properties of cocoa systems, the anthropogenic context in which they lie, their design and management, and the diversity of plants within them, would allow comparison of interventions designed to support biodiversity.

4.1.4. Potential drivers of plant diversity in cocoa systems

Interventions seeking to enhance biodiversity on cocoa farms mainly target the design of the production system, with a focus on agroforestry. Most studies of tree diversity on cocoa farms assume that tree biodiversity is the result of active choices of farmers (Gyau et al., 2015; Sonwa et al., 2014). Yet, many shade trees on cocoa plantations in West Africa regenerate naturally, and these “spontaneous” regenerating trees have been found to play an outsized role in delivering ecosystem services to farms (Kouassi et al., 2023). Thus, whilst farmers still select these trees (as they decide to keep them or not), the choice for particular species is not always designed *a priori*, and trees on farms are a product of ecological and historical processes as well as decision-making.

The routine management of cocoa is also likely to influence plant biodiversity. Fertiliser application can influence plant communities (Gough et al., 2000), and the regular weeding and planting of (useful native and non-native) plants influences the biodiversity of cocoa understoreys (Cicuzza et al., 2012). Shade management also plays a key role in determining the biodiversity of cocoa plantations. Typically, when cocoa is young and vulnerable to harsh sunlight, a relatively high degree of shade is maintained with trees (agroforestry systems) or bananas (monocultures) (Vaast and Somarriba, 2014). As cocoa grows and more sun is desired, shade can be thinned (Anglaaere et al., 2011). A greater diversity of shade trees is likely to be associated with a more diverse understorey, through seeding from the canopy, shading, and physical habitat provision (Bobo et al., 2006).

The landscape in which a cocoa farm is found influences on-farm plant biodiversity. Farms established in forested landscapes are likely to have a more diverse seed bank of tree diversity, and spontaneously-regenerated tree communities on farms are likely to be richer when surroundings are forested. Landscape forest cover positively influences biodiversity of forest birds in African cocoa (Sanderson et al., 2022), but its effect on plant diversity has yet to be investigated.

The remoteness of farms may lead to a higher diversity of tree species because people lack access to markets to sell timber, or to buy alternatives to natural medicine and fuel (Leblois et al., 2017). The same may be true for understorey plant diversity, as people value the non-timber forest products provided.

Finally, farm age and land-use history are important. In Côte d'Ivoire and Ghana farms tend to lose shade trees as cocoa plantations age (Ruf, 2011b), though recent evidence from Côte d'Ivoire found no relationship between farm age and tree diversity (Boadi et al., 2023). Clear-felling, repeated shade tree thinning, and burning are all part of cocoa land-use practices (Rolim and Chiarello, 2004). Long-term, intensive management of cocoa can mean that tree communities can be slow to return to a natural state after plantation abandonment (Arnold et al., 2021). Agroforestry systems can be established within existing forest, or by planting cocoa and other trees on otherwise open or degraded land (Jagoret et al., 2012). Cocoa agroforestry systems established on forest have been found to host more bird diversity than those established on open land (Martin et al., 2020).

A method capable of disaggregating the effects of different anthropogenic drivers is necessary to understand their relative importance and to design interventions for preserving and enhancing biodiversity in cocoa. Any framework needs to account for each of the three categories of anthropogenic drivers – farm management, land use history and landscape effects – as well as for their shared impacts (Shipley, 2016).

4.1.5. Modelling the drivers of plant biodiversity in cocoa

In this study, we aimed to create statistical models to disentangle the causal effects of direct and indirect anthropogenic drivers on plant biodiversity in cocoa. Such models, called path models would allow to quantify the relative importance of interventions on plant biodiversity . We conducted surveys on smallholder farms across Côte d'Ivoire, Ghana, Nigeria, and Cameroon. We combined data from interviews and biodiversity surveys on 668 plots spread across 167 farms. Farm selection aimed to achieve a spread of management types, landscape composition and land-use histories. We then used piecewise structural equation modelling (following Douma and Shipley, 2021) to estimate the effect anthropogenic drivers on tree and understorey biodiversity, in the context of their interactions, shared causes, and the intrinsic properties of systems that may influence biodiversity. We used the final models to estimate the relative condition of biodiversity under different scenarios designed to reflect interventions to enhance biodiversity in cocoa.

4.2. MATERIALS AND METHODS

4.2.1. Field survey sites and management protocols

Biological surveys and interviews were conducted between March and May 2022 in Ghana and Cameroon, and between March and May 2023 in Côte d'Ivoire and Nigeria (Figure 1). This represents the end of the dry season across the study region. Surveys were conducted on farms where CocoaSoils Satellite Trials are located (https://cocoasoils.org/satellite-trials/).

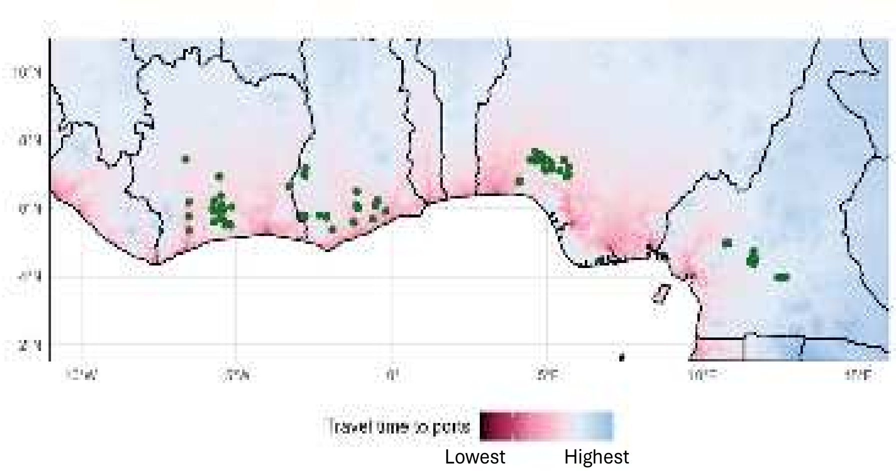


Figure 1. Map of all study farms across the four countries. Underlying colour represents the travel time to ports as used in modelling (log-transformed in this figure). Green points represent the farms where biodiversity was measured (not to scale).

Farms were selected from a wider roster of candidate Satellite Trial farms by stratifying by rainfall (Funk et al., 2015) and surrounding forest cover (Zanaga et al., 2021) where possible. The Satellite Trials comprise an integrated soil fertility management experiment established in 2018 with four "plots" (21 x 21 m grids) on each farm. These plots represent the unit of investigation for the biodiversity models in this study. Each of the four plots on a given farm was subject to a different management protocol (represented by the "Treatments" T1-T4):

- Insecticide was applied to all plots.
- T1 represents a control plot reflecting each farmer's current practices.

- On T2, T3, and T4, regular weeding is done either by hand or using herbicides. Fungicide application and phytosanitary harvest are also performed, sanitary and structural pruning of cocoa trees is carried out and fertilizer is applied.
- The main difference between the T2, T3 and T4 treatment plots is their fertilisation regime. No fertilizer is applied in T2, in T3 government-recommended fertilizers and rates are applied, whilst in T4 fertilizer composition and application rates are based on an offtake model (Vasquez-Zambrano et al., 2024).

4.2.2. Data collection protocols

4.2.2.1. Tree diversity

On every plot within each farm, each tree with any crown area overlapping the plot was recorded. For the purposes of classification, we counted any plant that had a stem diameter of over 10 cm with a canopy at or above the height of the cocoa. Tree height, trunk diameter, crown size, species, and position relative to the plot were all recorded. Trees with their trunk overlapping or within the borders of the plot were counted, whereas the trees outside each plot were only included in the canopy cover estimations. Farmers indicated the origin of trees, and each tree was classified as either: remnant (present before cocoa was planted), naturally-regenerated (which we term “spontaneous recruits”), or planted.

4.2.2.2. Understorey diversity

We sampled the understorey vegetation. In each plot, five uniform subplots were established. These formed a belt transect across the centre of the plot, 20 m long and 5 m wide. In each subplot, the identity and abundance of each plant species was recorded (except trees that had been counted in the tree survey). We recorded the origin of understorey plants, noting which had been planted by the farmer.

4.2.2.3. Land-use history

Farmers were asked about the age of the cocoa trees and the land-use history on each plot. When multiple answers were given for farm age (e.g., where some trees had died and been replanted) the age of the oldest cocoa trees was used to represent the date of most recent land-use change. The previous land use of each farm sometimes yielded complex answers that were simplified and made suitable for modelling by establishing, *post-hoc*, which responses indicated a “forest-derived” cocoa farm, and which indicated an “open-land derived” cocoa farm (we did not distinguish between farms derived from different open land systems such as cropland, fallow, or abandoned cocoa farms). For farms in Côte d’Ivoire, we were unable to collect detailed land-use history data, so we recorded the most relevant previous land use and reconstructed estimated land-use histories *post-hoc* with guidance from field technicians.

4.2.3. Data handling

4.2.3.1. Field data

All survey data was collected using Open Data Kit forms (Hartung et al., 2010), or handwritten tables matching the fields in those forms. We harmonised and merged the survey data in R, checking for any inconsistencies and correcting any persisting systematic measurement artefacts such as unit conversions. All species names were verified using Plants of the World Online (Royal Botanic Gardens, Kew, 2023), and misspellings and synonyms were resolved. Where only local names could be established, we used local and regional booklets and references and worked with local expert botanists to identify likely species names. In some cases, only a genus or family could be discerned, and a small number of plants went unidentified. To assess plot-level biodiversity metrics, pseudospecies “unknown” classifications were used to separate unidentified species from each other. We calculated understorey species richness, tree species richness, and abundance of remnant, regenerated, and planted trees.

4.2.3.2. Anthropogenic drivers and intrinsic properties

The georeferenced location for each farm in the survey dataset was used to attach key environmental variables to the dataset prior to modelling (Table S1). All geospatial driver data was processed using R (R Core Team, 2019) and/or Google Earth Engine (Gorelick et al., 2017) via the ‘rgee’ package. The full code used to process data into our modelling dataset is available at (https://linktocodeonzenodo).

4.2.3.3. Canopy cover

While shade tree density is a commonly-used and easily calculated metric for shade cover in studies on cocoa farms, it is inappropriate as a proxy for canopy cover as the crown sizes of trees are not accounted for. To estimate canopy cover, we produced a simple model of the trees shading each plot. First, we used the location of each recorded shade tree to map the position of each tree on the plot. We then used the crown radius measurements to estimate a circular crown above each shade tree. We calculated the shade caused by the tree by assuming vertical light projection (Figure S1). Finally, we calculated the area of the intersection of the canopies and the plot below to derive the proportion of the plot that was covered by at least one canopy (accounting for overlaps). This was carried out using the ‘sf’ package in R (Pebesma, 2018).

4.2.3.4. Landscape forest cover

Forest is often classified as vegetation 5 m and taller; this was problematic for our forest cover assessment as cocoa itself can grow to a height of over 5 m. To overcome this challenge, we first filtered the GEDI forest height dataset (Potapov et al., 2021) to only include trees above 10 m to create a “forest” layer. We then took a buffer of 2 km from each farm to represent the forest in the immediate surrounding area, and extracted the proportion of that area that was covered by forest. We extracted the human population density (Center for International Earth Science Information Network, 2018) and the accessibility of each farm to ports (Nelson et al., 2019) in the 1 km grid cell that the mean geopoint of the farm fell within using the ‘terra’ package in R.

4.2.3.5. Rainfall

We used 10 km buffers around each farm to extract rainfall information from the CHIRPS dataset (Funk et al., 2015). To account for the different temporal features of rainfall that may have led to variation in biodiversity measurements, we calculated the long-term (2000-2020) yearly average rainfall in each region, the rainfall anomaly in the year prior to the survey on each farm, the typical seasonal rainfall in each area in the four weeks preceding the survey date, and the rainfall anomaly in the four weeks immediately preceding each survey. This extraction was carried out in R and Google Earth Engine.

4.2.4. Modelling approach

We began with an overview of hypotheses related to the anthropogenic drivers of plant diversity in cocoa farms. We then ran simple linear regressions of different sets of variables on biodiversity, comparing a full range of intrinsic properties and anthropogenic drivers to anthropogenic drivers alone, and management variables only (Table S1). This provided information on the total proportion of variation that a simple model using our predictor variables could achieve, irrespective of interactions between drivers or a causal structure.

We then constructed and tested path models based on our set of hypotheses. Path models describe the dependency between variables through assuming direct and indirect causal relationships among them (Shipley, 2016). The consistency of these path models with the data, i.e. whether the hypothesized causal relationship could have generated the observed patterns of dependency between the variables, were tested against a so-called “saturated” model. The saturated model is a model that assumes that all variables are related to each other. Next, we used a likelihood ratio test to test whether the hypothesized models differed significantly from the saturated model, and thus whether the model built on our hypotheses could still sufficiently capture the observed dependencies between variables (Douma and Shipley, 2023). Then, we used the fitted models to investigate the statistically-expected outcomes of certain intervention scenarios in different contexts across the study region. We did this by changing the intervention variables by one unit and explore how the variable of interest would change in response to the direct and indirect effects of the intervention on the outcome variable. The path models represent different hypotheses about the causal links between variables (“paths” in Table 1) linked to plant diversity in cocoa farming systems. For example, tree diversity can affect understorey diversity by providing shade at the plot level (hypotheses D2 and F3, Table 1), or by directly seeding to the understorey below (hypothesis F4, Table 1).

4.2.4.1. Hypotheses

Table 1. The causal hypotheses applied to response variables by the path models and their potential mechanisms. For each driver, different effects on biodiversity (paths) are hypothesized. A causal effect is read as: changing the variable by unit will lead to a change in the child variable, irrespective of the value of other variables. The arrow in each box represents the hypothesised direction of causality, i.e., which covariate is thought to cause changes in the other. The symbols +, -, or +/- represent the hypothesised impact: positive, negative, or mixed.

Path	**Hypothesised relationship (arrows represent hypothesised causal paths)**
Farm design and management	
D1	Tree abundance(s) → Tree richness Remnant tree abundance (+) The more trees in a plot, the greater variety of trees is to be expected on average. Remnant trees comprise a different stock of species than those in planting programmes, so it is expected that they contribute more to richness. Regenerated tree abundance (+) The more trees in a plot, the greater variety of trees is to be expected. Regenerated trees could come from seeds of surrounding remnants or planted trees, so may contribute positively to richness (but not negatively). However, this also means trees of the same species are already likely to be nearby, so richness may be less affected by regenerated than by remnant trees. Planted tree abundance (+) The more trees in a plot, the greater variety of trees is to be expected. Though planted trees tend to come from a small stock of species, they are still likely to contribute to tree species richness.
D2	Tree abundance(s) → Canopy cover (+) The more trees in a plot, the greater the overall cover of the plot by tree canopies. This effect may diminish as shade tree density increases due to increasing overlap.
D3	Plot fertiliser treatment → Understorey diversity (+/-) More fertile soils can be more easily dominated by just a few species. However, this may be mitigated in agroforestry systems as many of the understorey species are planted. Conversely, this effect may be mitigated due to weeding activities.

Land-use history	
H1	Farmland-use history → Tree diversity (+ for forest-derived farms) Plots in forest-derived cocoa farms are more likely to retain remnant tree species and therefore have higher diversity. Plots established on degraded or non-cocoa land are less likely to have retained many trees, leading to low abundance of remnant trees and overall richness.
H2	Farm age → Tree diversity (+/-) As farms age, farmers may choose to adjust the shade tree density. For instance, trees are often used to shield young cocoa and are then removed as the crop matures.
H3	Years since primary forest → Tree diversity (-) The longer since an area has been primary forest, the more transitions are likely to have taken place, each one bringing the potential to lose originally-remnant tree species.
Landscape factors	
L1	Landscape forest → Plant diversity (+) Plots in landscapes with a higher proportion of forest habitat are likely to host richer and more abundant communities of both trees and understorey plants.
L2	Primary forest → Plant diversity (+) A higher area of denser, richer forest trees (characteristics associated with primary forest) near the farm is likely to contribute to a higher richness on farm, especially of spontaneously regenerating trees.
Intrinsic properties interacting with biodiversity and its drivers	
P1	Rainfall → Plant diversity (+) Rainfall (overall or at a critical point in the season) could determine the habitat limits for tree species in areas where cocoa is grown.
P2	Rainfall → Canopy cover (+) Greater rainfall is associated with higher productivity and more growth of shade tree crowns even at fixed levels of tree abundance
Feedbacks among elements of biodiversity	

F1	Tree richness → Canopy cover (+/-) Tree species have different crown sizes. More tree species results in greater variation in which trees contribute to canopy cover. This could have a variable or overall neutral effect on canopy cover, once abundance is accounted for.
F2	Vegetation structure → Understorey richness (+/-) Shade tree crown cover on plots creates the conditions in which many understorey species can thrive. Too much shade, however, may have a negative impact on understorey richness.
F3	Tree diversity → Understorey richness (+) The number and diversity of trees on a plot may have a direct positive impact on understorey richness due to habitat provision, as different crown types could lead to a variety of habitats for understorey plants, as well as through seeding where understorey plants are the saplings of the trees above them.

4.2.4.2. Path analysis

To assess our hypotheses about the drivers of biodiversity on cocoa plantations (Table 1), we constructed path models representing the hypothesized causal relationships among the variables in our study (Figure S2). To account for the possible influence of land-use history (two categories: x and y) on the causal strength between the other predictors and biodiversity, we implemented a multigroup analysis on the hypothesized model structure between plots with open- or forest-derived land use histories (Douma and Shipley, 2021). A multigroup analysis tests differences between groups in terms of the causal hypothesis and/or the strength of the causal relationships.

Hypothesized models were compared against a “saturated” model, i.e. a model where all variables were linked by causal paths, excluding only the paths between pairs of exogenous variables that were not of interest. We compared the likelihood of this model to the likelihood of models including only the relationships hypothesized. To do this, we used a log-likelihood ratio test to assess the probability that the difference in log-likelihood between the hypothesized and saturated model was due to chance, given the difference in their structural complexity (Douma and Shipley, 2023).

There are complex relationships between the forest cover in the broader landscape and the land-use history of the farms. However, unpicking their shared drivers is outside the scope of this study. To account for this, we allowed these variables to be correlated (represented as double-headed arrows in Figure 5). The following variables were assumed to have an unresolved causal relationship between them: forest cover, farm age, and farm 'years since primary forest'. These correlations were modelled with 'copulas' to account for correlated errors in each model (Douma and Shipley, 2023). Further, to assess the possible influence of land-use history as a grouping variable, we constructed four multigroup models allowing land-use history to differentially affect: 1) only the mean of the variables; 2) the strength of the causal relationships between the variables; 3) both the mean and relationships between the variables 4) means, relationships, and the dispersion of variables (Figure S2). From any models that were accepted by the log-likelihood test, we selected the one with the lowest Bayesian Information Criterion (BIC) (Schwarz, 1978) as our final model for the scenario analysis.

All models were constructed using the 'glmmTMB' package in R (Brooks et al., 2017). We modelled the count variables for tree species richness with a Poisson distribution, and understorey richness and the three tree abundance variables using a negative binomial distribution, to account for overdispersion. We modelled the canopy cover and landscape forest variables with a Gaussian distribution. All continuous predictor variables that were not also response variables in the models were standardised using the *scale* function before modelling.

4.2.4.3. Scenario development

To estimate the biodiversity impact of potential interventions, we used our final model to predict biodiversity values based on scenarios of on-farm interventions (Table 2). Well-studied and rigorous tests exist to test the consistency of causal hypotheses in the frequentist framework, in this study using the likelihood ratio test. While these tests are easily understood and commonly applied, piecewise SEMs cannot readily carry forward propagating errors to make predictions on hypothetical scenarios. To overcome this, we re-fitted our model's that were found consistent with our data in a Bayesian framework using the ‘brms’ package in R (Bürkner, 2017). Bayesian analysis has the advantage that it produces a posterior distribution of the parameter values, which then allows to be propagated through the causal chain by sampling from these distributions. When refitting the models in the new framework, we chose relatively uninformed prior distributions to allow models to converge as similarly as possible to the original model fits (flat for slope coefficients and student’s t about intercepts).

We defined a baseline scenario based on the mean values of each predictor, and five intervention scenarios based on simple interventions (such as planting more trees) and a range of existing standards for biodiversity-friendly or “regenerative” cocoa agroforestry. These are linked to certification schemes, national programmes (such as REDD+) or targets set by companies buying cocoa (Table 2).

Table 2. The scenarios investigated and the justification for including them in the study. Where scenarios are referenced, they represent the goals or standards set by various actors in the cocoa sector related to “biodiversity-positive” or “regenerative” cocoa.

Scenario name	**Description/rationale**	**Interpretation for modelling**
Baseline	No changes (intervention variables take median values from each context)	Median values of all predictors for each country and land-use history combination.
Côte d’Ivoire REDD+ strategy (United Nations Environment Programme, 2021)	50 trees per hectare. Overall mean in dataset is 80 trees ha $^{-1}$.	Use medians from national contexts, split 50 trees ha^{-1} between remnant, spontaneously-regenerated or planted according to the existing proportions in each country.
OFI cocoa and forests initiative report 2023 (ofi, 2023)	Increase the number of native forest trees planted to 20 per hectare, while	Use means from national contexts, divide 20 trees ha^{-1} between tree types following the existing proportions of remnant

	providing 30-40% shade canopy on the farms.	and regenerated, retaining the current mean number of planted trees, and fix canopy cover to 40% (assume that 40% cover can be achieved with 20 trees ha^{-1}.
Barry Callebaut/ Ghana Cocoa Board (Barry Callebaut, 2020)	Managing 18-20 mature shade trees per hectare of recommended species.	Divide 20 trees ha^{-1} between tree types (origins), with richness estimates following species in a list of preferred species in each of the countries (Asare, 2005).
		Fix the ‘maximum crown radius’ variable to 12.5 m, indicating (relatively) mature shade trees.
Tree planting	Comparison between spontaneous regeneration and planting programmes	Two additional “planted” trees per plot relative to national medians
Tree regeneration	Comparison between spontaneous regeneration and planting programmes	Two additional “spontaneous recruit” trees per plot relative to national medians

4.3. RESULTS

4.3.1. Variation in the anthropogenic drivers of biodiversity

Patterns in the anthropogenic drivers of plant biodiversity varied within and among the farms in each country, with some distinctive national patterns emerging (Figure 2). Ivorian cocoa farms typically had low shade cover and were found in non-forested landscapes (Figure 2a). About one-half were forest-derived farms and one-half were previously fallow land, mostly after an earlier period under cocoa (Figure 2c). Ghanaian farms were also often in highly degraded landscapes, had longer land-use histories and were mostly open-land-derived. Nigerian farms were younger and had shade comprising fewer different species than in other countries, though the forest cover in their surrounding landscapes was higher (Figure 2b). Finally, farms in Cameroon represented a mixture of young conversion from primary forest and from croplands established in the 1970s-1980s. Relatively few Cameroonian farms were open-land-derived, typically a direct conversion from previous cropland or fallow rather than cocoa.

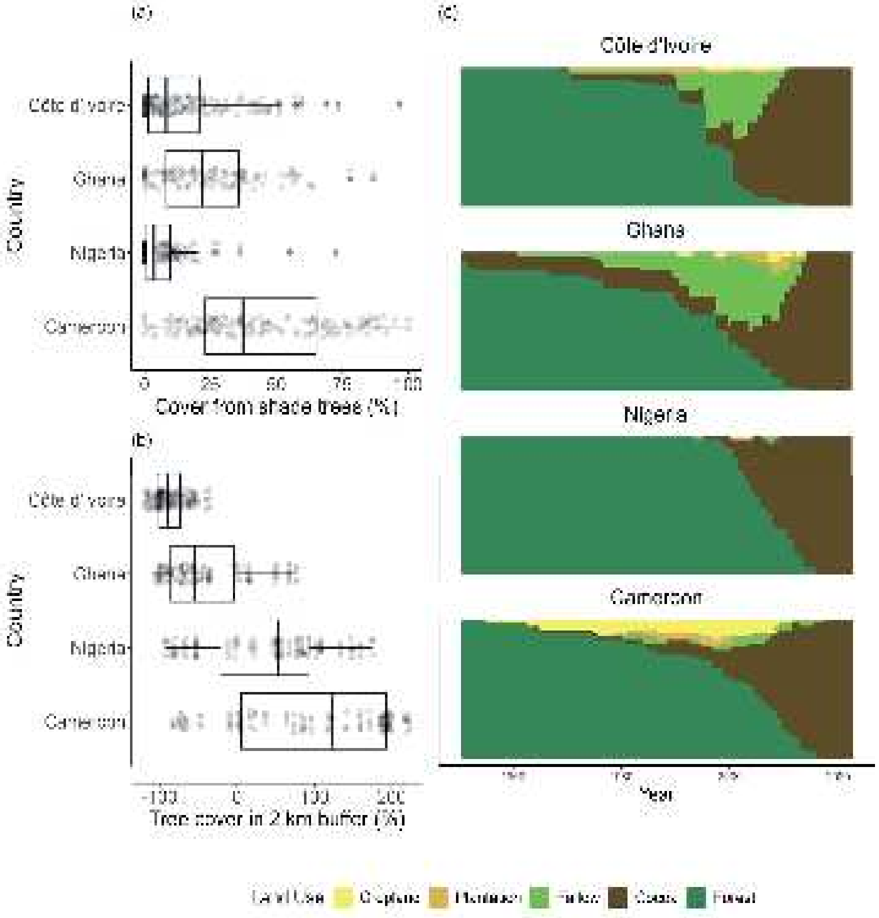


Figure 2. Differences in the distribution of three key drivers of biodiversity in the cocoa farms. (a) The distribution of plot shade cover levels for farms in each country. (b) The distribution of landscape forest in a landscape with radius 2 km surrounding each farm. (c) A reconstruction of land-use history at each farm in the analysis, built from interviews with farmers. The graph is composed by stacking the farm's histories. The colour in each row represents the different land uses in the history of a farm from 1950 (selected as a milestone before the earliest piece of information retrieved) up until the start of the biodiversity surveys in 2022. Farms in each country are sorted based on their earliest post-1950 conversion.

4.3.2. Biodiversity by country/region

Cameroonian farms held the highest on-farm tree diversity, with a mean tree species richness double that of the farms in any other country (Figure 3). Some parts of Côte d'Ivoire were comparable, particularly in the Centre region with higher rainfall. However, richness overall was higher in Cameroon, where 135 species were found over 42 farms, compared to 84 species over 49 farms in Côte d'Ivoire.

Understorey diversity was more similar across subnational regions but varied substantially within each. 38% of plots on farms in Nigeria and a small proportion (~5%) of plots in Côte d'Ivoire had no understorey plants whatsoever when surveyed. There was also some within country variation among the farms, mainly in the understorey diversity. For example, some farms in the Western, Central, and Eastern regions of Ghana had more diverse understories than farms in the Brong Ahafo or Ashanti regions.

