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Towards sustainable management in  
low-intensity agriculture:  
A quantitative framework to explore  
biodiversity and productivity outcomes

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## ABSTRACT

Conserving biodiversity and maximising agricultural productivity are both United Nations Sustainable Development Goals, however agricultural expansion and intensification are leading causes of biodiversity declines. Low-intensity agriculture (LIA) is promoted as a method to maintain biodiversity on agricultural land. However, implementing LIA is inhibited by conflicting reports on the impact on productivity. These conflicts are likely due to the presence of multiple stable states, each composed of different species abundances, and thus associated with different measures of biodiversity and productivity. As only one of these states can be observed at a time, it follows that small-scale observational studies can report conflicting conclusions regarding the biodiversity-productivity states achieved in LIA. Instead of relying on observations, if we could explore all potential biodiversity-productivity states simultaneously, an optimal state with high biodiversity and productivity outcomes could be identified. Investigating the system characteristics resulting in this state would then enable targeted sustainable agricultural management. To systematically explore state space in this way, novel quantitative modelling methods are needed. Accordingly, my first aim was to develop a community model capable of simulating the behaviour of a multispecies trophic web. I successfully developed the model using generalised Lotka-Volterra equations, incorporating dynamic consumption through a multi-species functional response. The second aim was to use the model to systematically explore the biodiversity-productivity state space of a simulated agricultural food web and then determine if multiple system states could be observed. Using a novel methodological framework, I successfully illustrated six system states were realisable for my multispecies trophic web. Finally, I aimed to identify which of these six states were optimal for sustainable management – exhibiting both high biodiversity and high productivity – and perform inference to ascertain how this state could be achieved via ecosystem management. One identified system state achieved these optimal properties and, by interrogating the conditions which allowed this state to occur, I discuss management guidelines for my LIA system. I conclude that the proposed modelling framework is a viable approach to overcome the restrictions of small-scale observational studies which fail to capture all possible realities of a system. With a worthwhile investment in further development, the model and framework have great potential to robustly and efficiently inform sustainable management decisions, achieving biodiversity and productivity goals simultaneously in low-intensity agricultural systems.

## INTRODUCTION

Competition for land-use is a preeminent global issue, with major conflict existing between protecting land of ecological importance and securing land for agriculture. Conserving biodiversity and ensuring agricultural productivity are equal priorities in the Sustainable Development Goals (United Nations, 2015), however agricultural expansion and intensification are leading causes of biodiversity losses, particularly in the tropics (Laurance, Sayer, & Cassman, 2014; Thrupp, 2000). This conflict will only worsen where the human population grows most rapidly (Cohen, 2003) – such as in Africa where the human population is projected to quadruple by 2100 – and where agriculture is essential for local food security and a primary income source (European Commission, 2013). These same tropical areas, with rapid population growth and reliance on agriculture, are also recognised as biodiversity hotspots (Fisher & Christopher, 2007). Therefore, biodiversity losses here will have a disproportionate effect on global biodiversity. To mitigate against this catastrophic trajectory, agricultural practices need to be optimised to sustainably manage land currently in use. This will be possible since many current practices result in a yield-gap – where farmers’ actual yields are lower than potential yields (Laurance et al., 2014). However, determining how yield-gaps should be closed is the subject of much debate.

Research investigating this biodiversity-productivity trade-off in agriculture has traditionally classed management approaches into two extremes – land-sharing or land-sparing (Kremen, 2015). Land-sparing is based on the idea that intensifying agriculture to increase yields on smaller areas of land will allow for more land to be spared and put aside for conservation purposes (Kremen, 2015). However, land-sparing is problematic for various reasons (see reviews by Kremen (2015) and Perfecto & Vandermeer (2008)). On a fundamental level, many farmers simply do not have the resources to intensify their farming effectively (Wessel & Quist-Wessel, 2015). But more importantly, when intensification of agriculture produces increased yields, the promised decrease in land used is unlikely to follow (Tscharrntke et al., 2012). In fact, it is frequently found that increased yields, and thus increased profits, lead to more deforestation as farmers are attracted to the area (Ruf, 2001).

An alternative, more appealing solution follows the land-sharing side of the debate. Low-intensity agriculture (LIA) is promoted as a way to maintain ecological integrity and increase biodiversity simultaneously on agricultural land. LIA has been highly opposed in the past due to the assumption that low-intensity inevitably results in vastly decreased yield in a biodiversity-productivity trade-off, however this assumption is not always correct (Tscharntke et al., 2012). For example, Clough et al. (2011) demonstrate that there is no inherent trade-off between overall species richness and yield in cocoa agroforests, where farmers grow the cocoa within a forested area supporting increased biodiversity. They conclude that managing land to increase biodiversity does not negatively affect productivity. Additionally, Gordon et al (2007) report that the most biodiverse coffee plantations are among the most productive management scenarios. Those opposing LIA have also cited research reporting that biodiversity in these areas cannot match “wild” areas, but this is not necessarily the case. One study found that bird and bat species richness was higher in agroforests than in neighbouring forests, while intensive monocultures were much more species poor (Harvey & González Villalobos, 2007). Philpott et al (2008) found similar results for ants, birds and trees for Latin American coffee plantations. Although species composition is often altered in LIA systems, with some forest specialists being excluded, by incorporating LIA practices such as agroforestry within a land matrix including natural forest patches, a more continuous yet diverse landscape is achieved (Harvey et al., 2006), allowing for regional biodiversity to be maintained more readily than in highly fragmented land-sparing regimes (Perfecto & Vandermeer, 2008). While research indicates LIA systems have the potential to retain biodiversity while simultaneously increasing yield, the conflicting reports of productivity outcomes inhibit the wide-scale uptake of these methods by farmers. Progress in this debate will help in closing yield-gaps and achieving sustainable management in agriculture.

The disagreement over the effectiveness of LIA is likely because most studies are small-scale, observational studies (Kremen, 2015). The key limiting factor of these studies is that only one version of the system can ever be observed, despite many potential outcomes existing. The composition of species present and their relative abundances within an ecosystem is referred to as its state. The existence of multiple system states is a phenomenon that occurs in many complex systems with intricate between-species

dynamics (Beisner, Haydon, & Cuddington, 2003). The observed state of a given system is determined by historical disturbances, such as local species introductions and extinctions (Montoya, Yallop, & Memmott, 2015). Since the observed state is informed by a history we may know nothing about, this is a poor indicator of the state a system has the potential to achieve. This is an incredibly important concept because each state has a distinct measure of biodiversity and productivity associated with it, due to their different species compositions. Thus, if we can identify all potential states of a given complex LIA system and quantify their biodiversity and productivity, we will discover if any state exhibit both high biodiversity and productivity. Identification of an optimal biodiversity-productivity state would support the LIA management strategy, and we can then manage the system to achieve both global goals simultaneously by manipulating species abundances to those which produced the optimal system state. It is worth noting here that I use the term “system state” rather than the common “stable state” as the definitions diverge in one small but significant way; while a stable state refers to an equilibria state, a system state refers to any state, independent of long-term stability. This is an important distinction to make since the interests of applied management are often over short, pre-defined timelines. Unfortunately, while multiple system states can exist, methods to identify them for a given complex system are limited.

Experimental approaches to identify multiple states are unlikely to present a solution, as the systems that generate these phenomena are too large and complex to manipulate effectively (Connell & Sousa, 1983; Schröder, Persson, & De Roos, 2005). Thus, modelling methods are often promoted as an effective alternative. However, these studies oversimplify food webs to solve systems of mathematical equations to determine the stability of a system, and then perturb the system and assess if the system changes state. A recent study using this method from Vial, Macdonald, & Haydon (2011) looked to identify the effect of livestock grazing on the persistence of a top predator by determining if grazing perturbations moved the system to an alternate state which excluded the predator. To do so, the system was simplified to a food chain consisting of only the focal predator, a single prey group and a single primary producer. However, as highlighted by Schröder et al (2005), only considering a small portion of a complex food web system says very little about the net effects of a given perturbation on the system as a whole. An additional limitation of many

current methods is that they look for stable states, but for constantly managed systems, such as agricultural land the transient states of existence are more relevant (Fukami & Nakajima, 2011). A third constraint of many current methods is that they assume interactions between species are constant through time to simplify models. However, interspecific connections are clearly dynamic throughout both space and time (Holt, 2002). In particular, generalist feeding is common and results in prey-switching dynamics, where generalist predators change their target prey depending on the availability of all its prey species (Smout et al., 2010; van Baalen, Křivan, van Rijn, & Sabelis, 2001). This behaviour is important to include in predictive models for two principal reasons. Firstly, it has been suggested that active prey-switching helps to stabilise complex food webs (Kondoh, 2003) and allows prey populations to persist through an emergent density-dependent effect (Kjørboe, Saiz, Tiselius, & Andersen, 2018). Secondly, dynamic prey selection by generalist feeders can increase both species richness and functional biodiversity in food webs (Ryabov, Morozov, & Blasius, 2015). Consequently, ignoring the dynamic nature of interspecific interactions may bias models away from achieving complex, biodiverse states.

The first objective of this study is to address these three methodological constraints by developing a holistic food web model capable of simulating the transient behaviour of a complex and dynamic system. My second objective is to use the model to systematically explore biodiversity-productivity state space of a simulated agricultural food web and then determine if multiple system states could be observed. By initialising the model in different states, one can explore the biodiversity-productivity outcomes achieved over realistic management timelines. I will then address the inverse problem of how particular outcomes of interest (i.e. an optimal state with high biodiversity and productivity) can be achieved practically. Thus, my final aim is to perform inference to inform management guidelines on how to cultivate an optimal biodiversity-productivity state through shifting systems to be in line with the desired initial regimes.

## METHODS

### Model System

The model system of smallholder cocoa agroforests typical of West Africa will be used, with expert opinion available from research carried out in Cameroon. This system was selected because currently little is known regarding the best management practices for growing cocoa, despite the product supporting over two million families throughout the West African cocoa belt, where 70% of the world's cocoa is grown (Schroth, Läderach, Martinez-Valle, Bunn, & Jassogne, 2016). In a global meta-analysis, De Beenhouwer et al (2013) indicate the best way to support biodiversity on cocoa plantations is to grow the crop in agroforest plots, i.e. under a diverse shade canopy. This helps to maintain vegetative diversity as well as support diversity of species at higher trophic levels. Unfortunately, cocoa is often slower to grow under shade and therefore often produces a lower yield than in intensive sun plots with no shade trees present (Clough et al., 2011). As a result, in the face of market pressure and with limited resource availability, farmers will often transform from low-intensity agroforestry to more productive sun plots, perpetuating further deforestation and threatening biodiversity. However, there are cases where shaded agroforests maintain sustainably high yields (e.g. Schneider et al., 2017). With the knowledge that it is possible for high biodiversity and productivity to be observed on the same piece of land, this is an appropriate system to begin developing the proposed methodological framework.

### Model Structure

The base of the model uses generalised Lotka-Volterra equations (GLVE; Equation 1) which describe how the population dynamics of a single species are affected by the other species it interacts with, whether antagonistically, or synergistically. For a given food web, there will therefore be as many GLVEs as the number of nodes (e.g. species, or functional species groups) in the web. In combination, these equations are used to model the behaviour of the whole community forward in time.

*Equation 1.*

$$\frac{dX_i}{dt} = X_i b_i + X_i \left( \sum_{j=1}^n a_{i,j} X_j \right)$$

The biomass of species  $i$  is denoted as  $X_i$  (with  $X_j$  being the biomass of species  $j$ ) and  $b_i$  is the species-specific intrinsic growth rate; this is the growth rate of a species when no other species are present in the system. The effect of species  $j$  on species  $i$  is denoted as  $a_{i,j}$ . This may be negative if species  $j$  is a predator of species  $i$  or positive if it is a prey item. Density dependence (the interference between conspecifics) naturally emerges from this formulation when  $i = j$ .