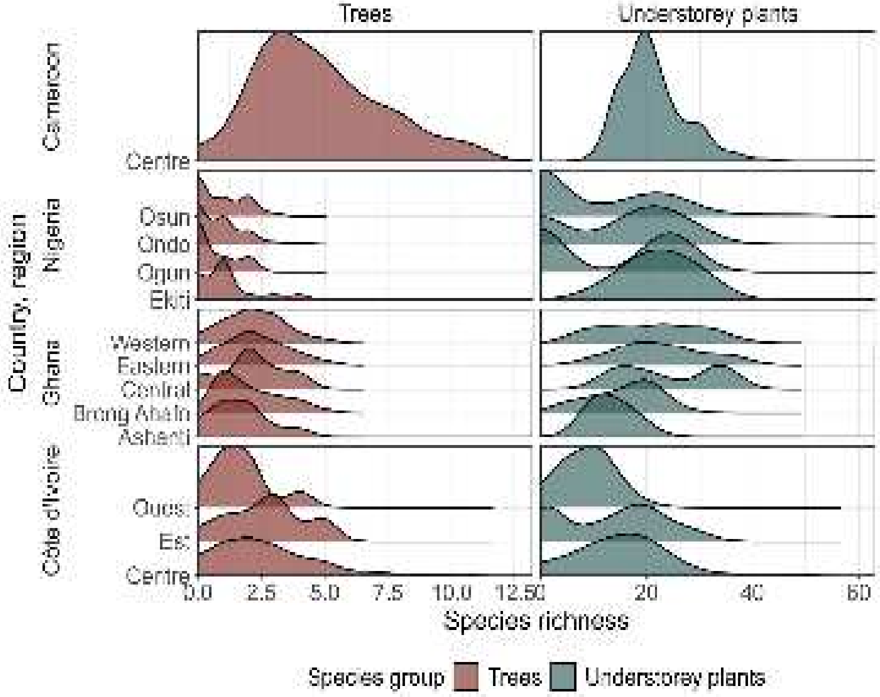


Figure 3. The distribution of tree and understorey species richness by country in the survey, divided by country and region.

4.3.3. Model fit and comparisons

Overall, 82% of the variation in tree species richness could be explained by the full complement of anthropogenic drivers and intrinsic properties investigated. This was much higher than for understorey richness, where only 21% could be explained (Figure 4).

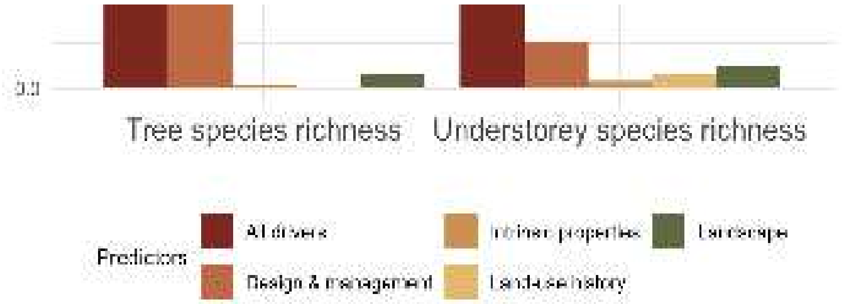


Figure 4. The R-squared values for simple linear models predicting tree and understorey species richness on plots. The size of the bars represents the unique variation explained by each category of predictors.

The explained variance dropped relatively little when the individual "design and management" and "intrinsic properties" were dropped, suggesting that there is a large 'shared' variance between these predictor groups. Yet, while drivers related to design and management contributed most strongly to the model's explanatory power for trees, drivers related to land-use history, landscapes, and design and management all held some unique explanatory power for understorey richness. When comparing models in the multigroup analysis of path models, only one of the potential structures passed the log-likelihood ratio test (df=178, Chi squared difference=71.05, *p*=0.15, Table S2). This was a highly unconstrained model where all paths and intercepts, as well as the dispersion parameter, were allowed to vary by land-use history. Ultimately, the path models were able to explain around 70% of the variation in tree species richness and 40% of the variation in understorey species richness without a multigroup analysis (Table S4).

Significant paths in the model varied between land-use history categories (Figure 5, Table S3). The only common driver of understorey species richness in farms of both land-use history categories was the largest crown size of shade trees, to which species richness responded positively, supporting hypothesis F3. Understorey richness in forest-derived agroforests responded negatively to landscape cropland cover, while understorey richness in open-land-derived systems responded negatively to forest cover and soil sand content, meaning there is mixed evidence for hypothesis L2, and the relationship between landscape factors and plant diversity is mediated by land-use history. Farms with different land-use histories also responded differently to rainfall: in forest-derived systems, understorey diversity correlated negatively with rainfall. In open-land-derived systems, understorey diversity responded positively to rainfall, in line with expectations of hypothesis P1.

In farms of both land-use history type, all types of shade tree contributed positively (though variably) to shade cover (hypothesis F1). They contributed directly but also indirectly to shade cover by enhancing tree species richness, which was associated with higher maximum crown size, and through canopy cover (supporting hypothesis F2). However, there was no evidence that tree richness had a direct positive impact on understorey richness, contradicting hypothesis F3.

We found no strong link between fertiliser application and understorey biodiversity (no evidence for hypothesis D3). Contrary to hypothesis H1, neither forest-derived nor open-land-derived farms were richer in tree or understorey species in the absence of other effects (Table S3, Figure S3a). Yet, farm age was found to have a positive influence on regenerated tree abundance in forest-derived systems (Figure S3f), and on planted tree abundance in open-land derived systems (Figure S3g), seemingly contradicting hypothesis H2. However, in forest-derived farms the relationship between age and remnant tree diversity was negative. On average, remnant trees contribute more to tree species richness than regenerated trees, so tree diversity would be expected to fall with age in forest-derived systems, supporting hypothesis H2 (Figure 5, Table S3, Figure S3).

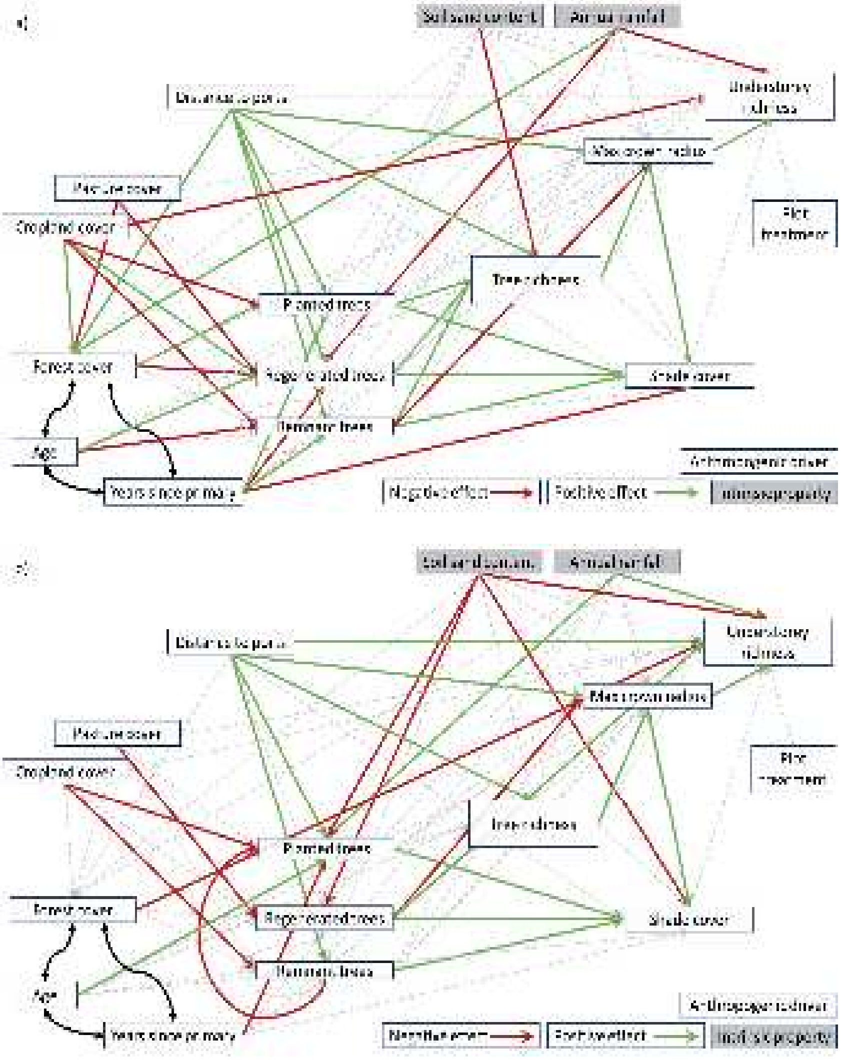


Figure 5. Final path models represented as graphs for each of the multigroup categories 'forest-derived' systems (Figure 5a) and 'open-land derived' systems (Figure 5b). Solid green lines indicate a positive relationship between variables, solid red lines indicate a negative relationship between variables. Dashed grey lines indicate no significant relationship at α=0.05. Solid black two-headed arrows represent where correlated errors were allowed in the model.

The abundance of trees of different origins had only a weak effect on maximum crown size once we accounted for overall richness. Tree abundance was also a driver of high tree richness, and trees of all origins contributed more to species richness in forest-derived systems. Spontaneously-regenerated trees contributed most strongly to species richness in forest-derived systems. Soil sand content was associated with lower tree species richness in forest-derived systems; this was not the case in open-land-derived systems. Overall, the total effect of tree diversity including richness and the three abundance variables on vegetation structure was positive.

Travel time to ports emerged as an important driver of tree diversity and vegetation structure in both forest-derived and open-land-derived systems. Tree species richness, the abundance of trees of different origins, and the maximum crown size were all consistently larger the further from port access a farm was located. This was also true for understorey species richness on plots in open-land-derived cocoa farms.

4.3.4. Scenarios of "regeneration"

Across all scenarios, the simple "planting" and "regeneration" scenarios were most commonly associated with increases in tree diversity, though the degree of expected richness increase was dependent on the history and national context in which the farms were situated (Figure 6). In some contexts, the 'REDD+' scenario gave rise to increases in tree diversity; including in contexts such as Nigeria, where tree density is typically below 50 trees ha^{-1} and most of these are planted trees of one or two species.

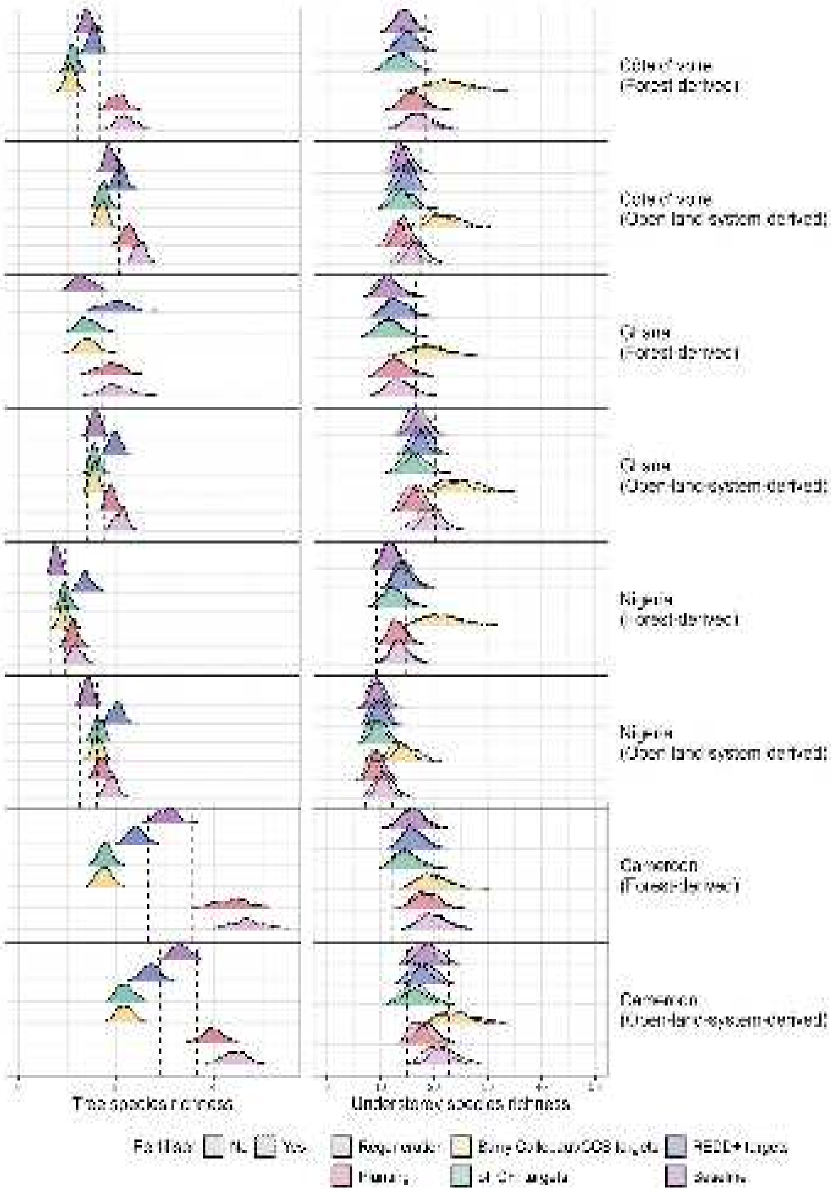


Figure 6. Mean expected plot-level tree and understorey species richness (per plot of 21m^2) in each country-history-treatment context, in response to six potential scenarios. The country and land-use history levels that predictions were based on are shown in groups on the right. The fill colour of the density plots represents the agroforest design scenario applied (Table 2). In the left plot (for understorey richness), two density plots are shown. These represent the scenario run on two datasets: one with treatments 1 and 2 applied (likely no fertiliser), and one with treatments 3 and 4 applied (with fertiliser). Vertical dotted lines show the 95% credible intervals of the baseline scenario in each context.

The ‘Barry Callebaut/GCB targets’ scenario was associated with the highest understorey species richness. This was driven by the requirement for the trees to be “mature”, here expressed by the “maximum crown radius” set to 12.5 m. The only context in which there was not a clear benefit to understorey richness from the specifications of the ‘Barry Callebaut/GCB’ targets relative to the baselines, was in forest-derived farms in Cameroon, where trees in our study tended to be mature, and the median size of shade tree crowns was already high.

4.4. DISCUSSION

4.4.1. Plant diversity and its drivers across four countries

Cocoa production systems in Cameroon were most diverse in terms of shade trees, and those in Nigeria were least diverse. This pattern emerged irrespective of country in our models, seemingly driven in part by farms having greater accessibility to ports in Nigeria, but also by the differences in management and design favoured in each country. Plots in Nigeria often had one or fewer shade trees (mean = 1.09 per 21m^2), which were also from a far more restricted pool of species – often only oil palm was present in addition to cocoa. These patterns ultimately reflect the priorities and preferences of farmers, but are also heavily influenced by national policies, such as the recommended cocoa planting density, which can limit the space remaining for shade trees (e.g., Cocoa and Forest Initiative, 2018).

In the models, understorey diversity was largely driven by the largest tree crown size available on plots, suggesting that the knock-on relationship between tree and understorey plant diversity is mediated by vegetation structure provided by trees (hypotheses F1 and F2), but not directly by the tree species richness (F3). However, overall shade cover was not identified as a predictor of understorey species richness once the largest crown size was accounted for. This suggests that there is an element of direct habitat provision linked to larger trees, to which some trees contribute disproportionately. The effect of large trees on understorey richness, irrespective of total canopy cover, could be linked to habitat variability, i.e. large areas with shade cover and other areas without, providing a spread of shaded and non-shaded niches on-farm.

From a conservation perspective, the vast majority of shade trees recorded in Nigeria are 'Least Concern' according to the IUCN Red List. By contrast, Côte d'Ivoire, Cameroon, and Ghana in particular hosted trees classified as Vulnerable, including *Sterculia oblonga*, *Entandrophragma candollei*, and *Terminalia ivorensis*. Further research into the trade-offs and synergies between species of conservation concern and species of value to farming communities is warranted to design sustainable agroforest that also contribute to biodiversity conservation.

4.4.2. Plant diversity and its drivers vary between farms with different land-use histories.

The plant diversity found in the plots (Figure 3), as well as its relationship with the drivers we investigated (Figure 5, Table S3), differed depending on land use history. This finding highlights the distinct characteristics of forest-derived and open-land-derived cocoa systems, which need to be taken into account when designing management plans to promote biodiversity. There was a key contextual difference between the two countries with many forest-derived farms: Nigeria and Cameroon. Farms were typically younger in Nigeria and held far fewer shade trees, with less diversity. Farms in Cameroon had retained much more of their shade, even when they had been converted from forest much earlier. This could be linked to higher population densities in Nigeria driving high demand for timber, as well as potentially differing perceptions of cocoa system multifunctionality between the countries.

Our results add weight to recent arguments that different baselines should be used when assessing the biodiversity impacts of farms with different land-use histories (Martin et al., 2020). Indicators and standards designed to assess and promote the biodiversity value and "regenerative" status of farms must use a relevant and well-established baseline. Failing to do so could de-value relatively diverse agroforestry systems and incentivise degradation and conversion to other land uses which do not incorporate significant tree diversity. Further, the conversion of natural habitats into cocoa is not an isolated industrial force; it is tied directly to extractive deforestation, poverty, and rural population changes, all of which must be considered (Ngouhouo-Poufoun et al., 2024; Orozco-Aguilar et al., 2021).

Open-land derived systems are more dependent on spontaneously-regenerated trees for their species richness than forest-derived farms. There is scope for policies and standards to promote biodiversity gain in cocoa systems where trees have been lost, as well as promoting the retention of remnant trees on farms (Rainforest Alliance, 2023).

4.4.3. Plant biodiversity in cocoa systems is influenced by external factors, but driven by on-farm management.

We found that some management practices were associated with enhanced on-farm plant biodiversity. As expected, both tree planting and allowing natural regeneration enhanced tree and understorey biodiversity. In the scenarios exercise, simulations allowing trees to regenerate led to increased species richness across all contexts, compared with planting and current baselines. This is because the spontaneously-regenerating stock is richer in species than the diversity of tree species provided or preferred for planting. Spontaneous recruitment would also be expected to have a higher beta-diversity, with different trees emerging spontaneously in various contexts.

Similarly, encouraging long-term growth of trees with large canopies was associated with gains in understorey diversity. We found that, while all trees contribute positively to crown sizes and canopy cover on plots, regenerated trees do so to a greater extent, as their crowns tend to be larger. This could be a unique benefit to the types of species that spontaneously regenerate on cocoa farms that could provide distinct benefits from planted species. As the bulk of the relationship between tree diversity and understorey diversity was mediated through vegetation structure, there are greater knock-on benefits for understorey biodiversity from regenerated trees. These findings imply that promoting natural regeneration as an efficient way to increase tree cover in West African agroforests (Kouassi et al., 2023), may also lead to greater biodiversity. There is evidence that spontaneously-regenerating timber trees in West Africa cocoa plantations grow faster, and reach a viable size for harvesting, faster than (trans)planted trees (Kouassi et al., 2024). On the other hand, planted trees may also provide targeted benefits to farmers, and can be selected in a way that is not achievable through regeneration alone.

The minor differences in plant diversity observed between plots with and without fertiliser use are likely to be explained by an unobserved common cause. For example, fertilised plots generally have higher cocoa productivity, and in response may have been weeded more attentively by farmers. Understorey plant diversity appeared to be resilient to current rates of fertiliser application. Increasing fertiliser use to maximise cocoa productivity could be compatible with maintaining plant biodiversity as a method of sustainable intensification. However, further research on the community composition of plants on cocoa farms relative to natural systems is warranted.

4.4.4. Scenarios suggest that current standards and targets are not ambitious regarding plant biodiversity.

Our simulations, which were grounded in the median conditions in each country, suggested that a typical plot in each of the country-land-use history contexts was already hosting sufficient tree and understorey diversity to meet current national and certification standards (Table 2, Figure 6). This suggests that, based on the evidence from our models and scenarios, current standards leave considerable room for future degradation and biodiversity loss on cocoa farms in most of West and Central Africa. In the most extreme case (forest-derived farms in Cameroon), tree richness could halve under the requirements of standards (Figure 6). Some gains in on-farm tree diversity could be achieved, such as on typical farms in Ghana and Nigeria, if the density of shade trees could be increased to 50 trees ha^{-1} following the REDD+ scenario. This reinforces previous suggestions that increasing the density of shade trees would have knock-on biodiversity benefits (Waldron et al., 2015).

Gains in understorey diversity would be expected under the conditions of the ‘Barry Callebaut/GCB’ scenario, in all contexts. Shade trees in our study were typically immature, especially on farms without remnant shade trees (which tend to be larger). While allowing more shade trees to grow to maturity (as in the ‘Barry Callebaut/GCB’ scenario) could have significant knock-on benefits for understorey plant diversity (Figure

6), this requirement could conflict with the need for farmers to derive benefits like timber from shade trees (Sanial et al., 2023).

There is no universally-agreed certification standard for biodiversity in cocoa systems. Incorporating three elements of biodiversity: high shade tree density, a diversity of native species, and the retention of trees until maturity, would be likely to ensure higher tree and understorey plant diversity within cocoa systems.

4.4.5. The EUDR and demand-side policy implications for biodiversity in cocoa

The accessibility of farms to ports was a more parsimonious explanation for both tree diversity and vegetation structure (maximum crown size, an important driver of understorey diversity) than any other combination of landscape-level effects. Timber harvesting is a key driver of deforestation in West Africa (Leblois et al., 2017), which brings into question whether cocoa production is a 'direct' driver of tree diversity loss. The pervasive negative impact of proximity to ports on all elements of tree diversity in cocoa indicates that, for much of West and Central Africa, irrespective of landscape condition, land-use history, and management and design options, cocoa systems face historic and ongoing external pressures from timber extraction – similarly to natural forests in the region.

Policies governing the international trade of cocoa will play an outsized role in the impact of cocoa production on biodiversity. The EU Anti-Deforestation Regulation (EUDR) aims to limit the amount of deforestation attributable to the commodities it imports by imposing a ban on imports sourced from land deforested after the end of 2020 (The European Parliament and the Council of the European Union, 2023). Even in forest-derived systems, cocoa is most often established on degraded and selectively-logged land; suggesting that producers should not bear the responsibility for tree loss on the basis of their cocoa production alone. The expansion of cocoa into natural habitats is linked to considerable forest loss (Kalischek et al., 2023). While important, this does not speak to the true details of tree diversity loss. If cocoa agroforests are established in already-degraded forests, it makes little sense to judge the ecological sustainability of such farms against a baseline of undisturbed forest. However, as income from cocoa can fund further deforestation and degradation, the full matrix of causality needs to be understood at a microeconomic level (Ngouhouo-Poufoun et al., 2024).

If cocoa is to be grown to supply importers that will not accept deforestation-linked products, open-land-derived cocoa production systems will become more common in all countries. Only naturally-regenerated trees contributed significantly to tree richness in open-land-derived systems (Figure 5b), so policies targeting the toleration of spontaneous tree regeneration, or those explicitly targeting planting for species conservation, will be key to biodiversity-positive cocoa in the future. Policies to reward such diversity-based planting schemes or regeneration would have great potential to increase the biodiversity value of millions of existing hectares of cocoa production systems.

Our results suggest that the long-term retention of spontaneously-regenerated trees is a key strategy by which on-farm biodiversity could improve in West and Central African cocoa systems. However, any suggestion of the potential impacts and benefits of enhancing plant diversity assumes that these interventions are resilient to external drivers – such as timber extraction. Improvements to tree tenure laws in the region (Damnyag et al., 2012) could incentivise natural tree regeneration on farms by protecting farmers' rights to the trees on their land, and promote the retention of trees to maturity (Fischer et al., 2021). This could help to secure ecosystem services for farmers and increase landscape-level tree cover and have knock-on benefits for plant biodiversity.

4.4.6. Caveats and extensions

Some inferences made during the scenarios exercise assume a space-for-time substitution, common in models of this type. In this approach sites of different ages are treated as an otherwise-comparable "chronosequence", where differences are assumed to be due to their different stages of development (Walker et al., 2010). This means that variation among the predictor variables is assumed to be causally linked to the biodiversity variables, and that changing the predictors in one farm to resemble another would lead to the biodiversity shifting to match. Inferences with this assumption are often criticised for ignoring the contextual factors that shape biodiversity on a given farm

(Damgaard, 2019). We attempted to overcome this weakness by using a well-stratified selection of farms that spanned all countries and a range of environmental conditions, as well as through a modelling structure that aimed to account for otherwise-unobserved causes of variation in biodiversity. Yet, we cannot be certain that changes made in one farm to closely resemble another would in turn cause the plant diversity to be similar.

The predictive power of the best-identified model varied widely among response variables. Most notably, while the hypotheses and data were able to explain a third of the variation in remnant tree abundance, they were only able to explain 8 percent of the variation in the abundance of spontaneously-regenerated trees. This supports the hypothesis that distinct causal processes shape the diversity of trees of different origins, and that modelling their abundances separately is best practice for trees in agroforestry systems. The final path model explained 70% of tree species richness patterns and 40% of understorey species richness patterns (Table S4); presumably because understorey vegetation is more responsive to small-scale environmental change than the canopy. For instance, variables that went unobserved in this study, such as weeding intensity or herbicide application, are likely to impact the understorey on a timescale not captured by our management variables.

Landscape forest cover was not a consistent predictor of on-farm biodiversity. Plant communities and farmers seeking specific ecosystem service benefits may therefore not benefit from landscape-scale restoration objectives, warranting more on-farm interventions for biodiversity. In contrast to studies on birds, we find that most plant diversity in cocoa is under the direct control of farmers, rather than a product of the natural environment. Reward schemes for retaining and increasing the use of diverse, native, and endangered tree species could therefore see a large area of West and Central Africa play host to significant further biodiversity within productive lands.

Cocoa yields in West Africa are already low and likely to further decrease as the impacts of climate change worsen growing conditions for the crop in existing production areas (Ariza-Salamanca et al., 2023). Together with the considerable costs incurred to clear land of cocoa, this may result in abandoned cocoa production systems emerging at scale as a land system, at least in the short term. Studies in Brazil and Trinidad comparing the diversity of recovering ecosystems in abandoned cocoa with fallow systems and abandoned open land systems, showing that tree communities do not recover quickly in abandoned cocoa (Arnold et al., 2021; Rolim et al., 2017b). However, no such studies have been carried out in African cocoa production landscapes, where comparing the economic and ecological outcomes of abandoning, regenerating, and restoring cocoa systems is critical to long-term decision making for people and biodiversity.

4.5. CONCLUSIONS

Increases in cocoa production are ultimately driven by demand from global commodity markets (https://tradingeconomics.com/commodity/cocoa) and national policy (MINEPAT, 2020). Such increases in production arise from a combination of expansion, intensification, and regeneration of cocoa farms; all of which have important implications for changes in on-farm biodiversity. Our study shows that considerable plant diversity remains on many cocoa farms. Further, elements of so-called “regenerative” agricultural practices – namely, the retention and restoration of complex, mature shade tree communities – may have direct or knock-on biodiversity benefits in West and Central African cocoa plantations. While land use history is key to explaining plant biodiversity, the evidence for plant biodiversity benefits from complex agroforestry practices are robust and consistent across farms derived from forest or from open land. In the face of increasing demand for cocoa produced in a way that does not contribute to overall trends in biodiversity loss, understanding the baselines and important drivers of plant biodiversity within cocoa farms should not be overlooked in favour of a sole focus on landscape-scale conservation. Ultimately, any drive for more “regenerative” cocoa production systems in terms of biodiversity must define the processes by which interventions will lead to biodiversity benefits, and rigorously monitor and evaluate their ability to do so *in-situ*.

Chapter 5. Mature, diverse shade tree communities are needed to reap broad biodiversity benefits in cocoa agroforestry systems.

This chapter is under review in the *Journal of Applied Ecology* as Maney, C., Hill, S.L.L., Giller, K., and Sassen, M.(2025) “Mature, diverse shade tree communities are needed to reap broad biodiversity benefits in cocoa agroforestry systems.”

ABSTRACT

Maximising contributions to livelihoods and minimising impacts on biodiversity are key goals of sustainable cocoa agriculture. We surveyed 168 cocoa farms in four West and Central African countries, to assess the diversity of shade tree community composition, structure, and functioning. We used these data to model the relationship between shade trees communities and ecosystem services, including cocoa yield, identifying the most important traits of trees and shade tree communities preferred by farmers.

Tree-level traits can be used to predict their benefits and downsides to farmers. Taller trees were considered more useful for construction, and fruiting trees for food. Traits such as evergreen leaf habit were linked to trade-offs between benefits to food provision and costs in the form of competition with cocoa. Similarly, farms with more trees, and larger trees, were more likely to provide provisioning ecosystem services like timber for construction for to sell, as well as cultural services like recreation/rest. Farms with more fruiting trees were more useful in providing food both for farmers and to go to market.

When shade tree diversity was low, maximum yields were predicted at low shade tree density, in line with current recommendations of 20 trees ha^{-1}. When shade tree communities were more diverse, maximum yields could be achieved at higher tree densities of up to 100 trees ha^{-1}, though they were lower overall. Typical agroforestry recommendations such as 30-40% shade cover can be achieved in a variety of ways, using tree communities that promote different values of cocoa systems. But this standard alone does not always accommodate benefits to yield and ecosystem service provision. Within these boundaries, compositional, structural, and functional traits of shade communities could be optimised to maximise yield and a number of ecosystem services simultaneously.

However, most yield and highly-valued ecosystem service benefits are dependent on large, mature trees, which can take longer than the productive lifespan of cocoa trees to grow. Guidance should move beyond shade cover alone to accommodate farmer preferences and the role of structure and function in supporting ecosystem services, including a steady supply of the most important types of trees to ensure sustainable production.

5.1. INTRODUCTION

Cocoa is a major commodity crop grown across the tropical lowlands of West and Central Africa. The majority of the world's cocoa is produced in this region, with the most important producing countries on the continent being Côte d'Ivoire, Ghana, Nigeria, and Cameroon. Cocoa farming is associated with deforestation and loss of biodiversity throughout its production region, including in protected areas (Kalischek et al., 2023). Biodiversity within cocoa farms is also at risk from tree removal and intensifying agricultural practices (Rolim and Chiarello, 2004). At the same time, cocoa systems are highly dependent on biodiversity for ecosystem services – the benefits to people that are obtained from natural systems (IPBES, 2019). Cocoa farmers value the services biodiversity provides to cocoa (e.g. pollinators, natural pest control) and more broadly (e.g. shading, wild foods, medicine) (Smith Dumont et al., 2014), but also experience trade-offs with biodiversity, largely due to excessive shade cover, competition, and increased disease pressure on cocoa (Ambele et al., 2023; W. J. Blaser et al., 2017).

Agroforestry – the inclusion of trees in agricultural systems – is commonplace across West and Central Africa. Therefore, a key question is how to design cocoa agroforestry systems that maximise benefits to yield and the ecosystem services favoured by farmers, while minimising trade-offs with biodiversity. The integrity and long-term health of forest ecosystems depends on their compositional, structural, and functional diversity (Carter et al., 2019). Yet, the extent to which these determine the processes underpinning ecosystem service provision in cocoa agroforestry is less clear. It has been suggested that the traits of accessory species (here, we focus on shade trees) could be key determinants of yield and of other ecosystem services (Wood et al., 2015).

There is considerable debate concerning the role of shade trees as essential service providers or hindrances to cocoa production (Abdulai et al., 2018a; Kohl et al., 2024). This highlights the complex and context-dependent nature of the role that agroforestry plays. A better understanding of the importance of shade tree community composition, structure, and function may help to maximise benefits and minimise trade-offs of the trees with cocoa (Blaser-Hart et al., 2021). Recent studies have investigated the role of shade trees and their traits in supporting cocoa systems. Composition, structure, and function are all suggested to be important in supporting cocoa systems and protecting biodiversity. However, trade-offs with shade trees are likely. For example, cocoa yields increase with distance from some shade trees (Kohl et al., 2024).

Cocoa systems vary widely, but typically host around half the species biodiversity of primary forest (Maney et al., 2022; Niether et al., 2020). There is limited evidence directly linking biodiversity and yields in cocoa, though studies in comparable agroforestry systems like coffee have shown that biodiversity is not necessarily always at odds with yield (Wright et al., 2024). Greater shade tree diversity is sometimes linked to better soil fertility (Wartenberg et al., 2020), and sometimes not (Wartenberg et al., 2017). The relationships between shade tree community composition and cocoa yields are therefore likely to be context-dependent, and to vary with the structural and functional traits of the trees. Generally, excessive tree diversity in cocoa systems is considered to generate more trade-offs than benefits (W. J. Blaser et al., 2017).

Structural traits of shade tree communities can also influence yield and other ecosystem services in cocoa systems (Jagoret et al., 2017). This is recognised by sustainability initiatives in the region, which typically target 30-40% cover from shade trees (Cocoa and Forest Initiative, 2018; Mondelēz International, 2023). Benefits from shade begin to tail off at shade cover above 30% due to increased competition for light, attracting pests, and allowing the spread of fungal pathogens (Blaser et al., 2018). The density of shade trees may be just as important as their canopy cover, due to below-ground as well as above-ground competition. Guidelines for shade tree density have been proposed (Barry Callebaut, 2023; Rainforest Alliance, 2023), though it is not clear on what scientific evidence these are based. However, other traits of the shade tree community are likely to be important. A study in Ghana concluded that yield, adaptation to climate change and climate mitigation benefits were highest with shade tree canopies that are elevated above the cocoa (Blaser-Hart et al., 2021).

Functional diversity of shade trees in cocoa systems varies widely from single tree species to highly multifunctional systems. Farmers in cocoa and coffee systems select for trees with certain functional traits, such as high leaf nitrogen content, low wood density (fast growth for wood production), and fruit production (Isaac et al., 2024). Shade trees with these specific traits also provide measurable benefits to ecosystem services (Addo-Danso et al., 2024; Sauvadet et al., 2020). In poor soils in Cameroon, shade tree litter traits predicted soil fertility: trees with readily-decomposing leaf litter increased soil C and N, although cocoa yields were not affected by the five trees investigated (Sauvadet et al., 2020). Pest arthropods abundance was diminished, and arthropods associated with ecosystem services were enhanced with denser shade in Cameroonian cocoa farms (Jarrett et al., 2023).

In this study we surveyed 168 farms across four countries: Côte d'Ivoire, Ghana, Nigeria, and Cameroon. We combined tree survey data, data on yields and functional traits of the surveyed tree species with farmer interviews, and developed statistical models of the relationship between shade tree communities and cocoa systems, to address the following questions:

1. Do the functional and structural properties of individual shade trees on cocoa plantations explain the values and trade-offs that farmers associate them with?
2. Is variation in ecosystem service at the farm level best explained by the diversity of shade tree species, shade tree structural traits, or shade tree functional traits?
3. How do the composition, structure and functional traits of shade tree communities affect cocoa yields?

5.2. METHODS

5.2.1. Data collection and processing

5.2.1.1. Site locations & ecosystem services

The sites selected for this study were located across Côte d'Ivoire, Ghana, Nigeria, and Cameroon, and were subdivided into one to five sub-regions per country (Figure 1). The 168 farms surveyed were participants in the so-called CocoaSoils Satellite Trials, an integrated soil fertility management experiment in which four plots on each farm are subjected to different management protocols with a focus on fertilization regimes (Vasquez-Zambrano et al., 2025). Yields are recorded regularly on these plots, with the earliest records starting in 2021. We surveyed the shade trees with crowns overlapping each plot, identified the trees and measured structural traits of each tree. These surveys were undertaken together with the farmers, who were asked about the relative benefits and trade-offs associated with each tree. Farmer interviews were open and conducted in the local languages; interview teams interpreted these and recorded responses in English. During analysis, we divided responses into eight main categories comprising six benefits and two trade-offs: construction/ timber, shade for cocoa, food (for consumption), marketable goods, medicine, fertility/ benefits cocoa growth, ‘competition with cocoa’, and ‘attracts pests/diseases’.

We also interviewed each farmer with respect to the overall value of their cocoa systems for several ecosystem services, namely construction, food, tools, fuel/firewood, medicine, marketable goods, ornaments and tradition, basketry and cordage, hunting, recreation, and future security (Sanial et al., 2023; Sassen and Jum, 2007; Sheil D. et al., 2001). We asked how farmers considered their cocoa systems to be useful for these eleven ecosystem service categories, with the possible interpreted options being “Not at all useful”, “Less useful”, “Useful”, and “Very useful”.

5.2.1.2. Compositional traits

For each plot and farm, we summarised the total abundance, species richness, and (inverse) Simpson index (Simpson, 1949), which represents the evenness of communities, with 0 being a single species and 1 being perfectly even. We transformed abundance into density by comparing the size of the plots (21 m^2) to one hectare.

5.2.1.3. Structural traits

We calculated weighted means for structural traits of each plot. Mean canopy height was weighted by crown size, mean crown size was unweighted, and tree height was weighted by tree basal area. We calculated total shade cover on each plot by recording the position of each shade tree relative to the plot and measuring its crown radius. Modelling each crown as a circular disc centred on the position of the trunk, we estimated the total overlap between all crowns and the plot, in order to exclude overlapping areas.

5.2.1.4. Functional traits

We gathered data on tree functional traits from the TRY database (Kattge et al., 2020). Out of necessity, we selected traits that had good coverage in the TRY database, aiming to filter the site data to remove only a small proportion of site data. We had to drop information on root depth, which was not available for any tree on over 50% of the plots. In the end, the selected traits allowed for a complete dataset of 445 distinct tree-containing plots. The final traits included were:

- Specific Leaf Area
- Wood density
- Leaf nitrogen content
- Nitrogen fixation capacity (classified as yes/no)
- Fruiting type (classified as none/fleshy/dry)
- Phenology type (classified as evergreen/deciduous)

These traits were available for 1832 of the original 2508 trees surveyed. 113 trees were identified to genus level only and were directly assigned their genus-average values for traits. 212 trees were not identified during the surveys, and complete trait data was unavailable for a further 464 trees species.

When assigning trait values, we started by identifying the TRY species IDs for all identified tree species. If a trait value was not available for a certain tree species, it was replaced with a genus-averaged value, if available. 61 trees were assigned trait values at the genus-level because species-level trait data was missing.

We calculated community-weighted means for each trait per plot, weighting by crown size if the trait was leaf-based, and otherwise by basal area. Community weighted mean trait values excluded trees for which trait data was missing, and plots without at least one measurement for each trait were excluded from the analysis.

5.2.2. Final datasets

Our final tree-scale dataset contained records of 1832 trees, each with a complete set of trait data. The farm-scale modelling dataset for ecosystem services covered 143 farm-level sets of interview response data and associated shade tree trait information. The final plot-scale modelling dataset for yields covered 441 plots on 143 farms, each with a complete set of yield and predictor variables.

5.2.3. Modelling approach

In all regressions, we tested and took steps to account for multicollinearity prior to model refinement. In the generalised linear mixed-effects regressions predicting tree-scale values and trade-offs, we used adjusted generalized standard error inflation factor (aGSIF) values with a threshold of 1.6 to flag and remove terms from highly co-linear predictor pairs (following Fox and Monette, 1992). In the generalised additive models (GAMs) of ecosystem services, we used 'concurvity', a measure equivalent to collinearity in the GAM setting, to identify highly "concurve" pairs of variables using a threshold value of 0.5 (Ramsay et al., 2003).

5.2.4. Tree-level benefits and trade-offs

To model tree-level benefits and trade-offs, we used mixed-effects logistic regression models for each category of value and trade-off. We constructed one model per benefit/trade-off, and tested for the effect of all the traits on that benefit/trade-off.

We used a farm-level random intercept to account for the random variation in the perspectives of respondents on the value of trees in general (irrespective of their traits). We tested the inclusion of this random effect by comparing the AIC of models with and without it. In all cases, it was found to significantly improve the models' fits. We then used backwards stepwise selection to identify the most parsimonious model structure using AIC values (Table S1).

5.2.5. Farm-level ecosystem services

To model farm-level perceptions of the ecosystem service values of cocoa, we created mixed generalised additive models (GAMs) using the ‘ocat’ fit family, to fit ordinal regressions predicting the Likert scale values assigned by the farmers to each the ecosystem service in the interviews. We considered GAMs appropriate for this question as we began without fixed expectations of the form of the relationship between expected complex relationships between traits and values. We had collected data from a wide range of sites across the West African cocoa-growing region, so we were interested in predicted effects within the range of our observations.

We constructed one model per ecosystem service category. We began by identifying the most informative level for a random intercept, testing no random effect, country-level random intercepts, and country-region combination-level random intercepts. We selected these using AIC and included them to account for patterns observed in differences between farmers’ perceptions of the ecosystem service values of cocoa farms across regions (Figure 1b, Table S2). We carried out an equivalent to typical linear regression model selection using the ‘shrinkage smoother’ approach (Marra and Wood, 2011). Here, the effects of variables not contributing to a parsimonious model are smoothed to zero during the fitting process, effectively removing them from the model while retaining information on which variables were tested.

5.2.6. Cocoa yields

To model yield relationships with community-weighted mean trait values, we fitted another GAM in the same manner as the ecosystem service models. When modelling the effects of shade tree community traits on yield, we used a normal distribution with a log link to ensure a normal distribution in the model residuals. We used a farm-level random effect to account for the large proportion of variation in plot level yields related to on-farm context, design, and management, which was not of concern for this analysis. Null model testing confirmed that a farm-level intercept outperformed a country or subnational region-level random intercept (ΔAIC = -714). We tested the model with a range of compositional, structural, and functional traits as potential predictors (Table S3). When modelling yield, we accounted for both the number of trees planted and the fertilisation regime of the plot. Again, the “shrinkage smoother” approach was used to refine the model (Table S3).

5.3. RESULTS

5.3.1. Shade tree traits vary by country

National shade cover averages varied widely, between 11% in Nigeria and 41% in Cameroon; shade tree density also varied between countries, though this difference was less pronounced. Mean shade tree sizes in Côte d’Ivoire, Ghana, and Nigeria were similar, but were much larger in Cameroon (Table 1).

Table 1. Mean values of shade tree composition and structure by country. All values represent plot means with standard error.

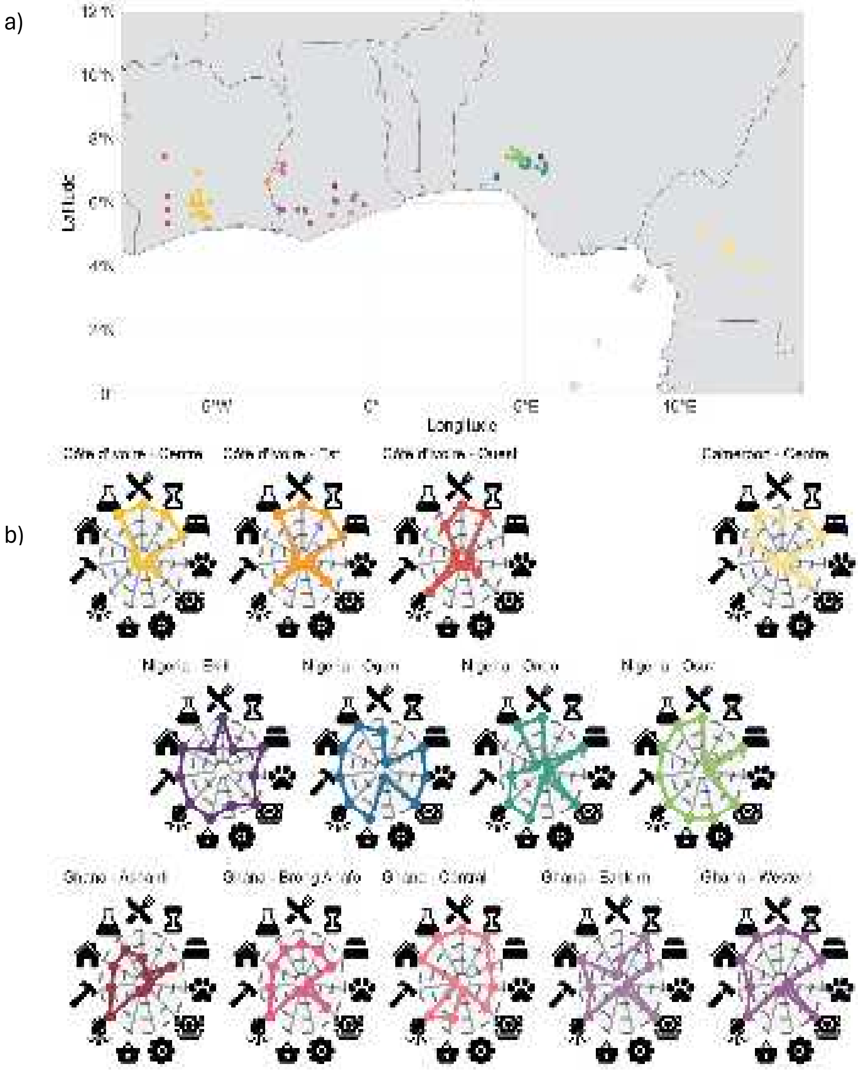
Country	**Shade cover**	**Shade tree density (trees ha^{-1})**	**Mean crown size (m^2)**	**Species richness (species per plot)**	**Simpson diversity (plot-level)**
Côte d'Ivoire	0.19 ± 0.02	99.54 ± 5.60	70.35 ± 6.73	3.12 ± 0.14	0.54 ± 0.02
Ghana	0.29 ± 0.02	77.01 ± 3.97	81.01 ± 5.25	2.48 ± 0.11	0.46 ± 0.03
Nigeria	0.13 ± 0.01	52.22 ± 3.25	65.65 ± 6.63	1.64 ± 0.09	0.25 ± 0.03
Cameroon	0.46 ± 0.02	159.63 ± 7.25	129.33 ± 7.11	5.02 ± 0.20	0.70 ± 0.01

Tree species richness and Simpson diversity were low in Nigeria, intermediate in Ghana and Côte d’Ivoire, and high in Cameroon, where plots typically held five distinct tree species.

5.3.2. Ecosystem service perceptions differ across subnational regions

In all regions, farmers considered cocoa systems to be “Very useful” for at least one of the ecosystem services in the survey (Figure 1). The ecosystem service value of food products other than cocoa was considered relatively important throughout the study area, most often reported as “Useful” or “Very useful” in all regions other than the Ashanti and Eastern regions in Ghana (Figure 1).

Cameroon was exceptional in that farmers did not typically consider cocoa systems of value for gathering firewood or producing fuel (Figure 1). The value of cocoa systems for ‘Future security’, defined as the role of cocoa systems as an investment that will provide value later in time, was noted in most areas. However, in farms in the Ashanti region of Ghana and in Nigeria, cocoa systems were not considered to be of value for this service (Figure 1). The value of farms for hunting was “Not Useful” in most regions. Exceptions were Ghana ‘s Central region and Nigeria’s Ekiti region, where cocoa systems were considered “Useful” for hunting, and the Ogun region in Nigeria where the most frequent response was “Very useful” (Figure 1).



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Food	**Future security**	**Recreation**	**Hunting**	**Marketable goods**	**Ornaments/ tradition**	**Basketry and cordage**	**Fuel/ firewood**	**Tools**	**Construction**	**Medicine**

Figure 1. a) Location of the farms studied, coloured by region. b) Spider diagrams show modal responses by region to the ecosystem services questionnaire: the four dashed lines represent each possible answer, "Not Useful", "Less useful", "Useful", and "Very useful", from the inner to outer ring.

5.3.3. Which structural and functional traits make trees good service providers according to the farmer?

Shade tree traits best explained the “construction” (R^2=0.19) and “food” (R^2=0.32) values of trees. Other values and trade-offs were explained almost entirely by the farm-level random intercept, such as the “competition with cocoa” trade-off ($R^2_{conditional}$=0.99). The “medicine” and “fertility” value of trees were least well-explained by the models (R^2=0.37 and 0.24 respectively) (Table 2). This suggests that most of the variation in tree-level perceptions of values and trade-offs depends on individual farmer preferences. Yet, significant effects of trait variables were also detected.

Farmers' perceptions of tree values and trade-offs were significantly related to different traits (Table 2). Trees with a higher leaf nitrogen content were associated with income, food, and lower incidence of pests and disease by farmers, though this trait was also associated with less construction value. Tree wood density was positively related to construction value, while trees with dense wood were considered less useful for providing shade to cocoa. Trees with dry fruit were considered less useful for food and construction, but were valued for medicinal uses. However, they were also associated with pests and diseases. Having fleshy fruit was a strong predictor of food value to farmers, and also positively related to construction value. Trees with fleshy fruit were also less strongly associated with perceptions of pests and disease, and considered less useful for medicine than trees without fruit, or trees with dry fruit. Tree height had a strong effect on construction value and was negatively related to food value. A wide diameter was not associated with any value, but farmers associated it with competition with cocoa. While crown size had a positive effect on shade value, the specific leaf area had a negative effect (i.e. thin leaves provided less shade). Both crown size and specific leaf area of trees were positively associated with pest and disease trade-offs. While evergreen trees were considered to contribute to food and medicine, they had a strong perceived link to pests and incidence of disease, and were unlikely to be associated with soil fertility. Finally, nitrogen-fixing trees were strongly positively associated with soil fertility benefits to cocoa, though they were also more likely to be considered to compete with cocoa and were unlikely to be considered useful for medicine.

Table 2. Model effects table showing the final structures of models, and how tree traits are associated with specific values and trade-offs by farmers. Cell colour represents significance threshold (lightest < 0.05, medium < 0.01, darkest < 0.001). Cell values are standardised effects (or in the case of categorical predictors, differences in intercept). Blank cells occur where terms were dropped from models during selection.

	Category	**R-squared (marginal)**	**R-squared (conditional)**	**Leaf N content**	**Wood density**	**Fruiting (dry)**	**Fruiting (fleshy)**	**Height**	**DBH**	**Specific Leaf Area**	**Crown size**	**Evergreen?**	**N-fixing?**
Benefits	**Construction**	0.19	0.75	-0.26	0.34	-0.46	0.80	1.72	-1.25				
	Shade	0.07	0.58		-0.43					-0.62	0.68		
	Income	0.02	0.70	0.30				-0.43			-0.49		
	Food	0.32	0.63	0.31		-0.12	1.20	-1.51				0.82	
	Medicine	0.06	0.37			0.48	-1.28	0.70			-0.39	1.03	-1.80
	Fertility	0.01	0.24									-1.75	1.92
Trade offs	**Competition**	0.00	0.99						0.45				1.97
	Pests/disease	0.02	0.93	-0.40		0.72	-0.61			0.46	0.51	1.98	

5.3.4. Which plot-level traits best explain farm-level perceived ES values and plot-level yields?

Plot-level traits related to the composition, structure, and function of on-farm shade tree communities were significantly related to the ecosystem services value to farmers in the interviews (Figure 2). Farms with lower mean tree abundance, trees with lower wood density, and most importantly a large proportion of their shade tree communities bearing fruit, were all more likely to have more ‘food’ ecosystem service provision. A larger proportion of fruiting trees was also found to be more useful for marketable goods, and ornamental and traditional services. Farms with more shade trees, and farms with taller shade trees, were predicted to be more useful for construction. However, higher canopies were negatively associated with hunting services. For fuel and firewood, the models predicted farms with larger community-weighted mean wood density to be more useful. For the perceived value of cocoa farms to future security, a larger number of low-wood-density trees was found to bring most benefit. No aspect of shade tree communities was found to have an effect on the usefulness of farms for tool-making, recreation, or medicine. While shade tree abundance and crown size were associated with slightly better recreation services, this effect was not significant.

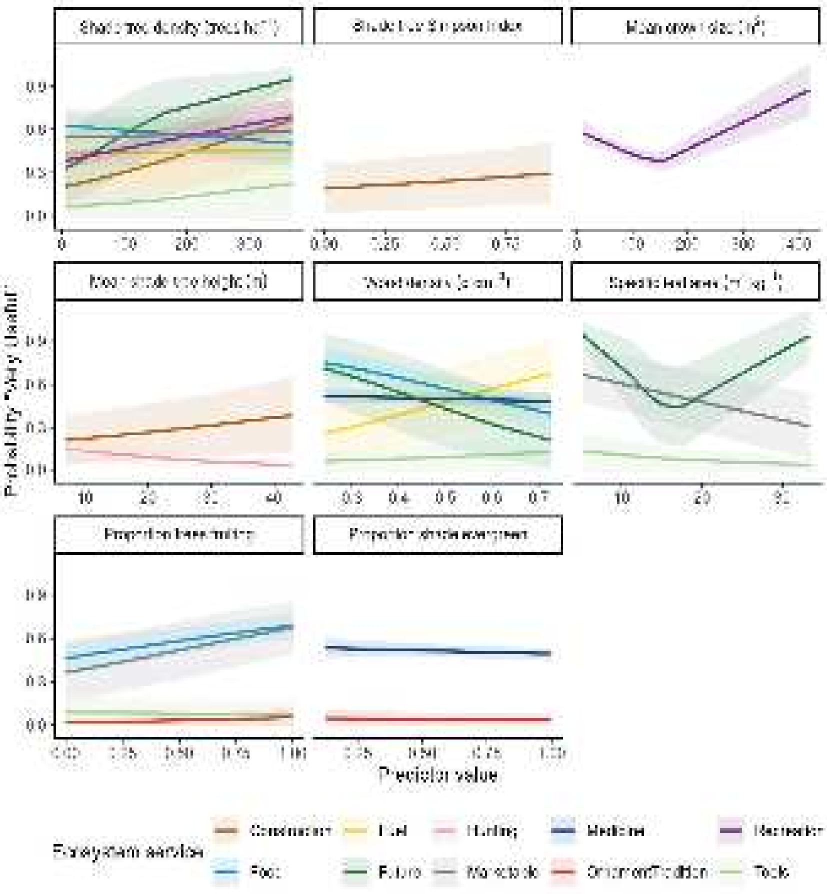

Figure 2. Predicted effects of community-weighted mean traits of shade tree communities on cocoa farms on the probability farmers' recognise their farm as "very useful" for certain ecosystem services (only non-zero relationships presented here – for full model output predictions and for all response categories see SI). Pale ribbons represent the standard error of predictions.