I then extended the model beyond the traditional GLVE form by allowing the interspecific interactions to be dynamic through time by incorporating a multi-species functional response (MSFR; Equation 2). The MSFR, a consumption model developed specifically for generalist consumers (Asseburg, Harwood, Matthiopoulos, & Smout, 2006; Smout et al., 2010), facilitates prey-switching by re-calculating the value of  $a$  in equation 1 through time for all interactions between generalist predators and their prey items.

*Equation 2.*

$$C_j = \frac{a_j X_j^{m_j}}{1 + \sum_{k=1}^n (a_k t_k X_k^{m_k})}$$

The consumption of prey  $j$  by predator  $i$  ( $C_j$ ) is dependent on both the biomass of prey  $j$  as well as the biomass of all alternate prey items,  $k$ , of predator  $i$ , at the previous time step.  $C_j$  is also a function of:  $a$  is a parameter indicating attack rate by predator  $i$  (not to be confused with the  $a$  parameter in equation 1),  $t$  is the handling time of prey  $k$  by predator  $i$ , and  $m$  is a parameter controlling the shape of the functional response. A Holling type 1 linear response is achieved by  $m=1$  and  $t=0$ , a type 2 hyperbolic response is produced when  $m=1$  and  $t>0$ , and values of  $m>1$  indicate a sigmoidal response, with larger values producing a stronger response (Smout et al., 2010).

Since  $C_j$  is the per capita, per unit time consumption rate of prey  $j$  by predator  $i$ , adjusted for the biomass of prey  $j$  present in the system, it represents the  $a_{i,j}X_j$  term in the predators' GLVE. This positive effect on predator  $i$ 's biomass is also adjusted for the efficiency of energy conversion of prey biomass to new predator biomass (for more details see method section 1b). Additionally, negative  $C_j$  also represents the effect of predator  $i$  removing biomass of

prey  $j$  in the preys' GLVE (where the prey species will become species  $i$  and the predator becomes species  $j$ ).

## **Overview of Framework**

The quantitative modelling framework we propose has five methodological steps:

1. Define the system
  - a. Construct the food web structure (nodes and connections)
  - b. Parameterise the single species dynamics and the food web interactions
2. Run simulations for a realistic management timeframe using different initial conditions to systematically explore state space
3. Quantify the biodiversity and productivity of the system at the end of each simulation
4. Identify the observed system states and their associated biodiversity and productivity characteristics
5. Perform inference to inform sustainable management decisions

All steps of the framework were carried out in the open source software R (version 3.4.2; R Core Team, 2017) using the RStudio interface (version 1.1.383; RStudio Team, 2016). Carrying out the full analytical process within open source software will allow for the framework to be easily generalised and replicated across any system of interest.

## 1a) Food Web Structure

The food web was inspired by a cocoa agroforest system, including complex interactions but remaining small in size. Since this is the first attempt at developing this complete framework, a smaller web allows for potential issues to be detected more easily throughout the process. It is common practice for food webs to group together species which have similar feeding interactions into “trophic species” (Pimm, Lawton, & Cohen, 1991), allowing this web to be small while avoiding removal of complex species interactions. Thus, any mention of species in this study refers to trophic species groups.

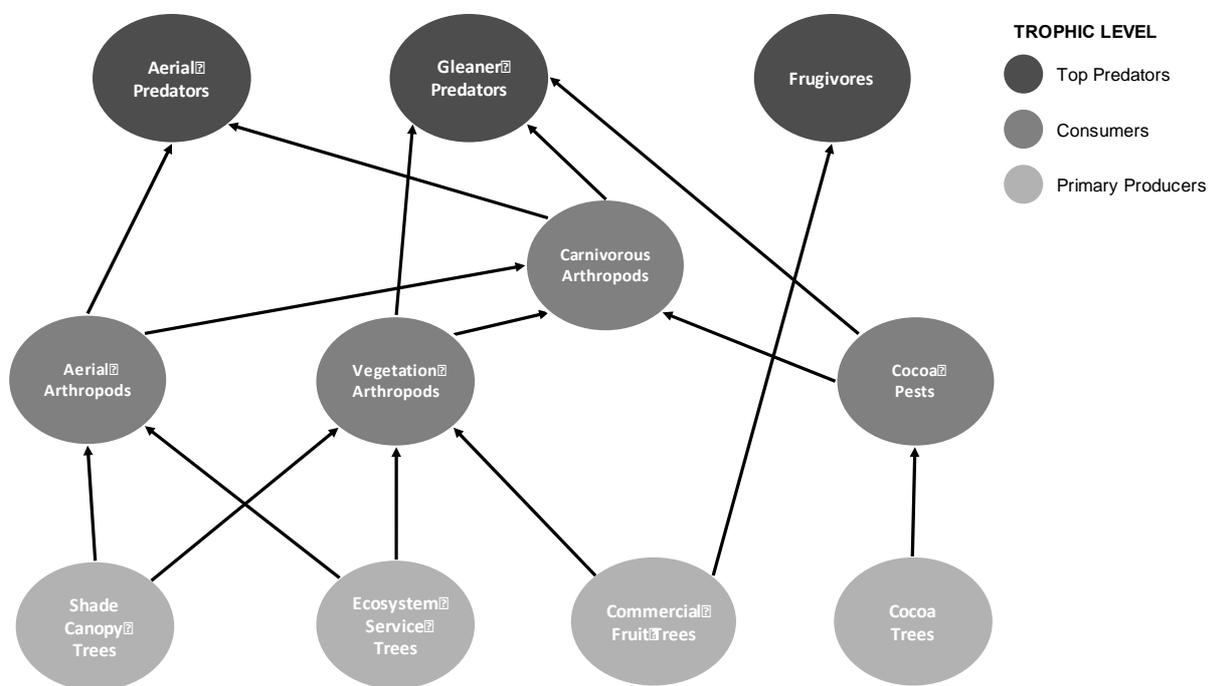


Figure 1. Food web resembling a cocoa agroforest. The nodes are trophic species groups based on foraging methods. Arrows indicate the direction of energy transfer through consumption.