Higher shade tree density was associated with smaller cocoa yields per hectare (Figure 3a). However, this negative effect diminished beyond around three tree species per plot – the median in our dataset at a density of around 50 trees ha^{-1} (Figure 3b). Similarly, the evenness of tree communities was associated with plot yields. Plots with relatively larger trees (mean crown size > 200 m^2 or with > 8m crown radius) were predicted to yield more cocoa than plots with similarly-composed communities of smaller shade trees (mean crown size < 200 m^2) (Figure 3c).

When model effects are combined (and on-farm conditions constrained to achieve 30-40% shade), we can identify optimal ranges of shade tree variables to promote larger yields. Overall, the largest yields (up to 715 kg ha^{-1}) are predicted under conditions of low shade tree density and evenness (a small number of few species). However, similar yields (up to 636kg ha^{-1}) were also predicted with greater evenness and a higher density of shade trees. Across the range of tree densities observed, greater evenness is associated with larger yields, at 30-40% shade (Figure 3d).

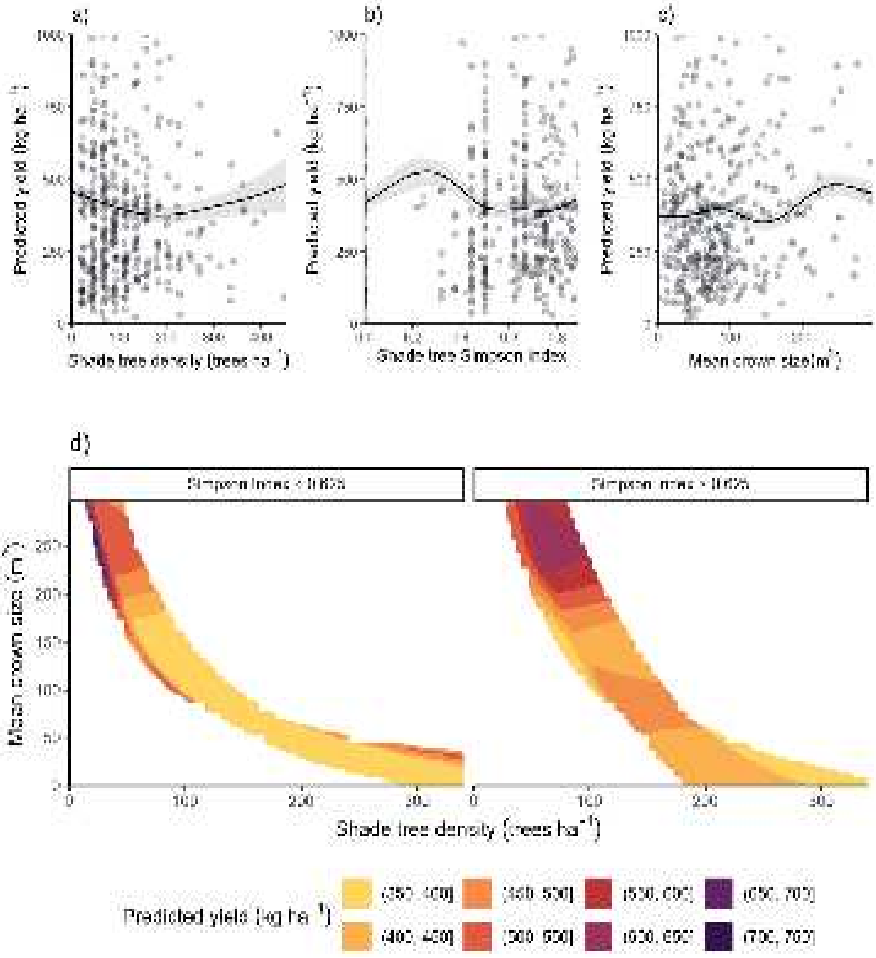

Figure 3. The individual (a, b, c) and combined (d) modelled effects of shade tree composition and structural traits on cocoa yield per hectare. The combined plot (d) is predicted within the bounds of achieving 30-40% shade. Grey ribbons in a, b and c represent the standard error of predictions.

5.4. DISCUSSION

5.4.1. Shade tree community traits help to shape ecosystem services and yield in smallholder cocoa farms

Compared to typical recommendations (for example, the Ghana Cocoa Board recommends 30%-40% canopy cover (Cocoa and Forest Initiative, 2018)), farms had less shade cover but higher tree density, suggesting that shade trees on farms do not contribute to shade cover as expected by sustainability criteria. This could be because shade tree crowns are either smaller than expected, overlap more than expected, or both. While this could be due to definitional differences of shade trees in criteria and this study, the average shade tree would need to be much larger than we found on the plots in order to meet both shade cover and common shade tree density guidance. We found that farms typically retain more trees than is necessary to meet tree density targets, but not more than 30-40% shade cover (Table 1). This was not the case, however, for the farms we surveyed in Nigeria, which were often without trees, or with a single species. One notable difference among countries was the perception of cocoa farms as important for providing future security. This was consistently strong in Cameroon and Côte d'Ivoire, variable in Ghana, and always weak in Nigeria (Figure 1b). This is reflected in the traits of tree communities on farms in each country. Farms in Cameroon and Côte d'Ivoire tended to have relatively rich tree communities, even occasionally including threatened species such as *Sterculia oblonga*, *Entandrophragma candollei*, and *Terminalia ivorensis*. These trees are valued for their timber, but are classified as Vulnerable or Endangered (IUCN, 2024).

Compositional traits (tree community abundance, richness, and evenness) were important in modelling the perceived ecosystem values of over half of the examined ecosystem services (Figure 2). Specific species are useful for purposes such as medicine and tools. For instance, *Morinda lucida* was valued widely for its anti-malarial properties, while *Celtis meldbraedii* was valued for tool provision in Ghana, where its trunk is used to make tools for food preparation. Where such species-specific services are desired, some diversity of shade trees on farms is necessary. Tree abundance was negatively associated with food provision services, reflecting that where fewer trees were present on farms, they tended to be fruit trees.

Structural aspects of shade tree communities were important for ecosystem services related to construction, fuel/firewood, marketable goods, and hunting. Farms are typically managed to maintain certain structural traits, reflected in tree density and shade cover targets. While such standards are compatible with ecosystem service delivery, they do not guarantee it. Our results show that ecosystem services are dependent on other factors, such as the height of shade trees (Figure 2). Achieving 30-40% shade cover could have a range of impacts on cocoa yield (Figure 3d). While the largest yields were predicted in farms with low shade density and lower diversity, nearly comparable yields were predicted in farms with a larger number of a wider variety of species (Figure 3d). When ecosystem services beyond supporting yield are favoured by farmers, our results suggest that a diverse mix of trees at a density of between 50 and 100 trees per hectare would achieve the best results within the constraint of 30-40% shade (Figure 3d). While many of the farms we surveyed fall within this range (Figure 3a, Table 1), it is more than the recommendations of certification boards and cocoa companies (Barry Callebaut, 2020; Cocoa and Forest Initiative, 2018; Rainforest Alliance, 2023). While mean shade tree height can have a positive effect on cocoa yields (Blaser-Hart et al., 2021), we found mean crown size to be a more parsimonious predictor in our dataset (though their strong correlation means these are not mutually exclusive and both analyses are compatible with the simplification to “larger” trees). Overall, our results support the idea that shorter trees compete more with cocoa trees, leading to negative impacts on yield.

Functional traits of tree communities on the plots were associated with only few ecosystem services. These were typically traits directly linked to the service, such as the link between fruiting trees and food. Further, no effect of community-weighted mean functional traits on yields was observed. The small overall importance of functional traits in these models may be due to the overall sparse density of trees on the plots. Typically, this was around five trees per plot which may explain the weak effect of community-weighted traits relative to the raw abundance of trees on a plot. Previous work has suggested that cocoa farmers favour trees with functional traits linked to soil fertility, wood provision, and fruit (Isaac et al., 2024). These are all supported by our results, as farmers linked nitrogen fixation to benefits to cocoa production, low wood density (and fast growth) to timber, and fleshy fruit to food provision (Figure 2). Our findings extend this to cover trade-offs such as competition with cocoa and pests and disease, highlighting tree-level traits such as DBH and leaf phenology respectively associated with these.

5.4.2. Altering tree community traits within current constraints could benefit biodiversity and ecosystem services.

Changes in designs and recommendations targeted at structural elements or compositional elements of shade tree communities will have different impacts on the values of the systems for farmers. Our results show the outcomes of these could be predictable, if the resulting trait changes are known, supporting recommendations for trait-based agroforestry design (Addo-Danso et al., 2024; Isaac et al., 2024). Our results also highlight the flexibility to tailor systems within existing recommendations. A small number of large trees, or more small trees can be used to achieve a certain shade tree cover (Figure 3d). For example, fewer large trees would likely lead to positive use values for construction, but less use for hunting (farmers discussed the inaccessibility of small prey in tall trees).

Alone, our results suggest that the 30-40% shade cover target is not useful to prescribe shade management. Recommendations to optimise ecosystem services and yield should instead indicate how the compositional, structural and functional traits of tree communities can be combined to maximise the most important outcomes for farmers. For instance, a farmer wishing only for highly-productive cocoa (but who still wished to meet agroforestry criteria) could use a small number of old, large shade trees to shade her/his cocoa trees (Figure 3d). Conversely, a farmer wishing to benefit from future timber values of cocoa trees, but who wanted yield as high as possible in the interim, could use a diverse range of fast-growing timber species at higher shade tree densities (~100 trees ha^{-1}) to maximise construction and future security value (Figure 2) while retaining relatively good yields (Figure 3d).

5.4.3. Cocoa agroforests have a challenging dependence on large trees

Larger (and typically older) trees are a key feature of farms where competition between different ecosystem services can emerge. Larger trees were considered more useful for several ecosystem services (Figure 2), and also provide canopy cover that meets targets while keeping an overall sparse density of shade trees, which benefits yields (Figure 3d). In fact, whether overall evenness of tree communities was high or low, the largest predicted yields were not achievable without large trees (Figure 3d). This is likely explained by the canopy height of larger trees, which is well above and less competitive with the cocoa canopy (Blaser-Hart et al., 2021). Large shade trees are also likely to buffer cocoa trees against climate extremes (Niether et al., 2018). This is notable, as on the farms we surveyed, tree mortality due to drought and heat was apparent in many low-shade patches. Furthermore, large trees are also associated with more biodiversity in the understorey (see Chapter 4/Maney et al. 2025). From an ecological perspective, there are knock-on benefits for other species groups from such large trees.

However, the main value of large trees (and the primary reason for farmers to retain them) is in timber for construction and to sell: a value that can only be realised when the trees are felled (Figure 1a). Therefore, there is a dilemma concerning large trees: they are simultaneously considered the most beneficial for cocoa production, and the most useful for extractive services such as construction. Younger, smaller trees are considered less useful, are more competitive with cocoa, and worse for cocoa yields. Thus, farmers may fell these trees and be unwilling to replant, or to allow more trees to spontaneously regenerate, due to the long period in which their replacements will be smaller, less useful, and potentially competitive with cocoa.

Shade trees take over 30 years to reach the stage at which they are harvestable for timber (Kouassi et al., 2024). Cocoa trees in agroforestry systems have a typical productive lifespan of 20-30 years (Wessel and Quist-Wessel, 2015), so cocoa agroforestry systems must be intergenerational with respect to cocoa planting in order to provide maximal ecosystem service benefits. Balancing a rich mixture of tree species to provide continual ecosystem services while supporting cocoa yields would also require ongoing efforts to plan and maintain shade, with the labour implication that carries.

Protections and enhancements of farmers' rights to trees – especially in the long-term, would be one measure by which the risk of permitting trees to grow could be reduced and the potential benefits could be realised (Addo-Danso et al., 2023). Local land tenure and inheritance procedures could also pose a barrier to supporting intergenerational tree retention. Yet, many farmers conserve naturally occurring species despite lack of tenure rights, so it is important to consider the other social and economic constraints that govern tree use (Asaaga et al., 2020).

5.4.4. Caveats and extensions

Results for ecosystem services (not yield) were based on farmer perceptions, so they are likely biased by the preconceptions of trees held by farmers, or influenced by training or extension advice farmers have received. Due to the nature of surveys, farmers may have focused on a particular sentiment towards a tree, meaning trees with both benefits and trade-offs may not have been counted. For instance, a farmer classifying a tree as useful for fruit may diminish any perceived trade-offs. Further, our study sites were not a random selection of farms, so we cannot claim that our results are representative of farms in the region as a whole.

We excluded oil palm (which is not a tree, but can contribute to shade in the canopy) in our analysis. While numerous on some farms, oil palms were associated strongly with a single ecosystem service (oil provision), and were not considered by farmers to provide shade to the cocoa. This 'oil provision' service was limited to this single species in the dataset, so we did not include it in the models to avoid biasing the responses for the smaller group of trees with similar traits to oil palm. Further, oil palms were typically not favoured on cocoa farms in most settings. Outside of Nigeria (where oil palms are very common), over half of the oil palms in the survey were noted by farmers either to have negative effects on cocoa production or be intended for removal by farmers. Understorey and other plants on the farms are also important (Kouadio et al., 2025). The plots on the farms also contained plantain, pineapple, banana, yams, and many other utilised species in the agroforestry systems that were not trees. Future research should investigate the impacts of joint canopy/understorey design on ecosystem services, including cocoa yield.

Finally, this study compared results at multiple scales of analysis. We detected a wider variety of important functional traits as important for ecosystem services at the tree level (Table 2; Figure 2). This shows how community-weighted means do not always capture the full complexity of relationships between shade trees and cocoa systems (Addo-Danso et al., 2024; Isaac et al., 2024). The position of individual trees relative to the cocoa, and individual differences in structural traits like height can also change how important or useful a tree is to farmers. These results warrant further assessments of tree- and community-level traits in cocoa, particularly regarding knock-on effects on other service providers such as arthropod pollinators.

5.5. CONCLUSIONS

Our results show that benefits to cocoa yield and valuable ecosystem services are mutually achievable at far higher shade tree densities than currently demanded by agroforestry standards. Traits at the tree, plot, and farm level are all informative in terms of predicting the perceived and realised benefits to cocoa agroforestry systems, and the most important features are the density, variety, and size of the shade trees. With necessary forethought and design, shade tree community composition, structural complexity, and functional traits can be tailored in a variety of ways to target the ecosystem services preferred by farmers.

Large shade trees are clearly of special importance on cocoa farms through supporting cocoa production and supplying vital ecosystem services. Yet farmers can only realise the monetary value of large trees by felling them. Promoting systems that would maintain a steady supply of maturing large trees is key to long-term sustainability in the region – we estimate it takes more than 30 years for a shade tree to achieve the height desirable for combination with cocoa. If biodiversity itself is explicitly favoured by policy makers and companies, it should be explicitly valued through a ‘biodiversity premium’ to be paid to retain such trees. As several tree species threatened with extinction were found on the cocoa farms – even in the countries with the most deforestation – this may prove to be a practical conservation strategy. Furthermore, companies wishing to promote agroforestry systems for the benefits they offer, must be prepared to provide support during the “growing pains” of transition where the benefits of a diverse shade tree community do not yet offset their negative impacts on yield.

Governments, certification boards, and private companies should carefully tailor their recommendations and interventions on the biodiversity of shade trees in cocoa systems to the local context. Such recommendations must consider how the composition, structure, and function of tree assemblages will impact overall ecosystem service provision, and what trade-offs might emerge through the life cycle of a farm. Doing so would acknowledge the trade-offs that shade tree biodiversity can bring, while allowing farmers to enjoy the yield and non-yield benefits of diverse agroforestry systems.

Chapter 6. General discussion

The research chapters of this thesis aimed to answer the questions, "Are plant biodiversity and cocoa production systems interdependent? And if so, how does this matter to decision-makers?" Chapter 2 showed the potential of cocoa systems to simultaneously impact and depend on plant biodiversity, in a study across a range of other commodity crops. Tree species were, though variably, associated with soil health, pollination services, and pest control services. Yet, the evidence on impacts of cocoa systems on tree diversity was mixed, and there is very little evidence for impacts and dependencies of cocoa systems on their understorey plant diversity. Respectively, Chapters 3 and 4 quantified the impacts that cocoa systems have on biodiversity a) across the range of land-use systems in areas of cocoa production, and b) within the range of smallholder cocoa systems in West and Central Africa. The relative 'intactness' of biodiversity, compared to minimally-impacted areas, varied by up to 50% among cocoa systems, though the land use history and nature of shade in the farms can account for most of this variation (Chapter 3). That said, cocoa agroforestry systems universally represent a more intact forest system than non-shaded land systems. The composition of biological communities in some cocoa systems rivals even mature secondary vegetation, highlighting that the role of cocoa agroforests in the conservation of biodiversity should not be discounted (Chapter 3). While Chapter 3 went a little way towards unpicking the causal relationships driving the disparity of biodiversity outcomes in cocoa, the subsequent field-based analysis in Chapter 4 addressed this directly. Testing the compatibility of our causal hypotheses with data collected from cocoa production systems in four countries revealed the importance of agroforestry design to biodiversity on cocoa farms. Yet, it also revealed the importance of factors out of the control of farmers. A nuanced approach to enhancing biodiversity in different contexts is needed, as the most important determining factors (such as tree density) depend on the land-use history of a site. Trees of different origins (planted, spontaneous recruits, and remnant trees) contributed differently to species diversity on farms. The traits of these tree communities were also important to determine the benefits and trade-offs they will bring to farms, as was shown in Chapter 5. Larger trees were valued highly for use and non-use services. They were also associated with the highest yields achievable within a constraint of 30-40% shade cover, but this brings the provisioning and supporting services they provide into direct competition with each other. For example, once a tree is harvested for construction or sale it no longer provides shade, contributes to soil fertility, or can be regularly used for medicine.

Throughout this thesis, I have explored a possible "feedback loop" between cocoa systems and biodiversity, showing that cocoa systems have the potential to play a role in supporting biodiversity despite being less biologically "intact" than forests, demonstrating the main factors that shape plant biodiversity that are under and outside of the control of farming systems, and how properties of the plant biodiversity in cocoa systems can shape both ecosystem services and cocoa yields. Below, I interpret and discuss these findings in three sections, each exploring a different perspective. I address how the results of this study are relevant for understanding developments in biodiversity modelling, how my findings can inform perspectives on the role of cocoa production systems in the conservation of biodiversity, and what they mean for cocoa and biodiversity in the face of policy and global change. In a fourth section, I break down the takeaways from the findings for different stakeholder groups.

6.1. SCALES, MODELLING, AND REFLECTING REALITY

6.1.1. Balancing generality, precision, and realism in biodiversity models.

It has been argued since the 1960s that ecological models are necessarily constrained in a three-way trade-off between precision, generality, and realism (Levins, 1966). A model achieving all three of these properties perfectly would be an exact replica of all relevant systems, which is impossible due to the high number of necessary parameters, the computational intractability of creating such models, and the difficulty of interpreting sufficiently complex models in a meaningful way (Levins, 1966). These arguments have proved prescient, even as computational power has risen exponentially; they certainly pervade the research in this thesis.

Chapter 2, the narrative review of evidence for and against interdependencies between cropping systems and nature, was necessarily the broadest piece of work. Practically, the evidence synthesized by this chapter was hard to quantify because a diversity of methods, metrics and types of results had to be combined to achieve sufficient information on each cropping system. A simple Bayesian framework helped to harmonise the conclusions of each piece of evidence into broadly supporting, neither supporting nor contrasting, or broadly contrasting the hypotheses I posed. But this chapter's simplifications were counterbalanced by its breadth, allowing some comparability between the different cropping systems and the two hypotheses.

Chapter 3 focused entirely on cocoa systems. This came with the clear benefit that quantified data on biodiversity could be incorporated into the models. Also, primary biodiversity data from non-cocoa land use systems like croplands and primary forests could also be incorporated, so a reasonable level of breadth could be maintained. However, nuance was lost in two important ways. Firstly, as high-quality data on biodiversity in well-characterised land-use systems was relatively sparse, the 'land use' predictor variables had to be condensed into a small number of groups. This meant that the level of detail necessary to inform specific actions or interventions to benefit biodiversity was not achieved in this chapter. The second way in which nuance was lost was in the biodiversity data itself. Rather than speaking to specific species or species groups, it was necessary to harmonise biodiversity data into two facets: species richness and presence-based composition similarity. This meant that the generality that the models in Chapter 3 gained by addressing many taxonomic groups was counterbalanced by the lack of precision on the responses of biodiversity to land use systems. This land system level of analysis is useful, as it provides a comparison between a wide range of land use types, placing cocoa systems on a scale where they can be compared to alternative land use systems. It also provided important evidence for the range of biodiversity outcomes across types of cocoa system, supporting the hypothesis that land use history is a key predictor of biodiversity. This level of analysis is also compatible with spatial data, as land use is commonly mapped across regions, making it useful for spatial planning and national statistics on biodiversity.

In Chapter 4, I focused on a detailed account of plant diversity on the plots in the study. However, the precision and realism gained the precisions and realism gained made it possible to suggest real-life interventions. The causal thinking approach to modelling was made possible by large quantities of harmonised, targeted data collection, and the use of established, experimental field sites meant that the important differences between otherwise-similar sites could be related to modelling variables.

Chapter 5 took a small step back into breadth. Here, I interviewed farmers to devise an index of ecosystem service provision. While this meant that ecosystem services (other than yield) could not be quantified, information was captured in a way that was relevant for farmers. Such interviews are a practical and important way to capture the perspectives of local people, beyond those that could have been pre-empted *a priori*.

Working at multiple scales when addressing a topic like this is essential. Starting with a wide focus, and allowing evidence to guide the subsequent research, has led to a fuller picture than would otherwise have been possible.

The most fundamental question regarding scales of modelling remains: can models usefully summarise intricate, intrinsically individual agricultural systems? This work, and its fieldwork component in particular, has led me to conclude that they cannot. There will always be more context in a system, and speaking to farmers on the ground revealed the naïvety of some of the modelling assumptions. In the farms I studied, there were hidden, unmeasured factors governing plant biodiversity. In one case in Ghana, a farmer indicated that trees useful for tool-making were not necessary on-farm due to their prevalence in nearby forests. In another case, I heard how farmers who valued pest control by red ants would transfer branches hosting them between farms. These were unique to individual systems and so could not be captured by models, yet this information was vital in putting together the picture of farm interdependencies with nature.

Regardless of the precision, generality, and realism targeted by modelling, on-the-ground knowledge and experience is essential. The best way to achieve this is to speak to people in land systems. Their collective knowledge provides context and realism that can make even the most sophisticated model seem ignorant. Further work exploring ways to incorporate these unique and complex narratives into decision-making, with or without the support of statistical models, is undoubtedly necessary.

6.1.2. Addressing and accounting for geographic data gaps.

Collecting and stewarding data on biodiversity in Africa remains a prominent challenge (Siddig, 2019). All major global biodiversity databases are sparsely populated for Africa, including the PREDICTS dataset (Hudson et al., 2017), BioTIME (Dornelas et al., 2018), TetraDensity (Santini et al., 2018), and the Global Biodiversity Information Facility (GBIF) (Beck et al., 2014).

Issues of data sparsity arose in every chapter in this thesis. In Chapter 2, I found a paucity of research on biodiversity feedbacks in Africa, instead relying on better-studied regions including Latin America and Indonesia for evidence. In Chapter 3, there was insufficient data to break results down by region. Again, data from outside Africa was needed to interpret the results. Even when using a large volume of data collected in West and Central African countries in Chapters 4 and 5, ancillary datasets often lacked sufficient coverage. For example, IUCN threat levels and assessments were missing for most of the understorey species and some of the trees (Figure 1).

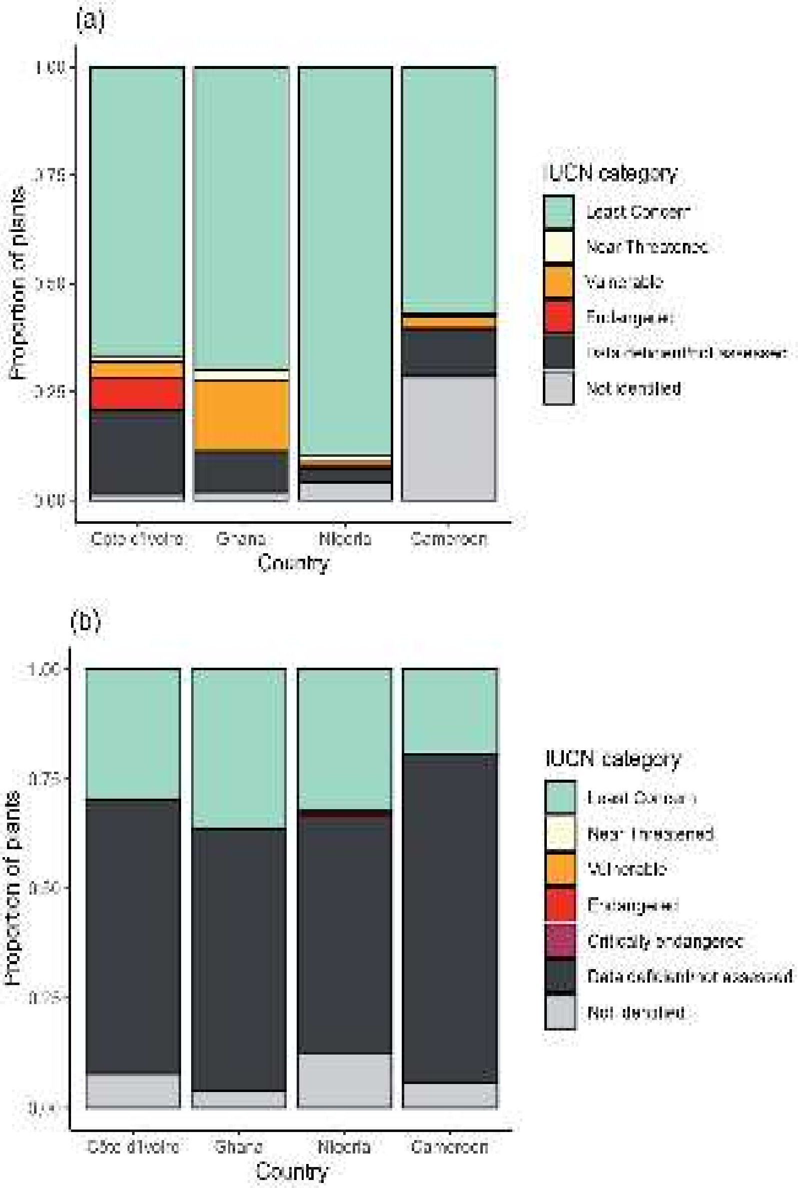

Figure 1. The IUCN categories of the tree (a) and understorey (b) species found in the surveys of cocoa farms in four West/Central African countries.

Similarly, in Chapter 5, the TRY database (Kattge et al., 2020) lacked trait data for some of the tree species in the survey which weakened the conclusions. In turn, this makes it more difficult to turn conclusions into recommendations. More comprehensive data collection and management is necessary to put African biodiversity on a level playing field with other regions with major biodiversity hotspots. However, some recent news is promising: the newest iteration of the TetraDensity database has good representation of African biodiversity for mammals (Santini et al., 2024).

In the meantime, there is a need for novel approaches to make use of what data is available without regressing African data to global means. An interesting extension to the work of PREDICTS would be a new analysis focused on West and Central African land systems to reconcile land use maps (including those created nationally) and knowledge of biodiversity responses to land use and land use change. One place to start could be the use of expert-based judgements about species group intactness in different African land use categories. For example, coefficients from the BIIAfrica expert-driven dataset (Clements et al., 2024) could be used as priors in an analysis designed to harmonise and contrast these expert judgements against what data there is available. This hybrid method could retain the benefits of both approaches to help decision-makers understand the context-dependent biodiversity impacts of land use change.

6.1.3. Global biodiversity models, scenarios, and nature futures

Chapter 3 reveals the magnitude of ‘biodiversity intactness’ in cocoa systems, but also a wide range of potential values. This contrasts strongly with how these systems have previously been characterised by global databases, which would typically group cocoa in with other cropping systems, with implications for national biodiversity statistics.

The Natural History Museum (NHM) (a co-founder and the host of the PREDICTS project) estimates that between 1970 and 2015, the Biodiversity Intactness Index of Ghana (-15%), Côte d’Ivoire (-11%), Nigeria (-4%) and Cameroon (-1%) fell, largely driven by an expansion of the “cropland” land use in each country (Figure 2) (Phillips et al., 2021). Though the metrics are not directly comparable, my results creating a similar model tailored specifically to areas of cocoa production suggest that these trends could be overestimated.

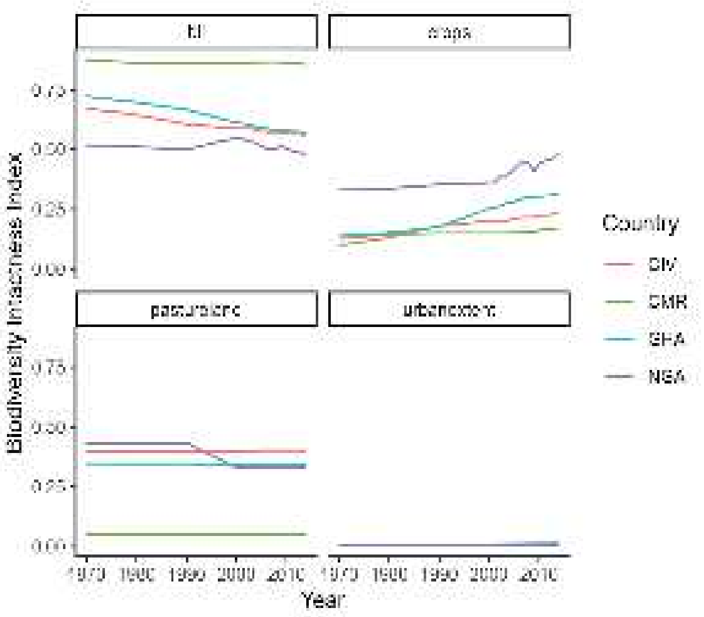

Figure 2. The NHM estimates of Biodiversity Intactness (BII) in the four focal countries in this thesis. Facets show BII as well as estimated cropland cover, pastureland cover, and urban extent in each country to indicate the drivers of change.

The directionality of the error depends on how cocoa systems are captured by the land use model. If areas of cocoa production are currently counted as cropland, associated biodiversity intactness impacts could be half as large as is reported – my coefficient for biodiversity intactness in cocoa agroforestry systems was up to two times the value of open land systems (Chapter 3). Conversely, if areas of cocoa production are not detected, and instead captured as forests, there could be missing biodiversity impacts. Accounting for this discrepancy in national biodiversity statistics is crucial in the four countries studied here.

Global scenario models of future biodiversity change should also account for the significantly higher biodiversity value of cocoa systems, and other perennial agroforestry systems, relative to other croplands. However, scenarios at the global level often must condense land use systems into broad categories (e.g., Pereira et al., 2024), so a more practical solution for national-level decision making may be to run smaller-scale scenarios of nature futures that are specific to regions (such as West and Central Africa) that can include a more representative range of land use systems.

Large regional- and global-scale integrated models of nature futures, such as integrated assessment models, cannot guide local actions. This is because they lack the context specificity to incorporate the most important drivers of biodiversity change in these systems. For example, in Chapter 4, key drivers were distance from ports and shade tree management. However, well-constrained, context-specific models rely on high quantities of good data, which is the crux upon which better understanding of biodiversity, cocoa, and people in West and Central Africa hinges.

6.1.4. Causality and assumptions in statistical biodiversity models

Biodiversity is a phenomenon which is uniquely difficult to experimentally manipulate, especially at the scales relevant to all species. Therefore, we should remain aware that a given statistical model may not represent the causal processes we assume it does. And it is always better to be explicit about the hypotheses and process models that we think our statistical models represent. For example, in Chapter 4, I test hypotheses about how land-use history drives biodiversity in cocoa farms (Figure 3). While I found that there was a significant difference between tree and understorey species richness between farms of different land-use histories even when controlling for other factors, there were always multiple process models that could account for the observed patterns, and multiple hypotheses underpinning them.

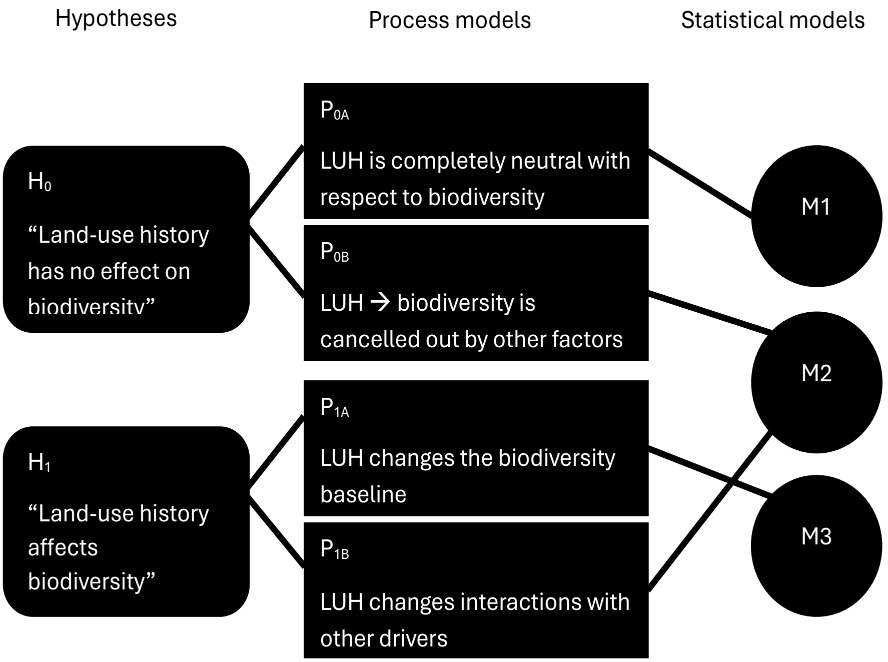

Figure 3. Adapted from McElreath et al. (2020), this diagram shows how hypotheses made in Chapter 4 do not represent distinct process/causal models, nor are either of those represented by a single statistical model.

In Chapter 5, I found that cocoa systems were valued differently between and within countries (Figure 5-1). It is not possible to unpick the causality here, as multiple causal paths could underpin the links between tree communities and perceived ecosystem services. Further, I did not have sufficient prior understanding of the social-ecological system to make appropriate hypotheses. Farmers could have an intrinsic view of the values of cocoa systems and what ecosystem services they should contribute to, so they decide to plant, permit and retain trees that fit that bill. Alternately, farmers have emergent views on the values of cocoa systems, based on the shade trees and other features of their farms they find useful and the ecosystem services they value. I consider the former more likely, as there is strong evidence that farmers take an active role in shaping the diversity and ecosystem services provided by trees in their cocoa systems (Sanial et al., 2023).

Ecology is increasingly dominated by statistical methods and empirical modelling. Black-box methods are on the rise from models of species ranges (Cole et al., 2023) to models mapping human pressures on nature (Keys et al., 2021). Large scale computing and digital twin methods drive us ever closer to the idealistic trifecta of models being precise, general, and realistic. Yet, we should question whether information derived from such models is as useful as it may seem, given that there will always be additional nuance to add and unpredictable drivers of change. Critically, by using these black-box methods with observational data, we become another step removed from understanding causality. So, while these novel statistical methods are impressive and useful in large-scale monitoring and prediction, they may actually present a hindrance to our understanding of ecological systems and their interactions with people.

6.1.5. Feedbacks and interdependencies in biodiversity models

In the introduction to this thesis, I presented the concept of biodiversity "interdependencies", and described how they could lead to feedback loops with negative consequences for people and nature. There is certainly evidence that cocoa systems degrade biodiversity, relative to natural systems (Chapter 2, Chapter 3). There is also evidence that more intensive practices, as well as external pressures, can also drive biodiversity loss (Chapter 4). Finally, there is evidence that some plant diversity in cocoa systems is beneficial for both yield and non-yield ecosystem services (Chapter 5). Thus, there is an extent to which cocoa systems drive feedbacks with biodiversity that could undermine the benefits they bring to people. From the evidence in Chapters 4 and 5 it is not unreasonable to suggest that cocoa systems in some areas could be reaching, or even be beyond, a "tipping point". Continued degradation of biodiversity in intensifying cocoa systems beyond the optimal level of plant diversity and shade cover could have simultaneous negative effects on species richness, yields, and ecosystem services.

6.2. COCOA AGROFORESTRY, LAND SHARING, AND THE ‘CONSERVATION ESTATE’

6.2.1. The value of cocoa systems for plant biodiversity conservation

Cocoa systems, including agroforestry systems, are typically considered by conservationists to be useful for connectivity within landscapes, but not from a species or ecosystem conservation perspective (Abada Mbolo et al., 2016; Asare et al., 2014; Oke and Odebiyi, 2007). This is reinforced by my examinations of the biological intactness of communities in cocoa agroforests relative to primary forests (Chapter 3) as well as the relatively few species that are of conservation concern found on farms (Chapter 4). One key problem with making, or keeping, cocoa agroforests compatible with species conservation goals is highlighted by results in Chapter 4 and Chapter 5. My results show that the largest, most mature “remnant” trees on cocoa farms contribute most strongly to species richness (Table 4-S3). Larger trees are responsible for knock-on biodiversity benefits for understorey plants (Figure 4-5). Shade is also linked to richer bat and bird communities (Ferreira et al., 2023a; Martin and Raveloaritiana, 2022). Therefore, the biodiversity value and conservation importance of cocoa agroforestry systems is tied to their most developed and mature ecological features.

At the same time, these trees are associated with higher yields (Chapter 5) and many ecosystem services (Chapter 5). Yet, the realisation of many of these services necessitates the removal of the trees (for example timber provision). While Chapter 5 suggests a potential generational cycling of service-providing mature trees to sustain benefits to ecosystem services and biodiversity, the ongoing removal of the largest mature remnants inhibits species conservation on farms. This is a key irreconcilable trade-off for West and Central African cocoa systems – and only payments for these trees are likely to keep them on farms in the future.

The regional context of biodiversity loss is of key importance when interpreting these findings. From the perspective of farmers seeking to gain ecosystem services benefits, cocoa systems may actually be more useful than secondary forests. An emergent problem across West Africa is that those tree species that are most highly-valued by local people are experiencing low rates of regeneration (Lykke et al., 2025). In other words, there are decreasing numbers of useful trees across size categories, so when large trees are removed, they are unlikely to be succeeded by the next generation. In Ghana, Nigeria, and Côte d'Ivoire, these patterns suggest that tree use is unsustainable (Lykke et al., 2025). My results suggest that most trees on cocoa farms are valued for ecosystem services (Chapter 4), and further, that the distribution of tree sizes on farms in Côte d'Ivoire, Ghana, and Cameroon is more even than in the study by Lykke et al., including more small trees than a similar study across all land uses in the region (Figure 4).

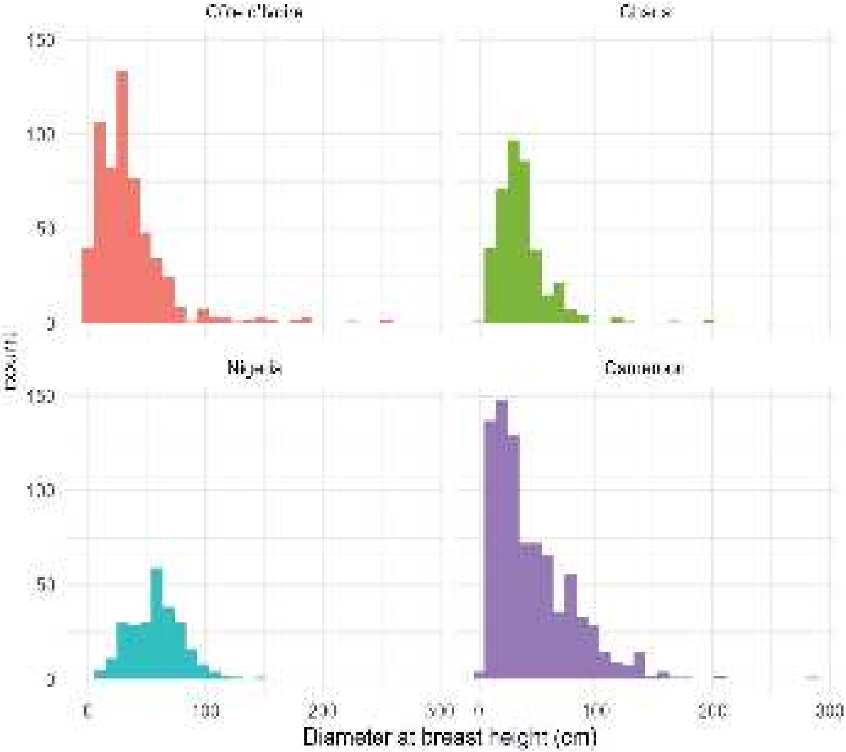

Figure 4. Diameter of trees on cocoa farms in the fieldwork studies.

This implies that on the farms in these three countries, we can consider tree use in cocoa systems to potentially be more sustainable than the national or regional averages. Data from Nigerian cocoa farms, however, shows low regeneration of tree species that more closely mirrors regional patterns, indicating that the study farms in Nigeria may be using their shade trees unsustainably. Cocoa agroforestry systems may therefore be acting as a relative biocultural refuge, providing healthier populations of tree species valued by local people than is otherwise achieved across the region. If the stewardship and regeneration rates of trees on cocoa farms could be extended to species of conservation concern, cocoa agroforestry systems could become a powerful tool for species conservation.

6.2.2. The usefulness of the land sharing-sparing debate for areas of cocoa production

Since its formal introduction, the land sharing-sparing debate has pervaded the field of biodiversity conservation (Green et al., 2005). The debate centres around whether it is 'better' for biodiversity if farming is concentrated on as little land as necessary to feed the world, operating intensively whilst strictly protecting non-farmed land (land sparing), or to integrate natural and farming systems to spread impacts thinly but broadly (land sharing). Papers targeting the debate continue to reach high-profile journals today (Bateman and Balmford, 2023). The most recent evidence syntheses have concluded that a land-sparing approach is most likely to protect species-level biodiversity, especially for those species of particular conservation concern (Balmford et al., 2025). However, an increasing recognition of the value of ecosystem services to farming systems means that what is best for biodiversity may not be best for farming (Grass et al., 2019). Not all services are "substitutable", and people value more aspects of farming systems than yield (Fitter, 2013).

Cocoa systems harbour less-intact biological communities than minimally-disturbed forests (Chapter 3). Thus, they cannot rival strict protected areas as a conservation tool. However, more complex agroforests can host communities of comparable intactness to mature secondary forests, including some species of conservation concern (Figure 1). Indeed, the loss of local biodiversity intactness from the simplification of a complex agroforest is expected to be just as large as the loss of intactness from the conversion of primary forest to complex agroforest. Thus, the expectation of biodiversity gains from concentrating cocoa production on existing farms to spare more land from conversion to 'land-sharing' agroforestry is false. Our results suggest that "intensification" in terms of shade removal would not necessarily improve yields, either.

I predicted that, so long as farms had at least a few large trees, yields would actually be higher with shade (Chapter 5). And that is without considering the other important ecosystem services provided by shade trees (Chapter 5). That said, there are certainly other approaches through which intensification (optimised fertiliser use, better pruning techniques, integrated pest management) could benefit yields and reduce demand for deforestation and biodiversity loss without the need to reduce tree cover in existing plantations.

Promoting "high yield farming" that is "less impactful than current industrial agriculture" (Balmford et al., 2025) is noted as the key component of a land-sparing approach. This approach would be most beneficial in forest-frontier areas where there are high-biodiversity value ecosystems to spare (Sassen et al., 2022), but even "high yield" cocoa systems can benefit from some diversity – and they currently have the most to lose. Where cocoa systems already dominate landscapes, a move towards sparing may enhance ecosystem services from remaining forest reserves, but on-farm sharing-based increases would be expected to deliver direct benefits too.

In the systems I have investigated, interdependencies mean that effectively sparing land for biodiversity may not really involve a great deal of reducing the extent to which land is shared with nature. At the very least, the distinction between sparing and sharing here is tautological. Better sharing, in order to spare, perhaps.

6.2.3. Do cocoa agroforestry systems belong in West and Central Africa's 'conservation estate'?

Political entities in Europe set explicit goals for agricultural biodiversity, such as to ensure that "at least 10% of agricultural area [is] under high-diversity landscape features" (European Commission, 2021). This allows for a positive public framing of biodiversity friendly agricultural activities. It recognises that many agricultural landscapes are highly degraded, and that there is a need to "bring back" biodiversity. In cocoa-producing areas of Ghana, Côte d'Ivoire, and in particular Nigeria, landscapes are also highly degraded (Kouassi et al., 2021). Yet, there is no similar target for this region. This means that instead of being recognised as positive recovery, biodiversity-friendly activities like agroforestry are instead sometimes characterised as mitigating losses. While this is the case in the context of direct forest conversion, many agroforestry systems are now second-generation (Figure 4-2b), so any positive contributions to biodiversity are missed. New targets are needed to recognise the transformed nature of much of the agricultural landscapes of West Africa – and the need to implement restoration even within agricultural landscapes. One route to doing so could be to define specific thresholds for management, biomass, or biodiversity over which farms are included in the ‘conservation estate’.

Recent research has investigated how disturbed and degraded forest systems may still contribute to overall biodiversity conservation (Ewers et al., 2024). They suggest that significant biodiversity benefits remain at biomass degradation levels up to 30% of those in undisturbed systems, and that only systems with 70% or more biomass losses had lost the majority of their biodiversity value. We did not estimate biomass losses in the cocoa systems, so further research would be needed to identify where different types of cocoa system lie against these thresholds. Though it is important to avoid “shifting baselines” when assessing long-term biodiversity change, the development of rigorously-defined thresholds for biodiversity-positive cocoa could bring recognition to farmers and countries that are successfully protecting and enhancing biodiversity through cocoa on an inter-generational timespan.

6.2.4. Contributions of cocoa systems to global biodiversity goals.

The Kunming-Montreal Global Biodiversity Framework (KM-GBF) was agreed in December 2022 by 196 Parties to the Convention on Biological Diversity (Convention on Biological Diversity, 2022). It lays out a vision for humanity “living in harmony with nature” by 2050, guided by four main “Goals”. The ‘2030 milestone’ is driven by the commitment to achieving 23 “Targets” that will in theory, if achieved, put the world on track to meet the 2050 goals.

Can cocoa systems contribute to the achievement of the outcomes of the KM-GBF? The goals and targets are designed to be achieved through the sum total of all contributions at a national level. Therefore, if some countries owe a significant proportion of their land or biodiversity impacts to cocoa production, then interventions on cocoa systems could help to achieve the goals of the KM-GBF. However, we must first assess whether changes to cocoa systems could contribute to these goals. Below, I focus on Goals A and B.

Goal A aims to “maintain, enhance, or restore” the “integrity, connectivity, and resilience” of all ecosystems by 2050. A key component of integrity is the compositional intactness of biological assemblages in ecosystems (Carter et al., 2019). The results of my biodiversity intactness models (Chapter 3) show that not only are cocoa agroforests more intact than nearby open-land systems, but they can in some instances rival natural regeneration (Chapter 3). Therefore, we can expect to enhance ecosystem integrity by establishing cocoa agroforestry systems on open-land using planted shade. Retaining and allowing further regeneration of shade trees in forest-derived agroforests could also contribute to the maintenance and enhancement of ecosystem integrity and Goal A in this manner. Another key element of ecosystem integrity is ecosystem structure. In my analysis of the drivers of biodiversity in cocoa (Chapter 4), I found that encouraging natural regeneration could lead to not just richer tree communities, but larger trees contributing more to canopy cover. In an environment with stiff competition for land, countries with large areas of cocoa production could consider the practicality of restoring 30% of their degraded land by 2030 (Target 2 of the KM-GBF), and whether encouraging more complex agroforestry practices would contribute to this goal, making it more achievable.

However, Goal A also aims to “halt human induced extinctions”. Even though the intactness models (Chapter 3) show some agroforestry systems with only a small fraction of their biodiversity missing, at wider spatial scales the patterns predicted by the models could still lead to extirpations and even extinctions, provided those lost species are the same everywhere. Particularly sensitive forest specialists, or species exposed to secondary threats like hunting in areas of cocoa production, cannot be protected by even the most complex agroforestry systems (Jarrett et al., 2021b). The dataset collected for Chapters 4 and 5 shows the overall dominance of non-remnant trees in most countries (Figure 5).

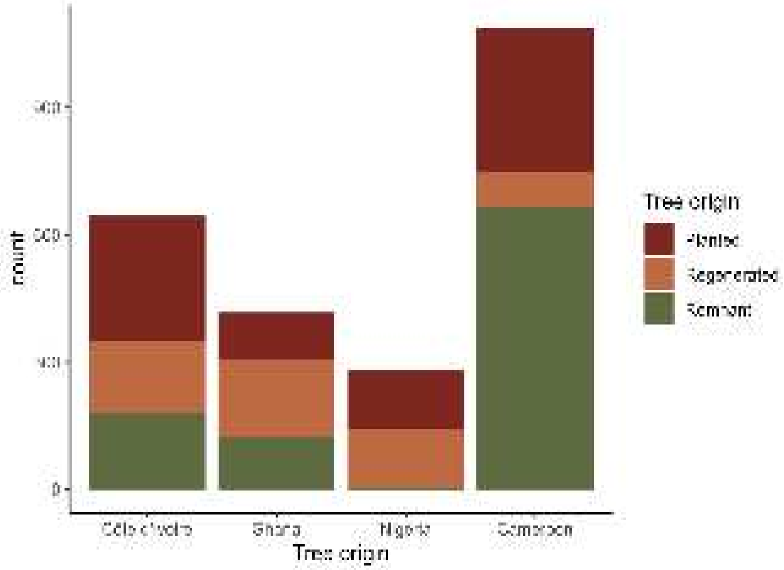

Figure 5. The origin of shade trees in the fieldwork dataset.

In Cameroon, there were many remnant forest trees, so those agroforestry systems could contribute to reducing extinction risk. There was also a relatively low proportion of threatened species in the dataset (Figure 1) – though again, in Cameroon especially the status of many of the species was simply not known. More efforts in threat classification are urgently necessary to determine the species conservation value of Cameroonian agroforestry systems.

Goal B aims to ensure that “biodiversity is sustainably used” and that “Nature’s contributions to people including…ecosystem services, are valued, maintained and enhanced”. There are clear routes for cocoa agroforestry systems to contribute to this goal: they are valued highly for ecosystem services in every region of every country we visited in the surveys (Figure 5-1b). Therefore, maintaining the current level of tree diversity on farms will help to maintain ecosystem services in the region. Furthermore, there are options for enhancing ecosystem services, including contributions to yield, by focusing on specific tree- and community-level shade tree traits such as wood density, tree size, and fruiting (Chapter 5).

The KM-GBF includes a monitoring component. National monitoring systems in the four countries could benefit from including the ecosystem service and biodiversity benefits garnered from the natural elements of cocoa agroforestry systems. Including and recognising these contributions would be a representative way to counterbalance the more measurable harm that cocoa expansion has done, and continues to do, to their biodiversity through forest cover indicators.

6.3. POLICY, PRACTICE, AND ANTI-DEFORESTATION REGULATIONS

6.3.1. Policy and standards do not yet best support productivity, ecosystem services, or biodiversity

It is time to revisit the standards and recommendations set for shade tree density and diversity on West African cocoa farms. Even though the study plots were selected for low(er) shade, they had higher plant diversity than would be expected from any of the standards tested in the scenarios exercise (Chapter 4, Figure 6). This means that there is significant room left for tree biodiversity loss on such cocoa farms, and there is an opportunity to valorise the “extra” diversity that currently exists.

Based on the models of shade tree communities’ benefits to farms (Chapter 5) and understorey plant diversity (Chapter 4), increasing shade tree density would be expected to yield multiple benefits for a farm currently meeting a standard of 20 trees per hectare. One additional large shade tree per plot (roughly 20 additional trees per hectare) could be expected to increase the productivity of such a farm by 100 kg ha^{-1} (assuming trees are relatively diverse) (Chapter 5), increase the likelihood of future security and construction services by 5-10% (Chapter 5), and significantly increase the species richness of the understorey (Chapter 4). Of course, this also depends on the agroecological context of the farm as well as the species of tree.