Based on field observations by Powell et al (Pers. comm., 2018), I identified 11 groups of species split across 3 major trophic levels to include in the cocoa agroforest food web (figure 1). The primary predators are birds and bat. I grouped these species by foraging method into aerial predators, gleaner predators, and frugivorous birds and bats. A single mesopredators group was selected containing carnivorous arthropods. I then split the herbivorous consumers into three groups – aerial arthropods (those who can fly), vegetation arthropods (those who live exclusively on vegetation), and finally cocoa pests.

The four vegetative groups are a fast-growing shade canopy, ecosystem service trees, commercial fruit crops, and the cocoa trees. For this system, I define ecosystem service trees as those which are consumed by the prey of both the gleaner predators and the carnivorous arthropods, since these groups act as natural biocontrol of the cocoa pests.

Feeding interactions between the groups are as detailed in figure 1, with arrows showing the direction of energy transfer. Three particular complexities are included. Firstly, the frugivores eating the fruit trees depicts a cross-trophic-level interaction. Secondly, within-trophic-level interactions are present through the carnivorous arthropods consuming groups at the same major trophic level. Finally, five out of the seven animal groups feed on more than one prey item, meaning generalist predator prey-switching dynamics are numerous in my food web.

## **1b) Food Web Parameterisation**

Parameterisation of the food web model requires two principal components: single species growth dynamics and multi-species consumption dynamics. The single species growth rates are governed by intrinsic growth rates and density dependence parameters. The animal groups have negative growth when no other species are present, while the primary producer groups have positive growth when in isolation. To stop the primary producer populations from exploding, density dependence is introduced to establish a carrying capacity (K).

Due to a lack of direct data on consumption and growth rates, biological first principles and expert opinion were used to parameterise the model. It was assumed that top predators would die out after ~8 weeks, the carnivorous arthropods would persist for ~4 weeks, and the other arthropods would only survive for ~2 weeks. Meanwhile, the primary producers were assumed to grow as follows: shade canopy trees take 3 years to reach  $K = 50,000$  kg/ha; ecosystem service trees take 7 years to reach  $K = 15,000$  kg/ha; commercial fruits trees take 5 years to reach  $K = 20,000$  kg/ha; and cocoa trees take 5 years to reach  $K = 30,000$  kg/ha.

To calculate the parameters that allowed these assumptions to be true in the model, I had to hardwire the time units within the differential equation solver (detailed in the method section 2). The cocoa trees were given a small, positive intrinsic growth rate and a small, negative carrying capacity. When the model was run with only cocoa trees it took 30 time units to approach K. Since K was expected to be approached within 5 years for this group, 6 time units now represented 1 year and the rest of the parameterisation was carried out using these units. Table 1 displays the final parameters and appendix 1 contains visualisations of the resultant single species growth trajectories.

*Table 1. Single species population growth parameters.*

<b>Trophic species group</b>	<b>Intrinsic growth rate (b)</b>	<b>Density dependence</b>
Aerial predators	-5	0
Gleaner predators	-5	0
Frugivores	-5	0
Carnivorous arthropods	-10	0
Aerial arthropods	-15	0
Vegetation arthropods	-15	0
Cocoa pests	-15	0
Shade canopy trees	0.9	-0.000018
Ecosystem service trees	0.4	-0.0000265
Commercial fruit trees	0.5	-0.000024
Cocoa trees	0.5	-0.0000165

The multi-species consumption dynamics were then built-in by first parameterising the single species consumption dynamics for each of the 15 predator-prey interactions within the food web. Equation 3 shows the single prey item version of the MSFR in equation 2, where predator group  $i$  consumes prey  $j$  at a rate of  $C_j$  per unit mass of predator.

*Equation 3.*

$$C_j = \frac{a_j X_j^{m_j}}{1 + a_j t_j X_j^{m_j}}$$

Since  $t$  is the inverse of the maximum consumption rate of prey  $j$  by predator  $i$  (Smout et al., 2010), biological first principles could again be used to parameterise these interactions. Once  $t$  was set,  $a$  and  $m$  were tuned to achieve a consumption curve which was sigmoidal

and had a gradual curve to the maximum consumption asymptote. The maximum consumption rates along with the calculated parameters for each interaction can be found in table 2.

The final step in parameterising the consumption interactions was to account for energy transfer efficiencies. Since not all prey biomass consumed is turned into new predator biomass, the new biomass gained from consumption had to be adjusted. The efficiency rate was assumed to be 40% for consumption of vegetation by arthropods, and of arthropods by carnivorous arthropods (within the range identified by Soo Hoo & Fraenkel, 1966). I assumed the efficiency for consumption of arthropods or vegetation by top predators to be half this at 20%.