Most sustainability recommendations for shade trees in cocoa agroforestry systems indicate a range of ideal shade cover of around 30-40%. Some also include a recommendation for a mixture of species (Barry Callebaut, 2020; United Nations Environment Programme, 2021), and some even recommend structural traits for tree sizes (Barry Callebaut, 2020). Standards also include a recommended shade tree density, though there appears to be no scientific basis for this choice. Canopy cover alone is insufficient to optimise farm cocoa yields, and other ecosystem services (Figure 3, Chapter 5). Yet, having a target for both canopy cover and shade tree density is confusing. Shade tree density will undoubtedly impact canopy cover, but the structure and choice of tree species will overwhelmingly impact the farming outcomes. Recommendations could instead opt for a range of traits linked to ecosystem service provision and yield support. One example is recommending the inclusion of 'mature' trees, which could be expected to involve larger trees with high, large crowns and the benefits they are expected to bring (Chapter 5).

6.3.2. Anti-deforestation policies and the attribution of blame

The EU anti-deforestation regulation (EUDR), set to go into force for large businesses in 2025, is a new import-side regulation designed to prevent imports of key commodities from deforested land (The European Parliament And The Council Of The European Union, 2023). Similar policies in other areas are set to go into place this decade, and all proposed regulations cover cocoa as a key deforestation-risk crop (Benyon, 2023; Partiti, 2020).

Practically, the enforcement and validation of these regulations depends on the reliable detection of forests, as opposed to other land uses. However, agroforestry systems – especially complex ones – can look like forests from space (Kalischek et al., 2023). It is notoriously difficult to identify agroforestry systems using remote sensing, particularly cocoa which is an understorey species in its native habitat (Escobar-López et al., 2024).

Existing cocoa land in agroforestry systems will almost all have been established before 2020. If too little effort is put into identifying cocoa agroforestry systems, many of the world's cocoa agroforestry systems could be subject to restrictions. The European Commission Joint Research Centre (JRC) has produced a map of "forest land in 2020" that can be used to screen areas for deforestation risk (European Commission. Joint Research Centre, 2024). For cocoa, this data and similar maps have already been shown to be low-quality (Moraiti et al., 2024) Based on the JRC map, how many of the farms in my dataset are incorrectly detected as "forest"? For reference, all the farms in the study were established prior to 2020, with the youngest plots of cocoa trees having been planted around 2015.

If we take a buffer of 250 metres from the centre point of the plots on each farm, and use a 50% threshold for classification, 44% of the farms in my study are classified as forested land. Furthermore, the more shade trees a farm has, the more likely is it to be incorrectly classified as forest by remote sensing methods (Figure 6).

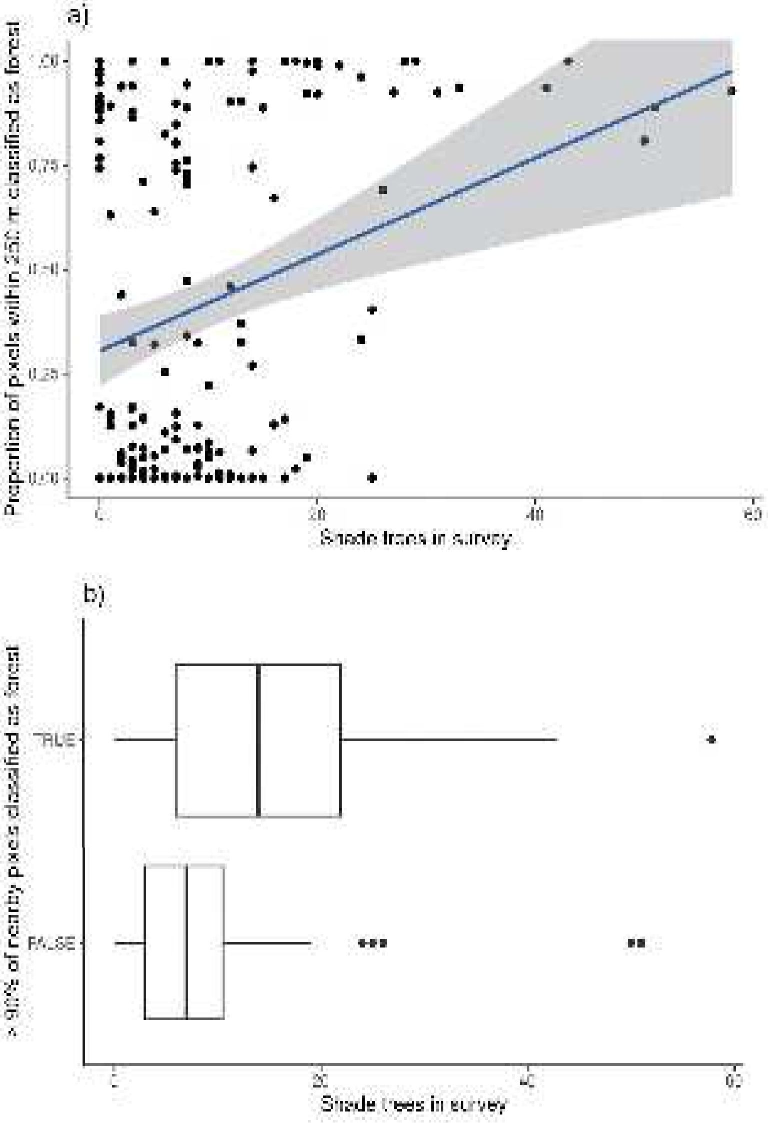

Figure 6. The likelihood of a farm being classified as a "forest" by the JRC anti-deforestation map relative to the number of trees in the survey.

Such remote sensing-based systems for measuring the risk of deforestation and biodiversity loss do not account for complex agroforestry systems. Agroforestry systems maintaining ecosystem condition and landscape connectivity, and re-agroforestry systems that were already mature in 2020 could be unfairly barred from import, despite being forest- and biodiversity-positive. Even though the wording of the EUDR is explicit in permitting agroforestry systems, importers may not wish to take the risk on areas supposedly covered by forests, and they may be unwilling to invest in the follow-up analysis necessary to validate results. Regional screening (classifying subnational regions as low- or high-risk for deforestation) makes this risk even higher. Companies seeking an easy approach to supply chain interventions to guarantee legal imports may screen out entire regions of cocoa production. This could incentivise farmers to switch to more destructive land patterns, producing non-regulated products, in precisely the regions where the legislation was intended to have the greatest benefits.

The processes underlying deforestation and the establishment of cocoa systems on previously-forested land are complex. The simple view that market demands drive deforestation for the purpose of cocoa production does not necessarily hold in West and Central Africa the way it may for soyabean in Brazil (Pereira and Bernasconi, 2025). Deforestation in West Africa cocoa landscapes typically begins with timber extraction, and cocoa is subsequently established on the degraded forests. Those responsible for the initial deforestation are unlikely to be same as those eventually growing cocoa. This is reflected in my models of biodiversity in cocoa, where the accessibility of sites (rather than farm management) was a major determinant of on-farm biodiversity (Chapter 4).

It is important for policies to consider the baseline state of biodiversity on cocoa farms when evaluating their contribution to deforestation and biodiversity loss (Martin and Raveloaritiana, 2022). Cocoa agroforestry systems, with simple or complex shade, are likely to host more biodiversity than systems derived from open land (Chapter 3). Forest-derived systems are richer in tree and understorey plant species than open-land-derived cocoa systems, but the composition of trees varies widely within both types of agroforest and open-land-derived farms with many spontaneous recruits can have high species richness that can be expected to increase over time (Chapter 4). If preventing biodiversity loss is a key aim of anti-deforestation regulations, a re-think is necessary to ensure the mitigating and enhancing effects of cocoa agroforestry from lower-diversity baselines can be accounted for.

The pixel-based approach of geospatial remote-sensing methods is also problematic for this use case. Imagine a farmer has access to the spatial data used to classify forest systems. She could simply use the map to decide where on her land to grow unregulated products, and where to grow regulated products (in areas not classified as forest). Importers could still buy her products with a “clean” conscience, but deforestation itself would be allowed to continue unfettered. In this sense, these deforestation regulations rely on farmers not having access to online resources, or training in using spatial data. While this is currently near-universally true for cocoa, it reflects patterns of global inequality and would not be considered useful for controlling the behaviour of farmers in wealthier countries.

A more nuanced, farm-based approach to anti-deforestation legislation in the global trade system would help to prevent perverse outcomes. This would require significant investment in national sourcing programs and monitoring databases, but some countries are already beginning to implement such mechanisms. For example, the Tanzanian Coffee Board recently announced its ambition to register and map all the country’s farms in aid of anti-deforestation regulations, as over 50% of its coffee is imported by the EU (Food Business Africa, 2024). If importer countries (and businesses) are serious about wanting to reduce their contributions to biodiversity and forest loss, they should invest the technology, effort, and resources into monitoring in a rigorous way.

6.3.3. Markets, cocoa prices, and mobilising funds

In April 2023, an historic pricing surge began for cocoa, where its price rose over fivefold in 12 months (Figure 7). Farms that were vulnerable to weather and climate events were hit across the region by an El Niño event, leading to governments revising their expected cocoa output down by over 40% (Reuters, 2024). Though these price increases have led to modest increases in the farm gate price of cocoa (Figure 8), this does not compensate for lost yields. Further, the “syndicated” system of cocoa buying in Ghana, with its dependence upon international lending for financing national cocoa purchases, means that the increase in prices could not be captured by farmers (Van Huellen et al., 2024).

Figure 7. The change in cocoa price both on the international market (blue) and at the farm gate in Ghana (brown) and Côte d'Ivoire (yellow). Taken with permission from KnowledgeCharts LLC.

Private sector interventions to reinvest this windfall into resilient farming systems could contribute to climate adaptation, biodiversity goals, ecosystem services, and sustainable livelihoods for farmers. Again, a certification demarking biodiversity and ecosystem service positive cocoa, sponsored by international importers, could help to bridge the disparity in local and international price increases through the specialty cocoa market (Van Huellen et al., 2024).

6.3.4. Climate change

We identified that farmers value cocoa farms highly for the future security that shade trees on farms bring (Chapter 5). However, to realise these benefits, shade tree communities (and the systems at large) must be resilient in the face of climate change in the region. Of the most common tree species in the dataset from West and Central African cocoa farms, species distribution models predict a range of likely climate impacts (Ariza-Salamanca et al., 2023). Common species in my data, such as

Pachylobus edulis, *Terminalia superba*, and *Carica papaya*, are expected to expand their ranges in West Africa under climate change. However, species such as *Ricinodendron heudelotii* are expected to undergo range contractions in the region, so may not form part of a resilient agroforestry system in certain climate contexts. Unfortunately, native species are expected to fare less well overall in medium-term climate change scenarios, so the conservation capacity of farms in the region may be limited (Ariza-Salamanca et al., 2023). Fruit trees from Cameroonian cocoa farms are also expected to undergo significant range contractions by 2050 (Gloy et al., 2023). Urgent steps should therefore be taken to enhance the resilience of cocoa systems to climate change. Agroforestry practices can play a role in this, but they must be tailored carefully to avoid emergent trade-offs (Abdulai et al., 2018b).

Shade trees, properly incorporated, can help to buffer microclimates for optimal cocoa productivity amid climate fluctuations (Kohl et al., 2024). Our surveys also indicate that this cooler microclimate is useful for people (Chapter 5). Most of the respondents indicating a “recreation” use value in the cocoa farms related this to a cooler microclimate, shade from the sun, which made the area the most attractive place to rest or relax available (Chapter 5). But more research is necessary to link these benefits to specific species and community traits: research using portable temperature sensors on farms with a range of shade types could help to inform farm design for this purpose.

There also remains a need to identify most functional pollinators and urgently take action to protect and enhance their populations in cocoa (Chumacero de Schawe et al., 2018). While recent research has identified that pollination and climate are both limiting factors in cocoa yield (Lander et al., 2025), pollinator species are also subject to the effects of climate change. Ensuring that populations of the species that cocoa depends most on are resilient to current and future climate change remains a key challenge to sustainable cocoa production. Identifying key species’ thermal tolerances, as well as interventions (including agroforestry) to boost the microclimatic suitability of cocoa farms for these species, is the most obvious immediate solution.

6.4. TAKEAWAYS FOR STAKEHOLDERS IN BIODIVERSITY AND COCOA

6.4.1. For national governments

"They will expand where no-one is looking"

This research has focused on African cocoa systems. For the EUDR, the vast majority of the monitoring effort will also go towards this region, leaving others relatively unmonitored. Crop production could expand in areas where monitoring efforts in support of anti-deforestation regulations are not being implemented, and bans are harder to justify. Agrcultural importers may already be preparing to make use of their multinational position to benefit from this. To speculate, for cocoa this new area could be in South America or Southeast Asia. Within African cocoa systems, this may mean a shift away from sourcing in Ghana and Côte d'Ivoire, towards Cameroon and other forest frontier regions. There, forest-derived agroforestry systems are harder to detect, and there is less data available to train machine-learning algorithms being employed elsewhere. This will continue so long as these regions are considered less material to mass markets.

Global monitoring programs and remote sensing-powered data layers should not limit themselves to those countries where commodities like cocoa are already prevalent, but aim to be able to detect cocoa-linked deforestation in wider regions. Governments of existing cocoa markets could support their farmers by introducing national monitoring programmes to support and "advertise" the positive impacts their agroforestry systems can have in context. Governments of emerging cocoa markets should invest, where necessary, into monitoring systems that can capture impacts as they emerge.

6.4.2. For private-sector importers and traders

"If you want biodiversity, just pay for it"

There is a growing interest from some corporate bodies in promoting, and in some cases compensating farmers for, sustainable and biodiversity-friendly practices. However, the restrictive and complex nature of finances surrounding cocoa trading has historically made it difficult to pass payments for ecosystem services and biodiversity-friendly actions to farmers (Van Huellen et al., 2024). But today, digital technologies such as "Mobile Money" could facilitate direct payments for biodiversity to farmers. Exploring unconditional, practice-based payments could be a compromise solution while capacity of biodiversity monitoring is developed. At present, the key barrier to this is authentication and transparency around payments.

6.4.3. For cocoa consumers

"Your PhD is on cocoa and nature. So, what chocolate should I buy?"

This research has focused on the features of cocoa farms that are likely to benefit or harm biodiversity and ecosystem services. However, in most of the national and land-use history contexts I investigated, real farms outperformed current standards in terms of plant biodiversity. Implementing the recommendations of most standards would not be expected to improve (plant) biodiversity relative to current conditions, except for areas with unshaded farms such as in Nigeria (Chapter 4). Though they are largely absent from corporate and certification criteria, the features most important for biodiversity gains or ecosystem service benefits include:

- Farms established on open-land systems (Chapter 3)
- Farms protecting and maintaining remnant trees (Chapter 4)
- Farms allowing natural regeneration of native tree species (Chapter 4)
- Farms harbouring threatened native species (Figure 1 in this chapter)
- Farms sustaining a healthy life-cycle of large trees (Chapter 5)

As traceability in supply chains improves, it will become more and more possible to make consumer choices based on these factors. But it will be the responsibility of brands themselves to engage with farmers and to implement these changes. As for what can be done now: brands with direct relationships with producers are more likely to be able to influence biodiversity-friendly practices – and their claims of biodiversity or other environmental benefits are more easily verified.

6.5. CONCLUSION

"I don't want to farm cocoa – I'm a taxi driver"

The final farm I visited during my fieldwork in Ghana made for stark contrast with many of the conclusions I have drawn from the overall dataset. The farmer in charge of the land, disillusioned by decades of shifting and often contradictory advice from extension officers, had decided to go against protocol and local recommendations, felling most of the shade trees on his plantation (Figure 8). The few trees that remained were also earmarked for removal: some had already been collared. This farm was hotter than other nearby farms. Dead cocoa trees with sun-bleached leaves made up patches of the remaining area. Perhaps this struggling productivity was the reason for a drastic shift towards full-sun farming. Or perhaps this was the result of shade removal. Either way, this farm was consigned to lose its remaining shade within a few years.

Figure 8. A Ghanaian cocoa farm where the majority of shade trees had been felled.

But the farmer was not necessarily wrong for doing this to his farm. General models of the benefits and trade-offs associated with trees cannot account for individual contexts. No-one would compensate him for the disservices he perceived in the trees: they attracted birds carrying the mistletoe parasite of cocoa trees. The timber from the felled trees could at least be sold. And the fate of the cocoa itself was not such a burden, as most of his income was from his job as a taxi driver in a local city. This situation is not unique: cocoa farming does not typically supply the majority of income for farmers achieving a living income today (Waarts et al., 2019). Despite narratives of the regeneration necessary to ensure the longevity of cocoa systems, the pattern in some instances appears to be a ratcheting-down of forest cover, biodiversity, and ecosystem services over time. Climate change will further destabilise cocoa production, despite some areas of increased suitability for the crop. Sustainability and biodiversity-friendly initiatives, however well-informed, must be made independently attractive for cocoa farmers.

Cocoa systems in West and Central Africa are at a crossroads. Concurrent shade simplification, forest loss, and climate change are fundamentally incompatible with sustainable cocoa production. In farms where tree diversity has been heavily impacted, overall biodiversity outcomes are worse, fewer ecosystem services are realised, yields can – in some contexts – be lower, and the future value of the land is diminished. Yet, establishing agroforestry systems that are beneficial to cocoa yields, biodiversity and ecosystem services is costly, and requires careful planning with context-specific accounting for farmer needs and historic baselines. Each country included in this study is at a very different point in its relationship with cocoa, and this needs to be accounted for in both research and practice. And if they are to succeed, sustainable practices must be made attractive to farmers based on their preferences and needs.

Cocoa agroforestry systems in West and Central Africa are no substitute for primary forests, or for strictly protected areas. But in the context of land-use history, external pressures, and agroforestry design, they can be a solution that maintains or enhances local biodiversity. For biodiversity and ecosystem services in cocoa systems, context is key, and we should not let the perfect be the enemy of the good.

7. References

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8. Appendices

8.1. Supplementary information for Chapter 2

8.1.1. Table 2-S1 Search terms in the initial evidence base construction.

	Pollination	**Pest control**	**Soil health**
Cocoa	(cocoa OR cacao) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(cocoa OR cacao) AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(cocoa OR cacao) AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Coffee	(coffee OR Coffea) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(coffee OR Coffea) AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(coffee OR Coffea) AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Cotton	(cotton) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(cotton) AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(cotton) AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Oil palm	("oil palm" OR "Elaeis" OR “palm oil”) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	("oil palm" OR "Elaeis" OR “palm oil”) AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	("oil palm" OR "Elaeis" OR “palm oil”) AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Rubber	(rubber OR "Hevea brasiliensis" OR Landolphia) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(rubber OR "Hevea brasiliensis" OR Landolphia) AND ("natural enemies" OR "biological pest control" OR (predator*)) AND ("biodiversity" or "abundance" OR "richness") AND (yield OR productivity OR production)	(rubber OR "Hevea brasiliensis" OR Landolphia) AND ("soil fertility" OR "soil health" OR "soil degradation") AND (biodiversity OR richness OR abundance OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Soyabe	(soy OR soya OR soybean OR "Glycine max") AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield	(soy OR soya OR soybean OR "Glycine max") AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*")	(soy OR soya OR soybean OR "Glycine max") AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR

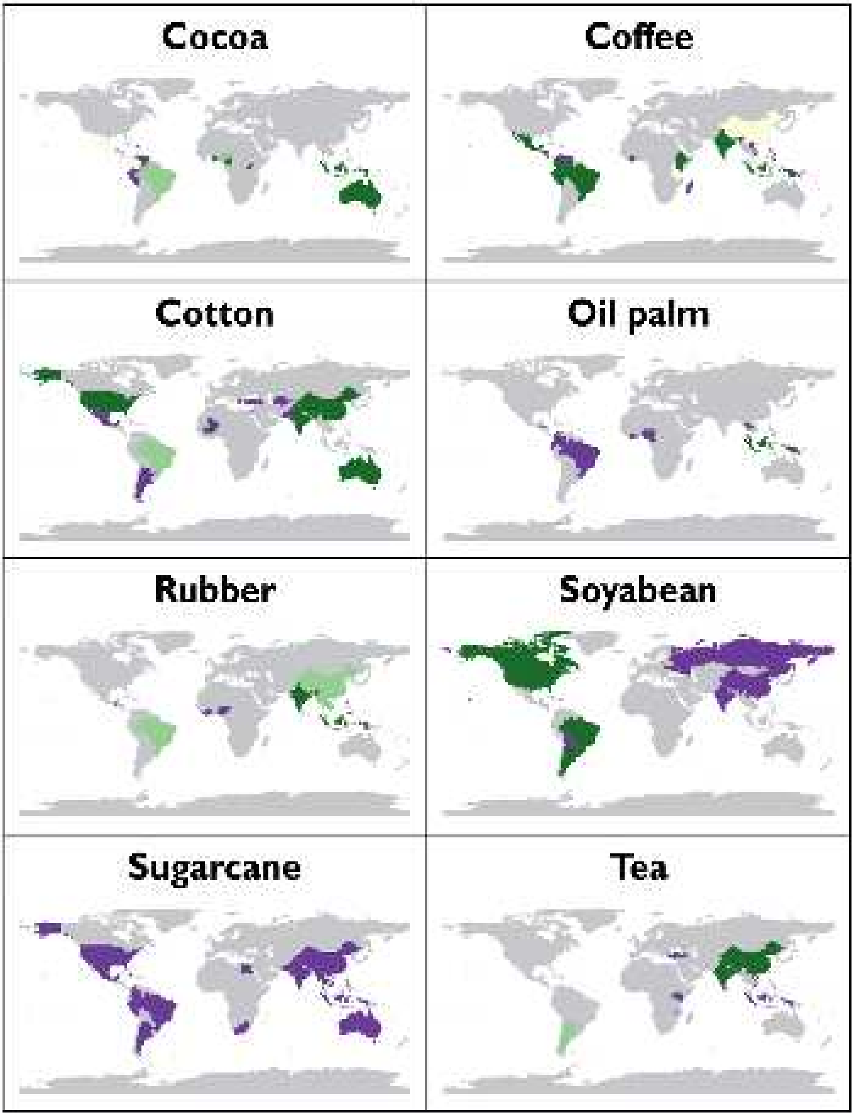
an	OR productivity OR "fruit set" OR "profitability")	AND (yield OR productivity OR "fruit set" OR "profitability")	"ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Sugarcane	("sugar cane" OR sugarcane OR Saccharum) AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	("sugar cane" OR sugarcane OR Saccharum) AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	("sugar cane" OR sugarcane OR Saccharum) AND ("soil quality" OR "soil degradation" OR "soil health" OR "soil erosion" OR "soil aeration" OR "soil fertility") AND (biodiversity OR richness OR abundance OR density OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")
Tea	(tea OR "Camellia sinensis") AND (pollination OR pollinator*) AND (biodiversity OR richness OR abundance OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(tea OR "Camellia sinensis") AND ("natural pest control" OR "natural enem*" OR (predator* AND "pest control")) AND (biodiversity OR richness OR abundance OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")	(tea OR "Camellia sinensis") AND ("soil fertility" OR "soil health" OR "soil degradation") AND (biodiversity OR richness OR abundance OR evenness OR dominance OR composition OR "ecosystem service*") AND (yield OR productivity OR "fruit set" OR "profitability")

8.1.2. Table 2-S2

A summary of the findings of the review, organised first by crop, then by ecosystem service, then by the mechanism by which facets of biodiversity support that service, and finally by the types of pressures the crops' production systems are purported to impact that facet. The final shaded column summarises both the risk posed by the loss of that biodiversity, and the likelihood of the crop production system impacting biodiversity.

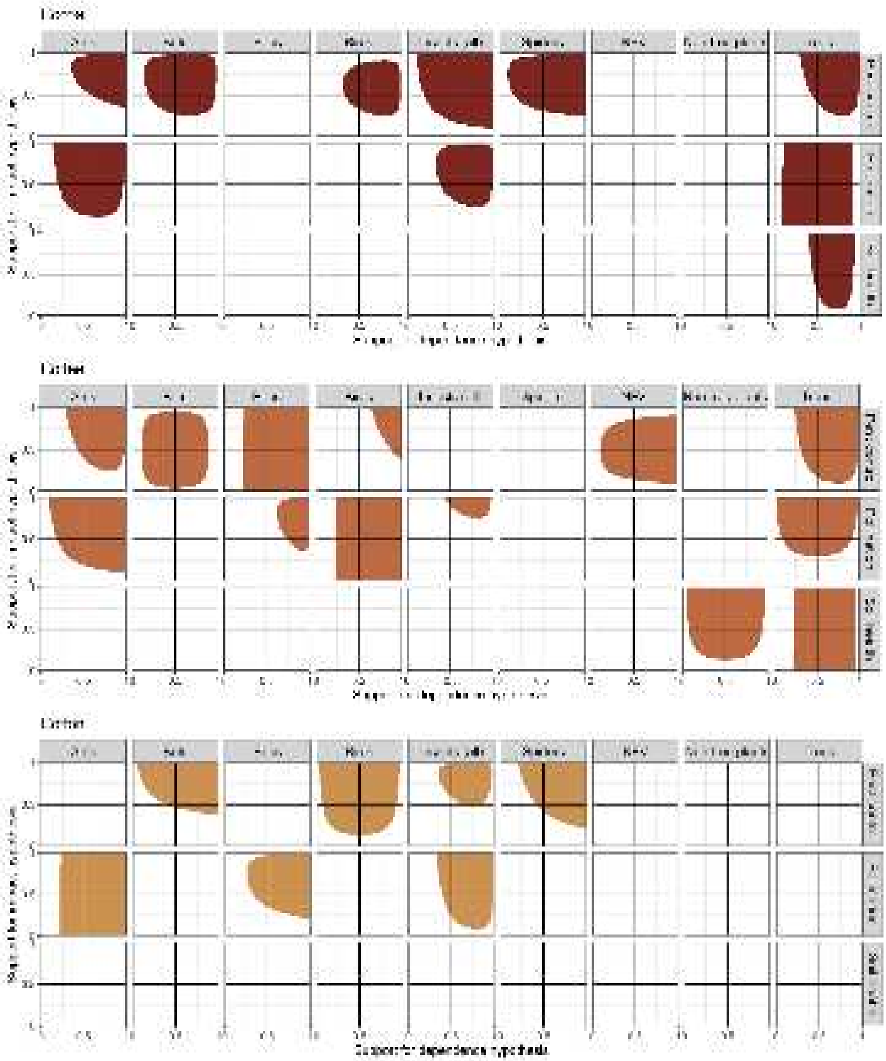
This summary table can be found in the supplementary information of the publication copy of this chapter, at https://doi.org/10.6084/m9.figshare.c.7430648.

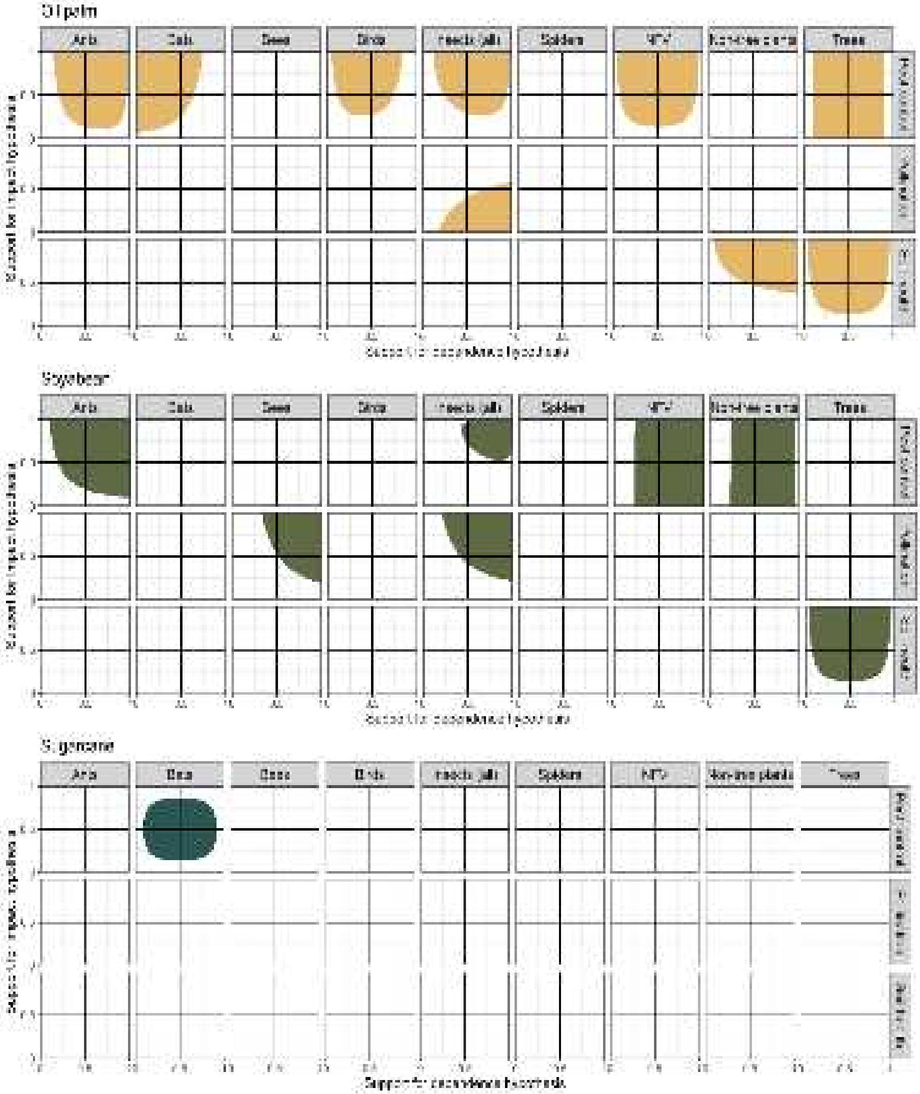
8.1.3. Figure 2-S1

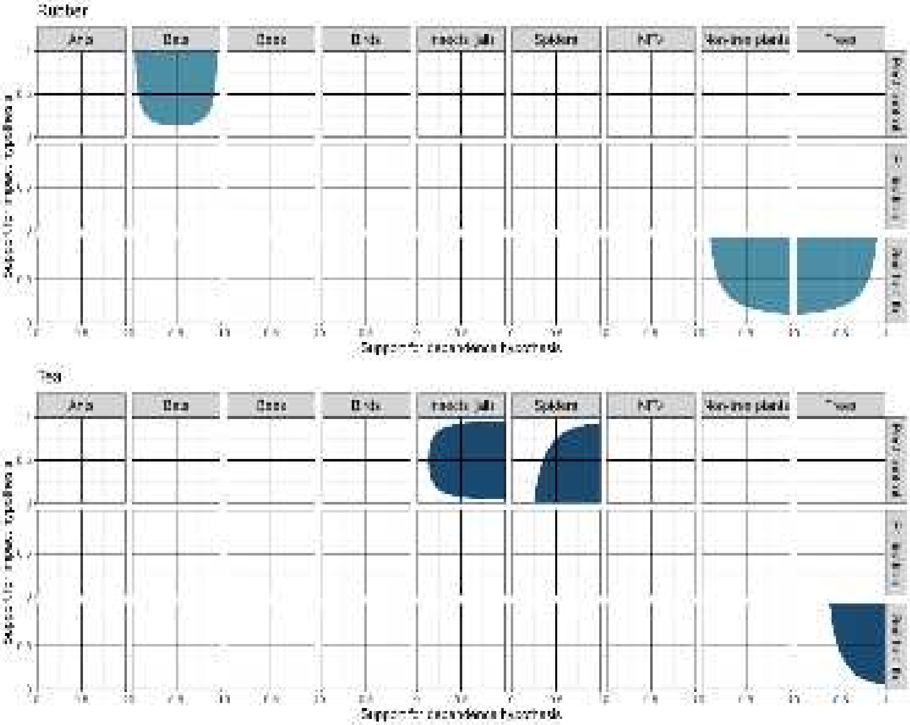


The geographic distribution of evidence from the initial literature search for ecosystem feedbacks in eight key commodity crops. Reference major production areas obtained from FAO for the period of 2011-2021 and include any country reporting a share of production at least 1% of the total for each commodity (Food and Agriculture Organization of the United Nations, 2020). The fill colour represents the presence and type(s) of evidence reported from studies in each country. Purple represents areas where production occurs, but no evidence was found. Light green countries represent where evidence for dependencies, but not impacts, was found. Light yellow countries represent where evidence for impacts was uncovered without evidence for dependencies. Finally, dark green areas show countries where evidence for both impacts and dependencies were found.

8.1.4. Figure 2-S2: disaggregated results by crop




Oil palm
Ants
Bats
Bees
Birds
Insects (galls)
Spiders
NTV
Non-tree plants
Trees
Support for impact hypothesis
Support for dependence hypothesis
Soybean
Ants
Bats
Bees
Birds
Insects (galls)
Spiders
NTV
Non-tree plants
Trees
Support for impact hypothesis
Support for dependence hypothesis
Sugarcane
Ants
Bats
Bees
Birds
Insects (galls)
Spiders
NTV
Non-tree plants
Trees
Support for impact hypothesis
Support for dependence hypothesis
0
0.5
1



The evidence bases for ecological impacts and agronomic dependencies of commodity crop production systems on biodiversity. Shaded areas mostly in the top-right quadrant are likely to support the hypothesis that interdependencies, feedback loops, and "intensification traps" could emerge due to crop-induced biodiversity change. The shaded regions represent the 95% percentile mass of the joint posterior distribution of findings' support for the impact and dependence hypotheses in the reviewed evidence. This therefore represents the likely outcome of seeking both evidence for dependence and evidence for impacts of a given cropping system via one of three ecosystem services.

8.1.5. Supplementary Information 2-1: full reference list for review data.

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8.2. Supplementary information for Chapter 3

8.2.1. Supplementary information 3-1 data collection for biodiversity responses to cocoa-driven land-use change

To gather further field data from studies comparing biodiversity in cocoa plantations to primary forests, we made Web of Science searches in September 2018, identifying studies with the following search terms:

(species-richness OR richness OR abundance OR community-composition OR biodiversity OR extirpat) AND (young OR recovery OR intensification OR over-time OR long-term OR new OR year) AND (land-use OR degradation OR restoration OR shade OR habitats OR agroforest* OR regime OR manage* OR chang* OR cultivate) AND (cocoa OR cacao OR theobroma)*

This returned a total of 198 potentially useful sources of data. 53 of these studies met study inclusion criteria of containing at least one site of cocoa cultivation, we were able to retrieve potentially useful data from 13, and 5 were incorporated fully into the PREDICTS database.

8.2.2. Table 3-S1

Numbers of species, organised by phylum, included in the analysis, and their distribution among studies.

Kingdom	**Phylum**	**Number of distinct taxa sampled**	**Number of studies containing phylum**
Plantae	Streptophyta	28	1
	Tracheophyta	2634	8
Animalia	Annelida	1	2
	Arthropoda	448	14
	Chordata	664	13
	Mollusca	32	1
Total		**3807**	**36**

8.2.3. Supplementary Information 3-2 Mixed-effects modelling of biodiversity responses

During model refinements, we used the optimiser “bobyqa” in the formation of each of the models. Models for species richness were selected with the aim of minimising their Akaike Information Criterion (AICc) value with respect to random- and fixed-effects structures. When constructing all models, random-effects structures were selected first, and as more specific terms (study to study/block) were added, models were rejected if their AICc was higher than, or less than a value of 2 lower than a less complex structure (simpler models rejected if they were significantly worse than the full model). In all models, all available random structures for fixed-slope models were considered. Site-level random effects were not considered for the compositional similarity models because modelling was performed on data from pairs of sites, not individual sites. Comparisons were similarly not drawn with within geographic blocks, so random effects in the compositional similarity models were limited to the study level.

8.2.4. Supplementary Information 3-3 Complete list of data sources

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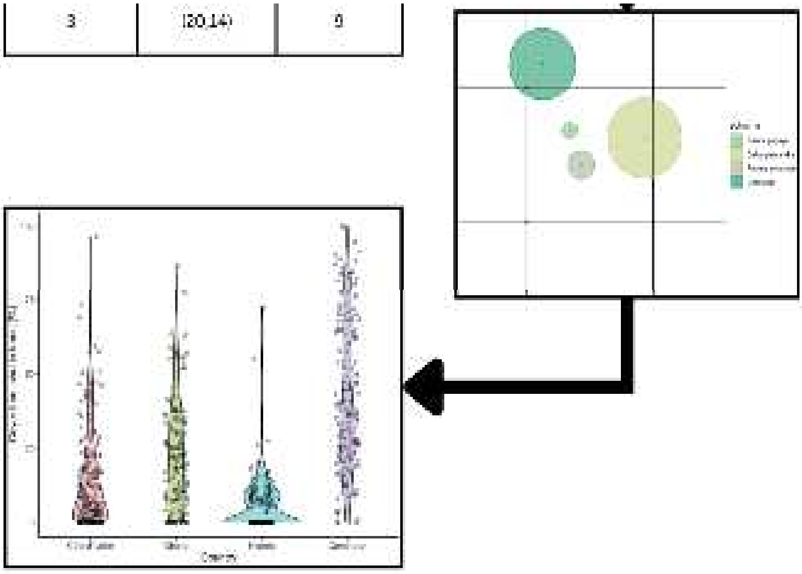
8.2.5. Table 3-S2

Evaluated model structures and associated assessment criteria for goodness of fit (AIC)

Response variable	Model structure	Rank	ΔAIC	Selected
Species richness	Null model: Species richness ~ 1	5	15838.20	
Species richness	Species richness ~ (1|Study) + (1|Block in study)	4	743.85	
Species richness	Species richness ~ (1|Study)	3	741.85	
Species richness	Species richness ~ LandUse + (1|Study) + (1|Block in study)	2	0.05	Yes
Species richness	Species richness ~ LandUse + log(Human population density) + (1|Study) + (1|Block in study)	1	0.00	
Community composition	Null model: Logit(Community Similarity) ~ 1	5	40276.6	
Community composition	Logit(Community Similarity) ~ (1|Study)	4	5411.4	
Community composition	Logit(Community Similarity) ~ log(Distance) + (1|Study)	3	3628.6	
Community composition	Logit(Community Similarity) ~ Land use Contrast + (1|Study)	2	1180.3	
Community composition	Logit(Community Similarity) ~ Land use Contrast + log(Distance) + (1|Study)	1	0.0	Yes

8.3. Supplementary information for Chapter 4

8.3.1. Figure 4-S1.



The process for establishing shade cover on each plot. Shade tree locations and crown sizes are mapped onto a 2D surface representing the plot, which is then summarised into a percent cover at the plot level.

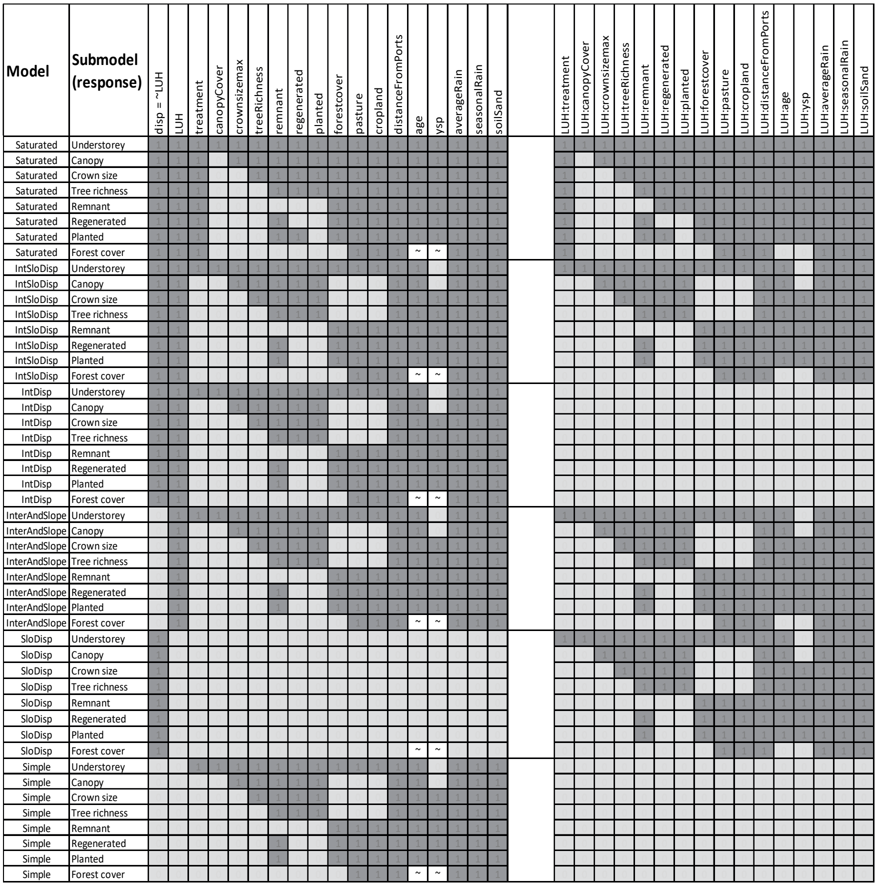
8.3.2. Table 4-S1.

Summarised description of the variables used in the multigroup analysis.

Category	Variable	Source	Range in data
Biodiversity response	Remnant abundance	Biodiversity surveys	0 - 17 (count)
Biodiversity response	Regenerated abundance	Biodiversity surveys	0 - 10 (count)
Biodiversity response	Planted abundance	Biodiversity surveys	0 - 15 (count)
Biodiversity response	Tree richness	Biodiversity surveys	0 - 11 (count)
Biodiversity response	Understorey richness	Biodiversity surveys	0 - 49 (count)
Biodiversity response	Canopy cover	Biodiversity surveys	0 - 1 (proportion)
Anthropogenic driver	Plot treatment	Biodiversity surveys	Factor (T1- T4)
Anthropogenic driver	Previous land use	Biodiversity surveys	0 / 1 (forest-derived / open land derived)
Anthropogenic driver	Age of cocoa trees on plot	Biodiversity surveys	5 - 55 (years)
Anthropogenic driver	Forest cover	GEDI (Potapov et al., 2021)	0 - 0.99 (proportion in area)
Anthropogenic driver	Landscape pasture cover	ESRI global Land use land cover 2022 (Karra et al., 2021)	0 - 0.64 (proportion in area)
Anthropogenic driver	Landscape cropland cover	ESRI global Land use land cover 2022 (Karra et al., 2021)	0-1 (proportion in area)
Anthropogenic driver	Travel time to ports	Global accessibility surfaces (Nelson et al., 2019)	43-604 (minutes)

Intrinsic property	Long-term annual rain	CHIRPS (Funk et al., 2015)	1094 - 1756 (mm)
Intrinsic property	Long-term seasonal rain	CHIRPS (Funk et al., 2015)	33 - 180 (mm)
Intrinsic property	Soil sand content	SoilGrids 250m (Poggio and de Sousa, 2020)	241 – 686 (g kg $^{-1}$)

8.3.3. Figure 4-S2.



Model	Submodel (response)	disp = ~LUH	LUH	treatment	canopyCover	crownsizemax	treeRichness	remnant	regenerated	planted	forestcover	pasture	cropland	distanceFromPorts	age	ysp	averageRain	seasonalRain	soilSand		LUH:treatment	LUH:canopyCover	LUH:crownsizemax	LUH:treeRichness	LUH:remnant	LUH:regenerated	LUH:planted	LUH:forestcover	LUH:pasture	LUH:cropland	LUH:distanceFromPorts	LUH:age	LUH:ysp	LUH:averageRain	LUH:seasonalRain	LUH:soilSand
Saturated	Understorey	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Saturated	Canopy	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Saturated	Crown size	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1		1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Saturated	Tree richness	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1		1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Saturated	Remnant	1	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Saturated	Regenerated	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
Saturated	Planted	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1		1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1
Saturated	Forest cover	1	1	1	0	0	0	0	0	0	0	1	1	1	~	~	1	1	1		1	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1
IntSloDisp	Understorey	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
IntSloDisp	Canopy	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1		0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1
IntSloDisp	Crown size	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1
IntSloDisp	Tree richness	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1
IntSloDisp	Remnant	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
IntSloDisp	Regenerated	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
IntSloDisp	Planted	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
IntSloDisp	Forest cover	1	1	0	0	0	0	0	0	0	0	1	1	1	~	~	1	1	1		0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1
IntDisp	Understorey	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Canopy	1	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Crown size	1	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Tree richness	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Remnant	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Regenerated	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Planted	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
IntDisp	Forest cover	1	1	0	0	0	0	0	0	0	0	1	1	1	~	~	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
InterAndSlope	Understorey	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
InterAndSlope	Canopy	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1		0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1
InterAndSlope	Crown size	0	1	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1
InterAndSlope	Tree richness	0	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1
InterAndSlope	Remnant	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
InterAndSlope	Regenerated	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
InterAndSlope	Planted	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
InterAndSlope	Forest cover	0	1	0	0	0	0	0	0	0	0	1	1	1	~	~	1	1	1		0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1
SloDisp	Understorey	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1
SloDisp	Canopy	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1
SloDisp	Crown size	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1
SloDisp	Tree richness	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1
SloDisp	Remnant	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
SloDisp	Regenerated	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
SloDisp	Planted	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1
SloDisp	Forest cover	1	0	0	0	0	0	0	0	0	0	0	0	0	~	~	0	0	0		0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1
Simple	Understorey	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Canopy	0	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Crown size	0	0	0	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Tree richness	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Remnant	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Regenerated	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Planted	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Simple	Forest cover	0	0	0	0	0	0	0	0	0	0	1	1	1	~	~	1	1	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

The structure of the path models tested in this analysis. A cell shaded in dark grey indicates a term was included in a model; a cell shaded in light grey indicates a term was omitted from a model. '~' characters indicate where a correlated error was included in the model.

8.3.4. Table 4-S2.

Final model diagnostic table for the path models evaluated.

Model	**df**	**Log likelihood**	**Chi-squared difference**	**p-value**
"Simple" – dispersion, intercepts, and slopes do not vary by group	93	-8101.06	457.89	0
Dispersion, intercepts free	110	-8027.59	310.96	0
Dispersion, slopes, and intercepts free	178	-7907.66	71.10	0.15
Dispersion, slopes free	180	-7945.54	146.85	1.19E-09
"Saturated" model	238	-7872.12	0	1

8.3.5. Table 4-S3.

Model summary tables for each path in the final path model.

Response		Estimate		Standard error		Z-value		P-value		Significance	
		Forest-derived	Open-land-derived	Forest-derived	Open-land-derived	Forest-derived	Open-land-derived	Forest-derived	Open-land-derived	Forest-derived	Open-land-derived
Understorey species richness	(Intercept)	2.49	2.36	0.15	0.17	17.17	-0.80	0.00	0.42	***	
	treeDivRichness	0.00	-0.01	0.07	0.03	0.06	-0.35	0.95	0.73		
	abundanceRemnant	-0.01	0.03	0.05	0.03	-0.11	1.30	0.91	0.20		

	abundanceRegenerated	0.05	0.07	0.06	0.03	0.78	2.57	0.44	0.01		*
	abundancePlanted	0.04	-0.01	0.05	0.02	0.73	-0.65	0.47	0.51		
	crownsizemax	0.06	0.06	0.02	0.01	2.57	4.53	0.01	0.00	*	***
	canopyCover	-0.04	-0.14	0.44	0.24	-0.08	-0.60	0.94	0.55		
	treatment2	-0.10	0.03	0.15	0.08	-0.67	0.33	0.50	0.75		

	treatment3	-0.11	-0.08	0.15	0.08	-0.73	-1.05	0.46	0.29		
	treatment4	-0.04	-0.06	0.15	0.08	-0.23	-0.80	0.82	0.42		
	forestcover	0.00	-0.17	0.07	0.06	-0.06	-2.98	0.95	0.00		**
	pasture	0.06	0.02	0.08	0.03	0.75	0.50	0.45	0.62		
	cropland	-0.21	-0.01	0.06	0.03	-3.41	-0.27	0.00	0.79	***	
	distance_ports	0.04	0.19	0.09	0.05	0.42	3.56	0.68	0.00		***
	averageRain.mm	-0.20	0.07	0.10	0.03	-2.09	2.33	0.04	0.02	*	*

	soil_sand	0.15	-0.22	0.08	0.03	1.77	-7.11	0.08	0.00	.	***
Shade cover	(Intercept)	-0.12	-0.07	0.07	0.07	-1.85	0.84	0.07	0.40	.	
	treeDivRichness	-0.01	-0.01	0.01	0.01	-1.43	-1.88	0.15	0.06		.
	abundanceRemnant	0.05	0.05	0.01	0.01	7.50	9.48	0.00	0.00	***	***
	abundanceRegenerated	0.02	0.04	0.01	0.01	2.91	5.99	0.00	0.00	**	***

	abundancePlanted	0.02	0.03	0.01	0.00	2.55	6.07	0.01	0.00	*	***
	crownsizemax	0.03	0.03	0.00	0.00	9.77	14.72	0.00	0.00	***	***
	distance_ports	0.01	0.01	0.01	0.01	0.90	1.49	0.37	0.14		
	age	0.03	0.01	0.02	0.01	1.34	0.71	0.18	0.48		
	ysp	-0.13	0.01	0.06	0.01	-1.99	1.00	0.05	0.32	*	
	averageRain.mm	-0.02	0.00	0.01	0.01	-1.44	-0.47	0.15	0.64		
	soil_sand	-0.02	-0.03	0.01	0.01	-1.32	-4.73	0.19	0.00		***

Largest crown radius	(Intercept)	3.64	3.25	1.53	1.58	2.38	-0.25	0.02	0.81	*	
	treeDivRichness	1.07	0.88	0.19	0.18	5.77	4.99	0.00	0.00	***	***
	abundanceRemnant	-0.30	0.15	0.14	0.13	-2.15	1.15	0.03	0.25	*	
	abundanceRegenerated	0.15	-0.34	0.19	0.15	0.78	-2.20	0.43	0.03		*
	abundancePlanted	0.08	-0.09	0.15	0.11	0.55	-0.76	0.59	0.45		

	distance_ports	1.75	0.52	0.22	0.21	7.99	2.41	0.00	0.02	***	*
	age	-0.38	0.03	0.46	0.24	-0.83	0.13	0.40	0.90		
	ysp	0.42	0.51	1.46	0.32	0.29	1.61	0.77	0.11		
	averageRain.mm	0.28	0.18	0.27	0.18	1.07	1.02	0.29	0.31		
	soil_sand	-0.26	-0.10	0.27	0.18	-0.96	-0.54	0.34	0.59		
Tree species richness	(Intercept)	0.01	0.48	0.38	0.38	0.03	1.24	0.98	0.22		
	abundanceRemnant	0.13	0.12	0.01	0.01	10.46	12.06	0.00	0.00	***	***

	abundanceRegenerated	0.21	0.14	0.03	0.02	7.03	9.03	0.00	0.00	***	***
	abundancePlanted	0.18	0.09	0.02	0.01	8.77	6.98	0.00	0.00	***	***
	distance_ports	0.29	0.12	0.05	0.04	6.33	2.88	0.00	0.00	***	**
	age	0.09	-0.02	0.11	0.04	0.82	-0.34	0.41	0.73		
	ysp	-0.07	-0.06	0.35	0.06	-0.21	-0.99	0.84	0.32		
	averageRain.mm	0.09	0.06	0.07	0.04	1.23	1.63	0.22	0.10		

	soil_sand	-0.17	-0.01	0.08	0.04	-2.26	-0.34	0.02	0.73	*	
Remnant tree abundance	(Intercept)	1.98	0.26	0.72	0.73	2.74	-2.34	0.01	0.02	**	*
	forest cover	0.03	0.27	0.17	0.15	0.16	1.83	0.87	0.07		.
	pasture	0.19	0.13	0.13	0.08	1.44	1.54	0.15	0.12		
	cropland	-0.50	-0.18	0.08	0.08	-6.10	-2.27	0.00	0.02	***	*
	distance_ports	1.24	0.38	0.16	0.15	7.57	2.57	0.00	0.01	***	*
	age	-0.62	-0.01	0.23	0.09	-2.69	-0.15	0.01	0.88	**	
	ysp	2.53	-0.09	0.70	0.13	3.62	-0.68	0.00	0.50	***	

	averageRain.mm	0.36	0.03	0.22	0.09	1.66	0.36	0.10	0.72	.	
	soil_sand	-0.28	0.11	0.20	0.09	-1.41	1.25	0.16	0.21		
Regenerated tree abundance	(Intercept)	-4.34	-0.15	1.26	1.27	-3.44	3.29	0.00	0.00	***	***
	abundanceRemnant	0.05	-0.03	0.07	0.04	0.65	-0.61	0.52	0.55		
	forestcover	-0.60	-0.11	0.18	0.16	-3.31	-0.73	0.00	0.47	***	
	pasture	-0.55	-0.32	0.22	0.11	-2.55	-2.92	0.01	0.00	*	**
	cropland	0.52	0.07	0.17	0.10	3.10	0.68	0.00	0.50	**	

	distance_ports	0.53	0.08	0.22	0.14	2.48	0.54	0.01	0.59	*	
	age	1.35	-0.07	0.38	0.13	3.57	-0.56	0.00	0.57	***	
	ysp	-3.72	-0.10	1.17	0.19	-3.19	-0.54	0.00	0.59	**	
	averageRain.mm	0.16	0.10	0.19	0.10	0.85	1.05	0.39	0.30		
	soil_sand	-0.62	-0.23	0.20	0.09	-3.09	-2.54	0.00	0.01	**	*
Planted tree abundance	(Intercept)	2.05	0.40	0.77	0.79	2.66	-2.11	0.01	0.04	**	*
	abundanceRemnant	-0.03	-0.11	0.04	0.04	-0.70	-3.03	0.48	0.00		**

	forest cover	-0.23	-0.15	0.12	0.14	-1.97	-1.07	0.05	0.28	*	
	pasture	-0.13	0.10	0.12	0.09	-1.12	1.09	0.27	0.28		
	cropland	-0.21	-0.27	0.10	0.08	-2.18	-3.45	0.03	0.00	*	***
	distance_ports	0.40	0.49	0.13	0.14	3.15	3.56	0.00	0.00	**	***
	age	-0.45	0.26	0.23	0.10	-1.91	2.54	0.06	0.01	.	*
	ysp	1.83	-0.28	0.73	0.15	2.52	-1.94	0.01	0.05	*	.
	averageRain.mm	-0.08	0.17	0.13	0.08	-0.61	1.98	0.55	0.05		*
	soil_sand	-0.06	-0.19	0.14	0.09	-0.42	-2.13	0.68	0.03		*