*Table 2. Multi-species functional response parameters for each predator-prey interaction in the food web. **MaxC** is the maximum per capita consumption rate per unit time of prey by predator; **a** is a parameter indicating attack rate on prey by predator; **t** is the handling time of prey by predator, equal to inverse **MaxC**; and **m** is a parameter informing the shape of the functional response.*

Predator	Prey	MaxC	a	t	m
Aerial Predator	Aerial Arthropod	60	0.001	0.0167	2.7
Aerial Predator	Carnivorous Arthropod	15	0.005	0.0667	2.6
Gleaner Predator	Vegetation Arthropod	40	0.00075	0.025	2.5
Gleaner Predator	Carnivorous Arthropod	20	0.005	0.05	2.7
Gleaner Predator	Cocoa Pest	40	0.0025	0.025	2.6
Frugivore	Fruit trees	500	0.00000002	0.002	2.7
Carnivorous Arthropod	Aerial Arthropod	60	0.01	0.0167	2.2
Carnivorous Arthropod	Vegetation Arthropod	60	0.01	0.0167	2.2
Carnivorous Arthropod	Cocoa Pest	60	0.0075	0.0167	2.2
Aerial Arthropod	Shade Canopy	500	7.5E-11	0.002	3
Aerial Arthropod	Service trees	500	0.000000002	0.002	3
Vegetation Arthropod	Shade Canopy	500	7.5E-11	0.002	3
Vegetation Arthropod	Service trees	300	0.00000001	0.0033	2.8
Vegetation Arthropod	Fruit trees	150	2.5E-09	0.0067	2.7
Cocoa Pest	Cocoa Tree	500	5E-10	0.002	2.9

## 2) Model Simulation

Simulations were used to explore biodiversity-productivity state space. When multiple system states exist, state space can be thought of as a landscape with peaks and troughs, with stable states located in the troughs (Beisner et al., 2003). Troughs can have different widths and depths, with larger troughs representing stronger basins of attraction for the system to be drawn towards. If a system is initiated at different areas of state space, it will be drawn towards different states. Therefore, by running the model numerous times, starting each simulation with different initial conditions, one can effectively explore state space and identify the states present for the defined system. Since I am interested in the transient dynamics, I am not looking to identify the stable equilibria states in the troughs, but instead common areas of state-space the system will be attracted towards.

In the food web model, the initial conditions are the edible biomasses of each trophic species, which in combination represent the systems' initial biodiversity-productivity state. For each simulation, the initial biomasses were selected from a random uniform distribution, with a lower limit of 0 (indicating the node is locally extinct) and an upper limit equivalent to a theoretical maximum biomass per hectare. A theoretical maximum was used as the upper limit instead of commonly observed value to avoid biasing the simulations to fall towards only commonly observed stable states. The maximum values were established from a combination of information in the literature, unpublished data, and expert opinions from field researchers (Powell et al, 2018, Pers. Comm.).

The Initial conditions along with the single species growth parameters and the consumption parameters from section 1b are fed into a custom function containing the model. I wrote this function to read the number of nodes in the food web based on the number of parameters, and then construct and parameterise a full set of GLVEs including the MSFR. See Supplement 1 for the model function code. To solve the set of dynamical generalized Lotka-Volterra differential equations contained within the function through time, the ode function from the deSolve package was used (Soetaert, Petzoldt, & Setzer, 2010). Simulations were run for 20 years each, with updated dynamics being reported every 2

months. 10,000 iterations of the model were run, with the initial and final conditions being stored for each iteration. See Supplement 2 for the simulation code.

### 3) Quantifying Biodiversity and Productivity

After the model had been run, the biodiversity and productivity for the initial and final conditions of each iteration of the model were quantified. Biodiversity was calculated in two ways, the standard Simpson diversity and a novel weighted Simpson diversity measure. The standard Simpson measure accounts for species evenness using relative biomasses of the species present. However, in a multi-trophic system such as my food web, there are inherent differences in biomass between trophic levels which should not influence the calculation of evenness. Additionally, since trophic species groups are used, the different species richness levels represented by each group need to be accounted for. Therefore, a weighted Simpson diversity measure was devised using biomasses adjusted by an inherent bias and a group richness measure (equation 4). Details of both the inherent bias and richness parameters can be found in appendix 2.

*Equation 3.*

$$\text{weighted biomass} = \frac{\text{observed biomass}}{\text{inherent bias}} * \text{group richness}$$

Productivity was measured as the dry mass of cocoa beans produced in kilograms per hectare, which is the industry standard measure. Abenyega & Gockowski (2003) report that a cocoa pods weighs 400g on average and produces approximately 40g of dry bean mass. Therefore, I calculated productivity as 10% of the cocoa biomass present in the system.

### 4) Identifying System States

To identify the observed system states found, the biodiversity and productivity of each iteration of the model were plotted in biodiversity-productivity state space. Two plots were created, one for each of the two biodiversity measures. The high number of overlapping data points made the plots difficult to interpret, so kernel density estimation was then used to produce heat maps. This was carried out using the `kde2d` function within the MASS package (Venables & Ripley, 2002). The resultant heat maps visually demonstrate the areas

of state space the system was most likely to be observed in. The optimal state was identified as the state with the highest measures of both biodiversity and productivity.

### **5) Inference for Sustainable Management**

The initial conditions for simulations leading to each of the identified states were separated and interrogated separately to assess commonalities and differences that would result in each state. More specifically, the initial biomasses of each trophic species which allowed for the optimal state to be observed were interrogated. Finally, the final biomasses of each trophic species which compose each of the final states were examined to identify particular groups important for the maintenance of the high biodiversity and high productivity characteristics of interest.

## RESULTS

### Identifying System States

Figure 2 shows the kernel density heat maps which were produced both before and after 10,000 simulations of the model. Figures 2A and 2B use the standard Simpson diversity measure, while figures 2C and 2D use the novel weighted Simpson diversity measure. In figure 2A, we can see that the standard Simpson diversity is highly influenced by the cocoa biomass present in the system, with lower biomass appearing to increase the biodiversity space explored by the initial conditions. This is due to the bias towards the inherently more massive vegetation groups in this measure. This bias has been effectively flattened by the weighted Simpson diversity measure. I therefore adopt this measure for all further exploration of biodiversity.

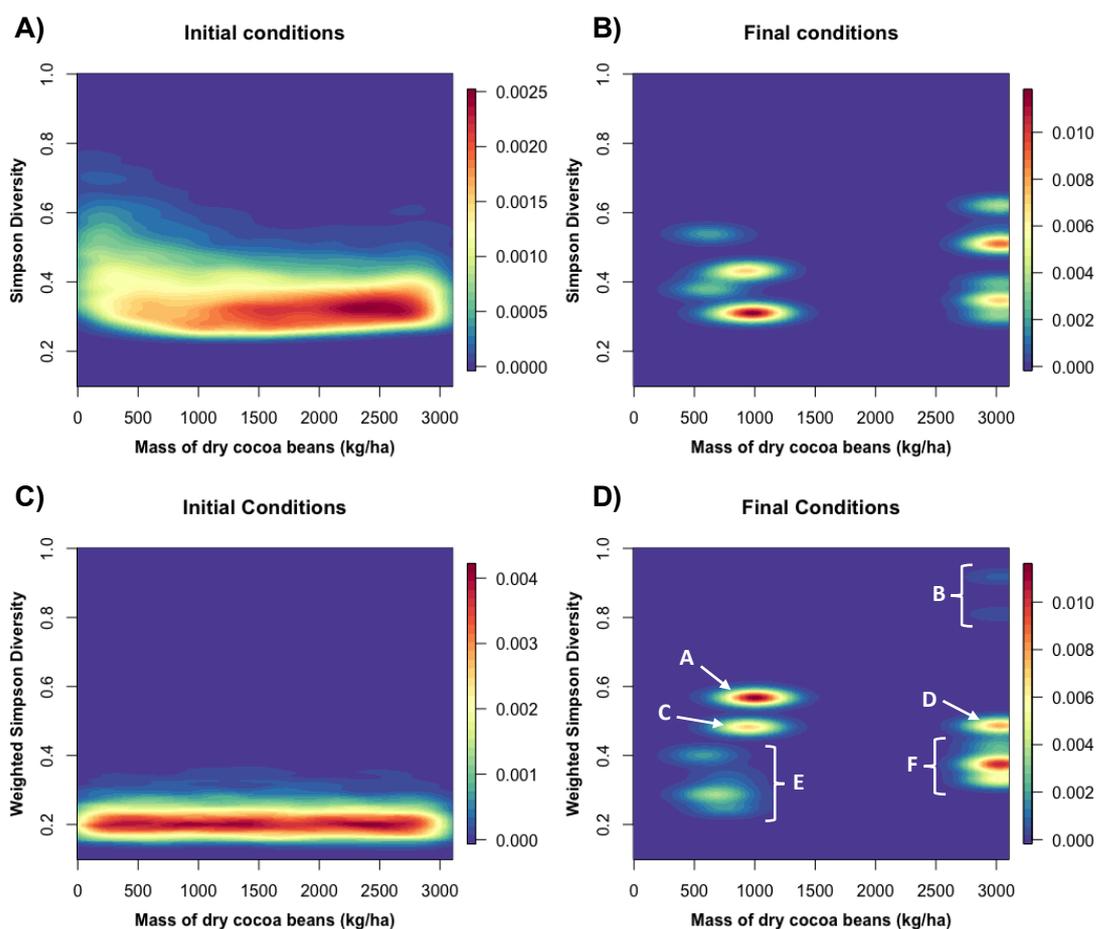


Figure 2. Heat maps of biodiversity-productivity state space. Plots A and B use the standard Simpsons diversity measure. Plots C and D use the weighted Simpson diversity measure. Productivity is measured as dry mass of cocoa means in kilograms per hectare. Plots A and C illustrate the initial conditions of the system explored through simulations. Plots B and D show the conditions of the system 20 years after the initial conditions, clearly demonstrating heat spots have emerged. In plot D, the heat spots have been given an ID ranging from A to F, corresponding to the plots in figure 3. The legend indicates the density with which each area of state-space is observed.

Multiple heat spots, or system states, have been identified after 20 years (Fig. 2D). The observed system states are bifurcated in relation to productivity, with cocoa trees either reaching approximately carrying capacity and producing  $\sim 3000\text{kg/ha}$ , or being constrained to productivity ranging from  $\sim 400\text{-}1500\text{kg/ha}$ . These states will be referred to as high productivity and low productivity, respectively. In terms of biodiversity, the observed final states illustrate a range of biodiversity outcomes in both productivity states. I have identified these as high, mid, or low biodiversity states. In figure 2D, the six combinations of biodiversity and productivity states have been identified. States A, C, and E all have low productivity, and high, mid and low biodiversity, respectively. States B, D, and F all have high productivity, and high, mid, and low biodiversity, respectively. State B is therefore identified as the optimal state, exhibiting both high productivity and high biodiversity.

### **Inference for Sustainable Management**

While it is clear from figure 2C that a large range of initialisation state space was explored, it is not clear which areas of state space produced which of the final observed states. For management purposes, this is important to identify which conditions a system can be initialised at to achieve optimal outcomes. Figure 3 explores this through an initial conditions heat map for each of the six system states identified in figure 2D.

The common trend which produces systems of high productivity is that cocoa is initialised very low, or already high. Initialising the system with intermediate cocoa biomass results in low productivity states. These trends appear to be independent on biodiversity, with large ranges of biodiversity space explored in all six states. Figure 3B indicates that the optimal state can be achieved throughout a wide range of initialisation values. Exploring the optimal initial conditions further, figure 4 illustrates that initialising any of the animal species groups at any point throughout their range can result in optimal states. The same pattern is observed for the ecosystem service trees and the commercial fruit trees. The two groups which show clustering within their ranges are the shade canopy trees and the cocoa trees. The shade trees follow the same pattern observed in cocoa, with either very low or high initial biomasses, with no intermediate values resulting in the optimal state being observed.