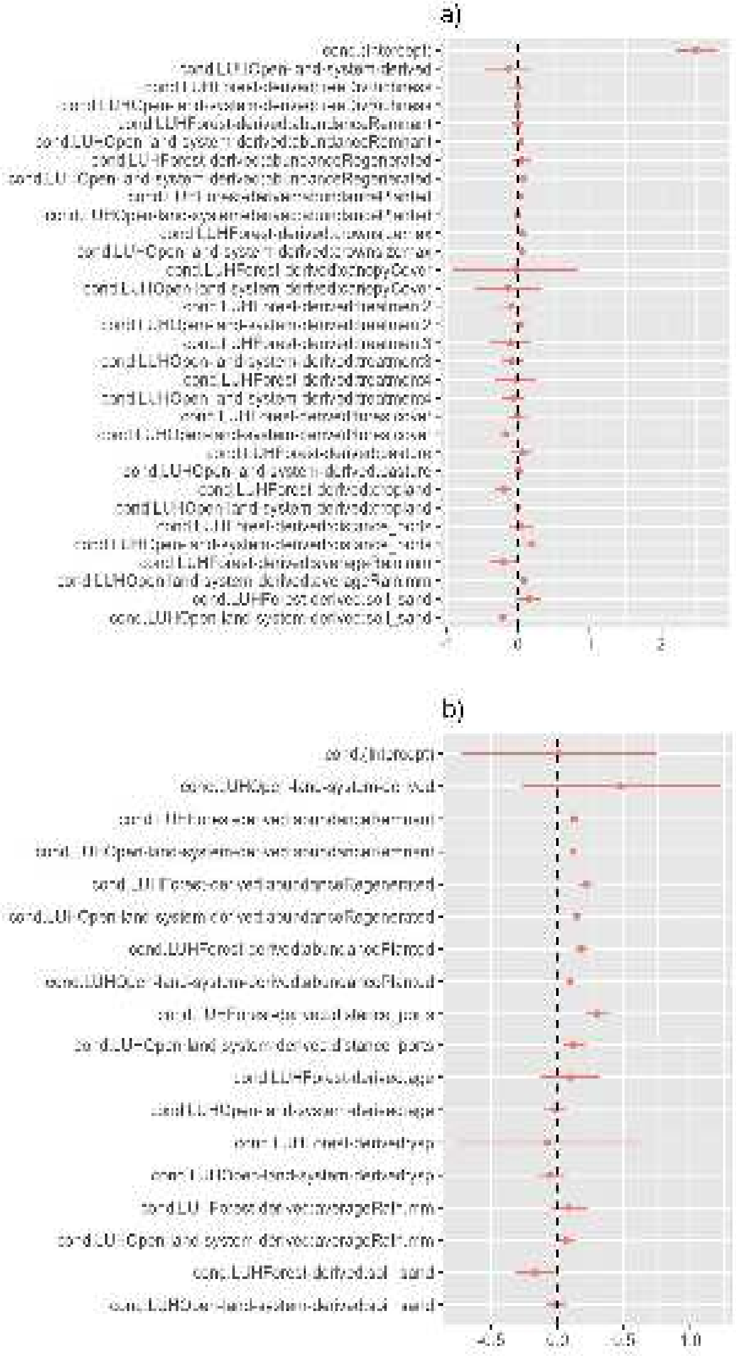
Landscape forest cover	(Intercept)	0.32	-0.23	0.06	0.06	5.79	-8.77	0.00	0.00	***	***
	pasture	-0.52	-0.31	0.06	0.03	-9.43	-10.56	0.00	0.00	***	***
	cropland	0.18	-0.02	0.05	0.03	3.98	-0.53	0.00	0.59	***	
	distance_ports	0.71	0.69	0.05	0.03	15.69	20.47	0.00	0.00	***	***
	averageRain.mm	-0.09	0.20	0.08	0.03	-1.16	6.99	0.25	0.00		***
	soil_sand	-0.01	-0.04	0.07	0.03	-0.07	-1.35	0.94	0.18		

8.3.6. Table 4-S4.

Table of ‘Bayesian R2’ values for each sub-model in the most parsimonious structural equation model. The 95% credible intervals are included for each R2 value.

Response variable	**Estimate**	**Est Error**	**Q2.5**	**Q97.5**
Understorey plant richness	0.398808	0.031673	0.331955	0.455493
Canopy Cover	0.73049	0.009586	0.710043	0.747824
Crown size (max)	0.478681	0.01978	0.438104	0.51409
Tree richness	0.717069	0.00953	0.695824	0.733066
Abundance (Remnant)	0.483702	0.039724	0.399374	0.553026
Abundance (Regenerated)	0.243364	0.078533	0.116113	0.416043
Abundance (Planted)	0.233497	0.047204	0.148443	0.332844
Forest cover	0.59445	0.015473	0.562309	0.622706

8.3.7. Figure 4-S3.



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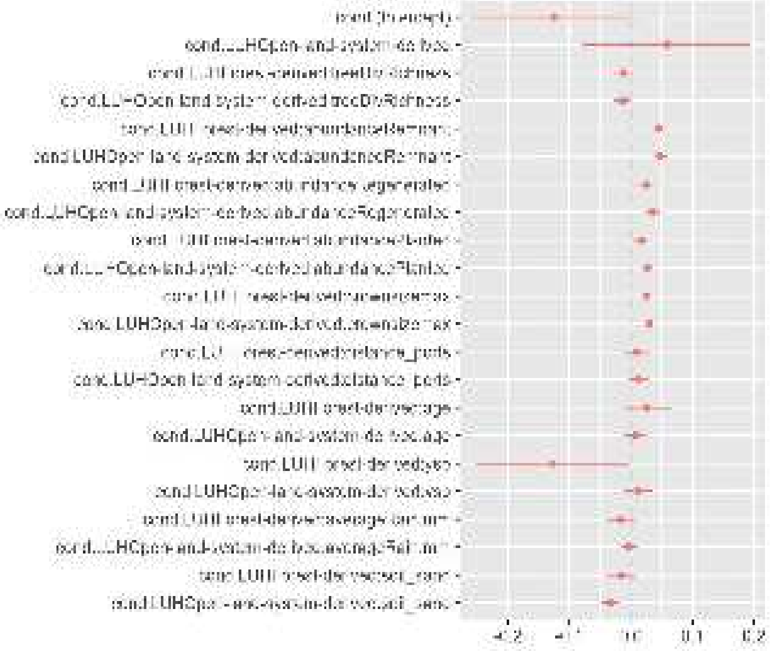
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cond.LUHOpen land system derived.age
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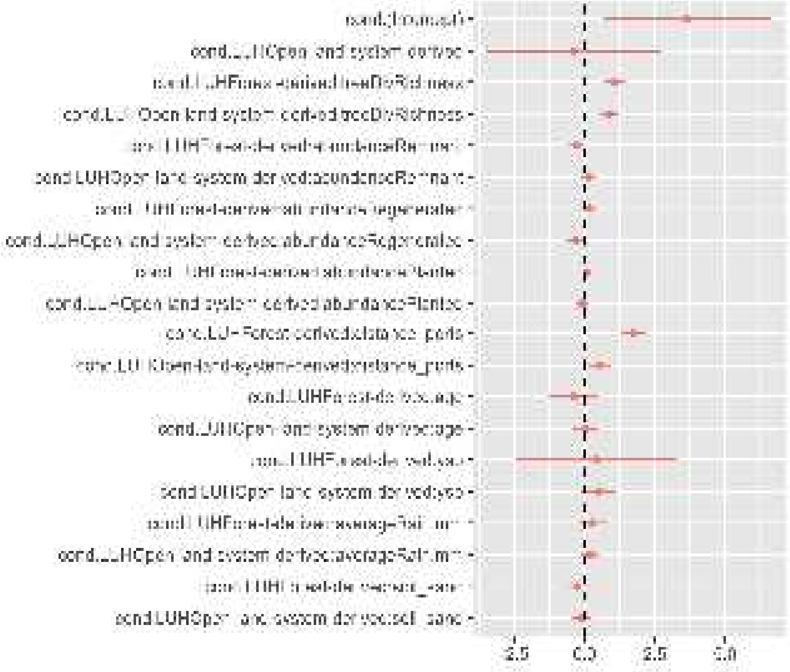
d)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5.0

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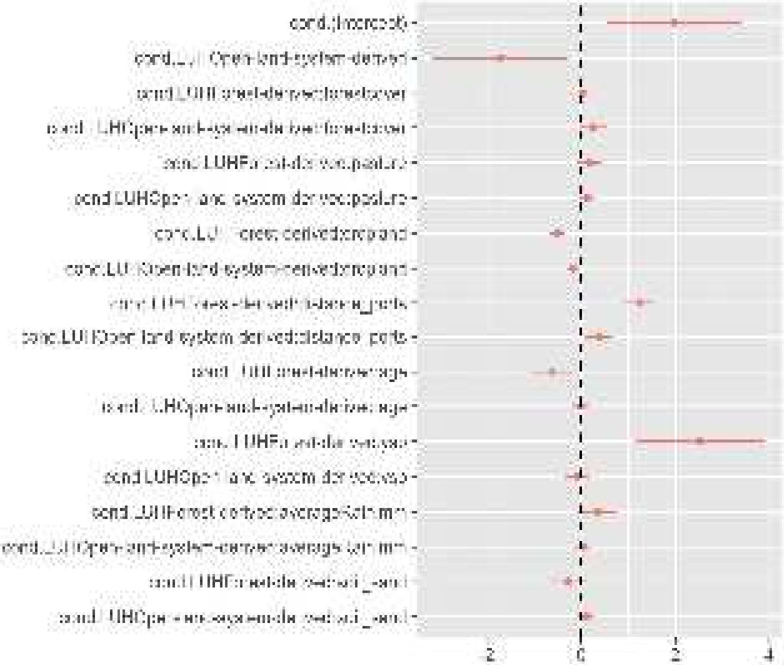

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cond.LUHForest-derived:ysp
cond.LUHOpen-land-system-derived:ysp
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cond.LUHOpen-land-system-derived:averageRain.mm
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4

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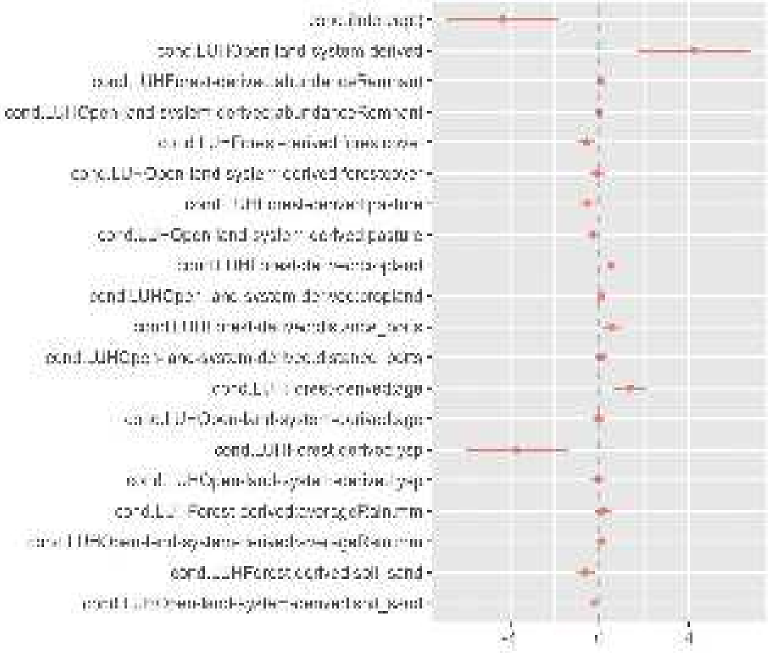

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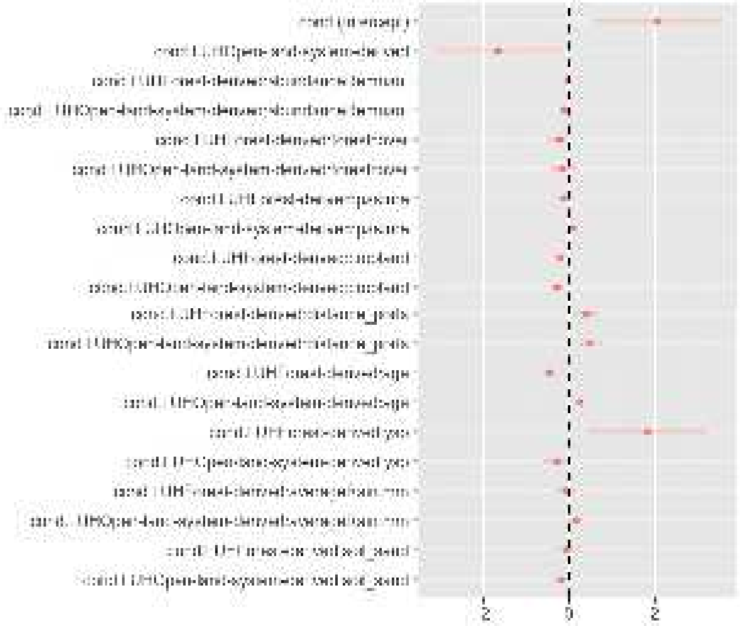
g)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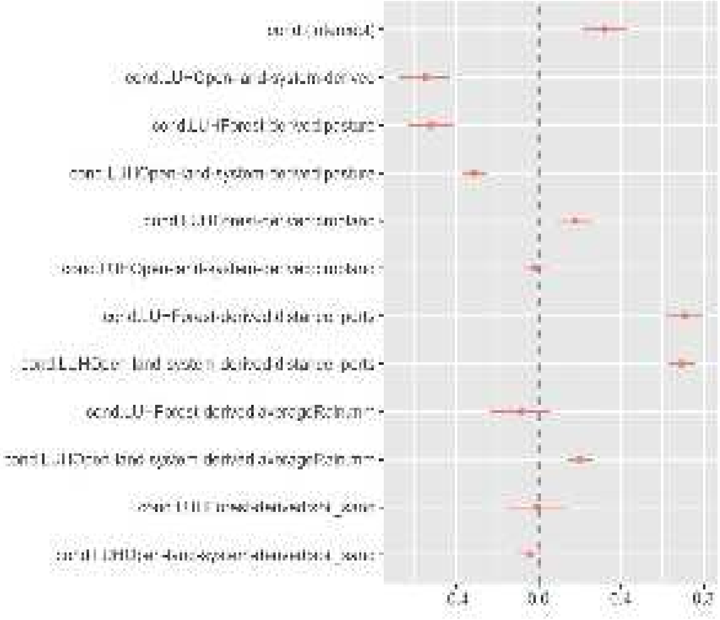
0
2

h)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Model effects plots for the final biodiversity path model. a) Understorey richness, b) Tree richness, c) canopy over, d) max. crown size, e)remnant abundance, f) spontaneous recruit abundance, g) planted tree abundance, h) forest cover

8.4. Supplementary information for Chapter 5

8.4.1. Table 5-S1

Model comparison table for null (left) and final (right) models for each of the values/trade-offs in the tree-scale models.

Model	AIC (Null)	AIC (Final)
Construction	1327.321	1162.707
Shade	1436.529	1306.477
Income	991.0461	922.5915
Food	2032.764	1574.485
Medicine	1032.902	970.6435
Fertility	432.4616	402.012
Competition	556.9206	549.2225
Pests/disease	556.9206	549.2225

8.4.2. Table 5-S2

Model summary tables for the ecosystem service GAM predictions, post-refinement for concurvity.

	Construction	Food	Fuel	Future security	Hunting	Marketable goods	Medicine	Ornaments/ tradition	Recreation	Tools
(Intercept)	0.11	3.299	0.467	1.23	-1.511	1.691	0.557	-2.782	0.544	-0.905
Num.Obs.	143	143	143	143	143	143	143	143	143	143
AIC	297.9	254.3	295.3	249.5	283.7	324.4	353.5	177.5	333.3	264.9
RMSE	1.05	0.7	1.1	0.9	1.14	0.98	1.29	0.82	1.19	0.99

8.4.3. Table 5-S3

Model summary table for the final yield model.

	Plot yield		
Predictors	Estimates	CI	p
(Intercept)	5.77	5.65 – 5.89	**<0.001**
plot ID [2]	0.03	-0.03 – 0.09	0.282
plot ID [3]	0.15	0.09 – 0.21	**<0.001**
plot ID [4]	0.24	0.18 – 0.29	**<0.001**
Smooth term (treeDiv abundance)			**0.008**
Smooth term (treeDiv simpson)			**<0.001**
Smooth term (function crownPropEvergreen)			0.361
Smooth term (function nfix)			0.590
Smooth term (functioning woodDensity)			0.146
Smooth term (canopyCover)			0.279
Smooth term (meanCrownSize)			**<0.001**
Smooth term (cacaoTrees scale)			**<0.001**
Smooth term (ST ID) (Random)			**<0.001**
Observations	441		
R^2	0.943		

9. Summary

Global agriculture has, over the course of its development, brought biodiversity under more threat than any other driver. Consequently, the ecosystem services that biodiversity provides have increasingly been lost. Sometimes, these losses can be accounted for, or "substituted". When they cannot be substituted, for intrinsic or contextual reasons, we can consider an agricultural system to be "interdependent" with biodiversity. Interdependencies, and the destructive feedback loops they imply (intensification leads to degradation, leads to a need for further intensification), are grounded in ecological theory, yet it is hard to evaluate if real-world systems are currently experiencing their effects. We can use data to model the effects of land-use on biodiversity, and to model the reliance of agricultural systems on ecosystem services. However, these relationships are very hard to generalise, and context-specific data is required to make confident inferences.

To assess the evidence for interdependencies with biodiversity in commodity crops, I reviewed the relevant literature for evidence for two hypotheses: that commodity crops depend upon specific species groups for their productivity, and that they, by way of expansion or intensification, impact those same species groups (Chapter 2). I studied eight commodity crops: cocoa, coffee, cotton, oil palm, rubber, soyabean, sugarcane, and tea. I examined literature that directly concerns biodiversity and productivity. Overall, I found evidence that most commodity crops both impact and depend on biodiversity, though this was less clear in sugar cane. For some species groups, such as bats in coffee, evidence was more available but less universally positive. Critically, there was clear evidence for the impacts and interdependencies of cocoa systems on plant diversity.

Cocoa has a particularly interesting relationship with biodiversity. Cocoa systems have replaced high-biodiversity tropical forest ecosystems, and so large biodiversity declines across West and Central Africa are attributed to the expansion of the crop across the "cocoa belt". At the same time, some cocoa systems are themselves fairly diverse with agroforestry that is said to benefit biodiversity and ecosystem services. Despite this potential, cocoa sustainability programmes rarely include a specific biodiversity component.

The remainder of my research focused specifically on cocoa. The variety of cocoa-producing systems globally is large, from simple monoculture systems in full sun to complex, forest-like agroforestry systems with a large density of trees, which support diverse animal communities. To establish a baseline for the typical quantity and variation in “how much” biodiversity cocoa systems can support, I gathered primary data on biodiversity in cocoa systems, also collecting data on other land systems from the same studies (Chapter 3). Following an established framework for estimating the “intactness” of biological communities, I fitted models describing the species richness of sites, and the similarity of community compositional to undisturbed areas. I compared two categories of cocoa agroforestry system, based on whether they had “planted” or “natural” shade. This was used to compare biodiversity intactness between cocoa systems with different land-use histories. I found that cocoa systems are typically similar to secondary forest systems and host more biodiversity intactness than that of open land systems such as cropland and pastures. Planted shade systems and naturally shaded systems had similar species richness, but the community composition differed greatly. Natural shade communities were much more similar to primary forest communities, and were comparable to mature secondary forests in similarity at around 90%. Conversely, a much lower similarity in planted shade systems caused their overall intactness to be 50% or less relative to primary forests. Yet, even planted shade agroforestry systems outperform open-land systems in intactness, showing that where landscapes are already degraded, even simpler agroforestry systems could lead to biodiversity gains.

Context is key to understanding how cocoa production and biodiversity interact. While studies on the impacts of cocoa have typically taken a landscape perspective, I focused on the plant diversity found within cocoa farms for my further research. In order to derive management guidelines to safeguard and enhance biodiversity in West and Central African cocoa systems, it is necessary to understand what drives biodiversity on and off farm (Chapter 4). To do this I developed a “causal model” of how biodiversity responds to driving factors. To test a joint set of hypotheses about how relevant variables may interact, I fitted path models designed to evaluate these against field data from 668 plots on cocoa farms where biodiversity was sampled on cocoa farms in Côte d’Ivoire, Ghana, Nigeria, and Cameroon. I found that while there were important links between farm shade management and tree and understory plant biodiversity, underlying factors such as land-use history, landscape composition, and soil types also governed plant biodiversity on farm.

This also means that the existing base stock of shade and tree diversity must be taken into account to improve biodiversity on cocoa farms, as well as underlying factors that may have influenced this biodiversity in the past. The most impactful actions to take differ based on spatial context, the history of a farm, and the number and type of trees currently present (remnant, spontaneous recruits, or planted trees). One key variable that dominated biodiversity patterns, as well as patterns in other causal factors such as vegetation structure, was the distance of a site to the nearest port. Taken as a proxy for the overall intrusion of human activities into a landscape, this shows how different strategies are necessary across the range of variation in areas in West and Central Africa. In Nigeria, where typical farms have only one or two species of planted tree, allowing spontaneous recruits on farms would enhance biodiversity both in trees (clearly) and in the understorey, especially if spontaneous recruits are allowed to grow to large sizes. However, in areas such as Cameroon, retaining remnant trees is the most impactful action, especially in the face of increasing land conversion and landscape accessibility in the region.

I found that the minimum requirements for a range of current sustainability standards in cocoa are insufficient to protect existing plant diversity. This was because tree density and diversity were already much higher in most contexts than required to meet sustainability criteria. Nigerian farms were the only context in which this was not the case. I suggest that new criteria that are focused explicitly on biodiversity impacts are needed to preserve the additional biodiversity on farms, as well as to recognise and reward it.

The most appropriate actions for improving biodiversity on a cocoa farm also depend on the ecosystem services that biodiversity can provide. This is the most important factor when it comes to designing biodiversity-friendly cocoa that is both ecologically and economically sustainable. To assess how farmers perceive trees, tree communities, and the ecosystem services they provide, I carried out a detailed analysis of the benefits and trade-offs associated with trees on cocoa farms (Chapter 5). Traits of individual trees were somewhat predictive of their usefulness to farmers, as well as their likelihood of certain trade-offs being associated with them. For example, while trees with large canopies were considered good for shading cocoa, they were also more likely to be perceived as contributing to pest and disease outbreaks. Other patterns pointed to special traits of certain trees: for example, nitrogen-fixing trees were associated with fertility benefits, but were unlikely to be considered useful for medicine. Using the predictive power of tree traits can help to design sustainable cocoa systems, for instance by providing saplings of trees with traits considered useful for filling gaps in ecosystem services perceived by farmers.

I also fitted general additive models (GAMs) describing how farmers respond to the composition, structure, and functional diversity of trees on cocoa farms in terms of the ecosystem services they provide. At the farm level, having more trees, and larger trees, was linked to perceptions about cocoa systems providing construction services, areas to rest and relax, and future security. Farms with fewer fruiting trees were perceived as contributing more to food security and marketable goods.

Finally, I compared the traits of tree communities to plot-level data on cocoa yields to examine if there were relationships between tree diversity and productivity on cocoa farms in the region, beyond that which is already well established (i.e. that a shade cover of 30-40% is optimal for productivity). Within the bounds of 30-40% shade cover, the density of trees needed to achieve the largest cocoa yields of around 700 kg ha-1 depended on the diversity of the trees. When tree community evenness was low (more of the same types of tree), sparse tree density of around 20 trees ha-1 was expected to achieve the largest yields, but when the evenness was higher (a more diverse spread of more types of tree), the largest yields were predicted to occur with greater densities up to 100 trees ha-1. In all cases, larger trees were more effective in providing larger yields. I use these findings to suggest that a “one size fits all” approach to sustainable agroforestry design is unlikely to maximise yields and other ecosystem services in all situations, so a context-appropriate method to enhancing biodiversity and ecosystem services on farms would be a better approach to sustainable cocoa production. Most biodiversity, ecosystem service, and yield benefits are associated with large trees, which can take over 30 years to reach maturity (and usefulness). As cocoa systems have a productive lifespan of 25-30 years, this means that shade management needs to be multi-generational to be effective.

My general discussion (Chapter 6) builds on the strong interdependence of plant biodiversity and the multiple uses and benefits of cocoa systems. The design and underlying context of cocoa farms is key to understanding both the baseline degree of biodiversity on farms, and how to improve it for both conservation and ecosystem services, including cocoa yields. Combining insights from top-down, global-scale models with models grounded in field work shows the necessity of both, while acknowledging that only the field-based models can effectively guide specific actions on farms and, in doing so, can add nuance to potentially oversimplified global views of biodiversity. Cocoa systems have value for biodiversity conservation, though this value is governed by local context. Despite wider trends of unsustainable tree use in West Africa, cocoa farms may be using trees sustainably. Diverse cocoa systems are thus an important part of the West Africa's conservation estate and contribute to global biodiversity goals. Current standards fail to take into account the diversity of contexts governing biodiversity and ecosystem services in cocoa systems, so new standards to protect biodiversity are needed. The protection and continuous supply of large trees, which are disproportionately valuable to farms, should be a key target of future standards for ecologically and economically sustainable cocoa. Current import regulations such as the EU anti-deforestation regulation (EUDR) fall short for cocoa systems: the false-positive detection of agroforestry systems is a major shortcoming of existing data-driven approaches to preventing commodity-linked deforestation in West and Central Africa. Practice, governance, and private sector priorities all need to shift to reflect the nuanced, carefully-implemented changes needed to provide cocoa that halts and reverses biodiversity loss and that provides for local communities in a way that is robust and resilient in the face of climate change.

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