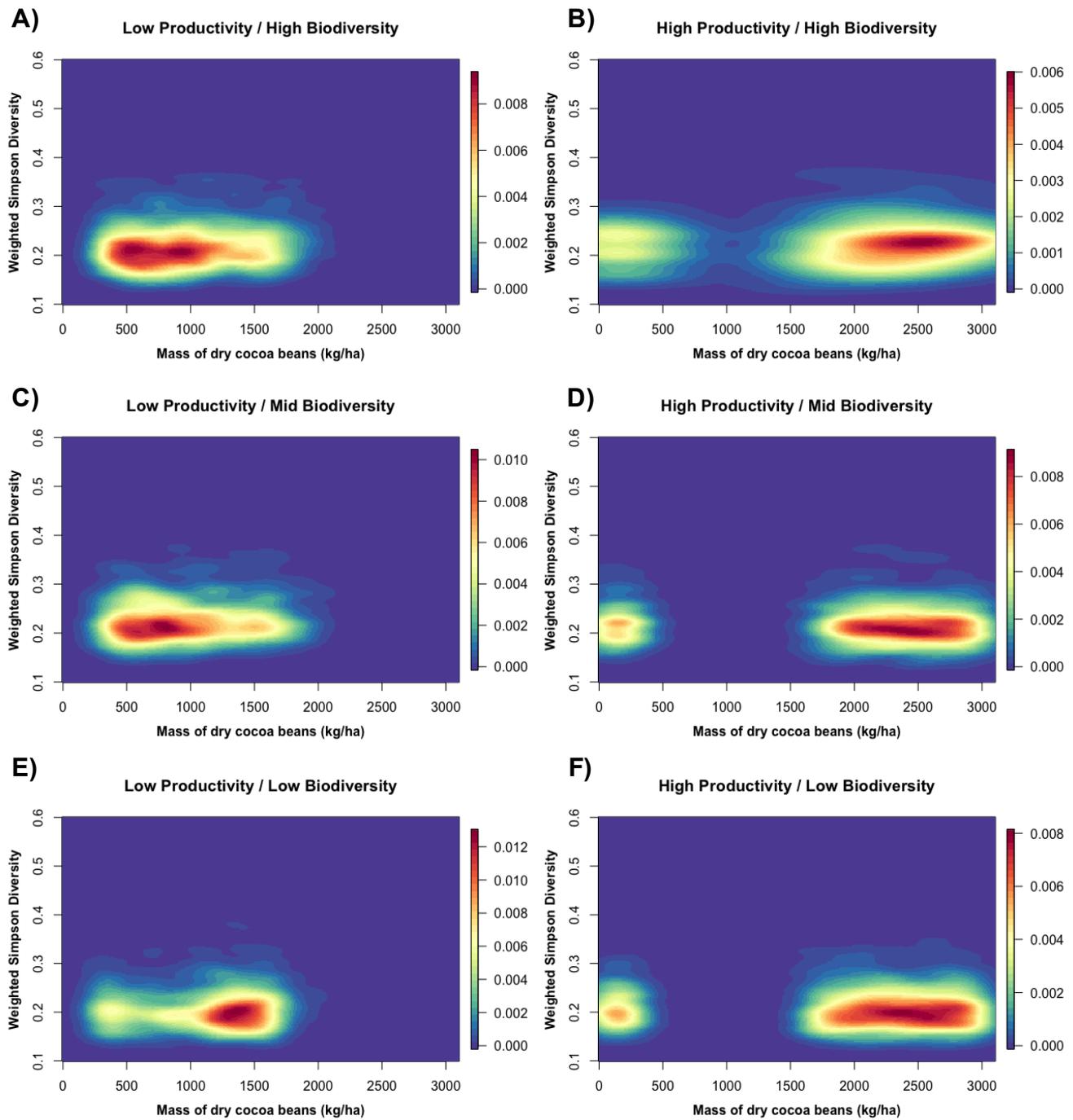


Figure 3. Heat maps demonstrating the initial conditions which resulted in each of the identified heat spots in figure 2D. The left column of plots result in low productivity states while the right column results in high productivity states. The rows result in high, mid, and low states of biodiversity, respectively. The legend indicates the density with which each area of state-space is observed.

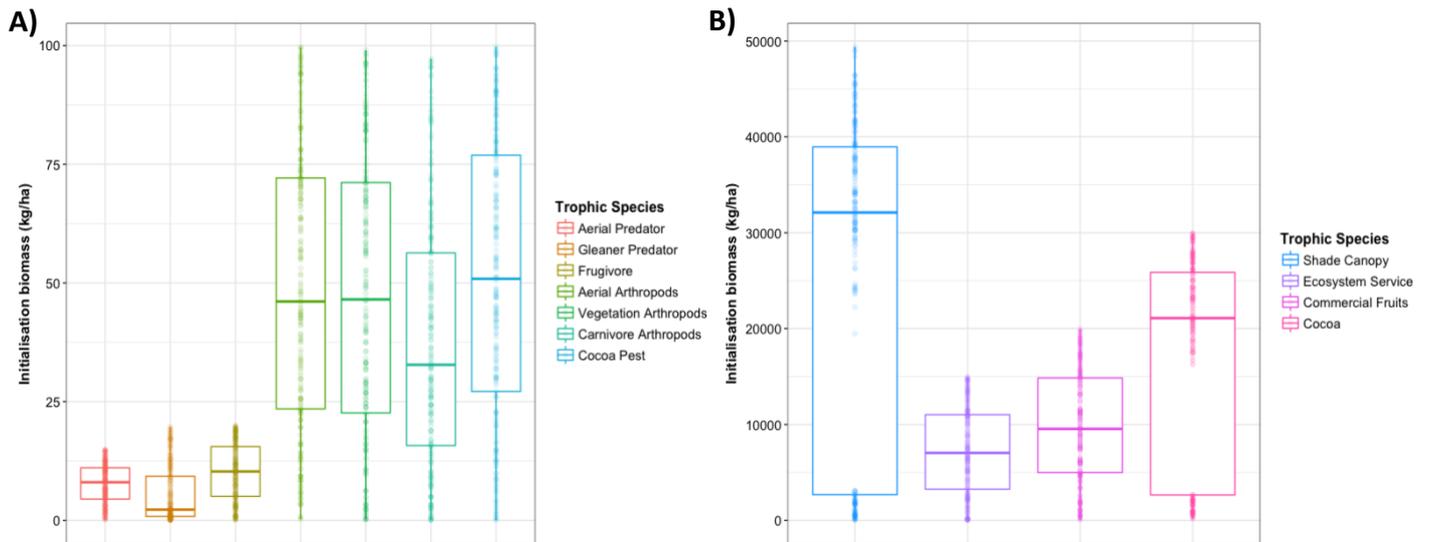


Figure 4. Boxplots showing the initial biomasses of each trophic group resulting in the optimal system state with high biodiversity and high productivity. Plot A contains the animal groups and plot B contains the vegetation groups. The boxplots were produced using ggplot2 (Wickham, 2009). The bold line within each box indicates the median value, the lower and upper limits of the boxes representing the second and third quartiles respectively, and the lines demonstrate the minimum and maximum values. Data points are overlaid to demonstrate the spread of data.

An additional point of interest is exploring which species are present in the different system states at the end of the simulations. By looking at this, groups that are important for maintaining particular biodiversity-productivity states can be identified. Once again, the common trends are clearer in productivity, and less obvious for the biodiversity states. Figure 5 shows the common trend for achieving high productivity is a lack of pests, with all high productivity states having no pests, while all low productivity states do. Other animal and vegetation groups are variable both within and between states. A common trait for the low biodiversity states is a bifurcation in the shade canopy biomass, being either very low or at approximately carrying capacity. The shade canopy never reaches carrying capacity in the mid and high biodiversity states. Both high biodiversity states are the only states which can support high biomass of the aerial predators.

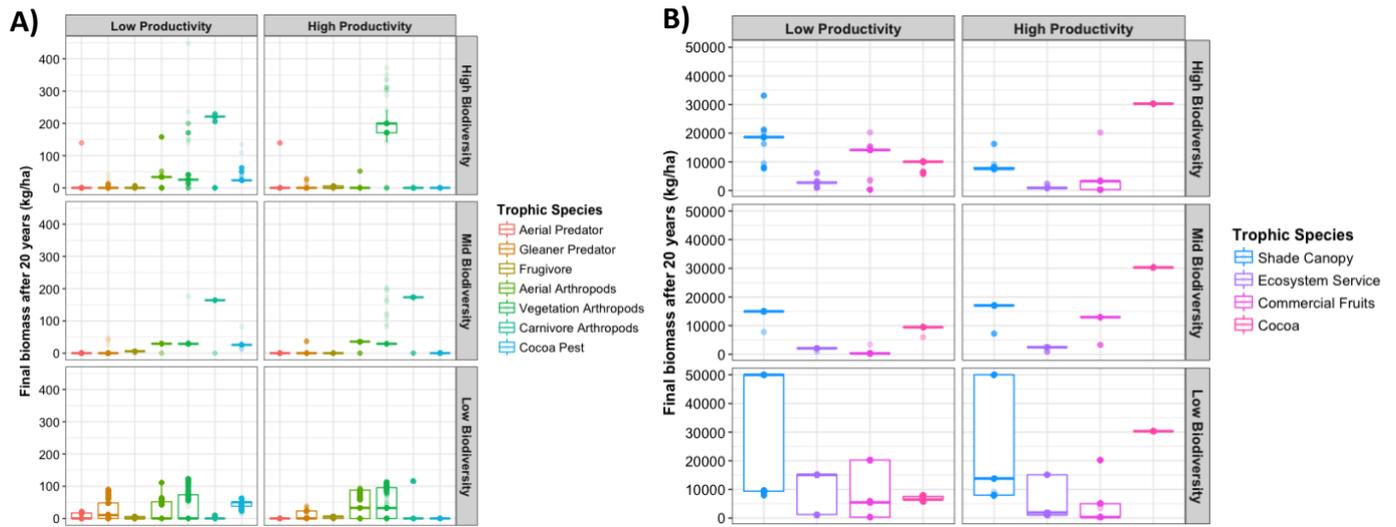


Figure 5. Boxplots illustrating the final biomasses of each of the trophic groups for each of the six observed states. Plot A contains the animal groups and plot B contains the vegetation groups. The boxplots were produced using ggplot2 (Wickham, 2009). The bold line within each box indicates the median value, the lower and upper limits of the boxes representing the second and third quartiles respectively, and the lines demonstrate the minimum and maximum values. Data points are overlaid to demonstrate the spread of data.

## DISCUSSION

### Assessment of Objectives

I have developed a novel and complex food web model, incorporating dynamical prey-switching through a multi-species functional response. I demonstrated the application of this model through a step-by-step methodological framework exploring the potential biodiversity-productivity states realisable by a low-intensity agriculture system. After 10,000 iterations of the model, with each iteration starting from different initial conditions, it was established that this method is capable of identifying multiple biodiversity-productivity states for a given system. Moreover, this was achieved over realistic management timescales by looking at transient dynamics rather than equilibria states. Thus, I have successfully achieved the first and second objectives to develop a model capable of handling complex and dynamic food webs and simulating their behaviour through a specified period of time to identify multiple system states.

The final objectives of this study were to ascertain if an optimal biodiversity-productivity state – exhibiting both high productivity and high biodiversity – could be achieved in the simulated low-intensity cocoa agroforest system, and to investigate how management towards optimality, and thus sustainability, could be directed. It was determined that within 20 years, a state exhibiting these optimal characteristics can be realised in my cocoa agroforest system. A preliminary investigation demonstrated that to achieve high cocoa productivity, cocoa had to be initialised at either extremely low or high biomasses, with shade canopy trees following the same pattern (figures 3 and 4). All other trophic species groups were initialised throughout their entire range to result in the optimal state. The explanation for the polarization in the two vegetation groups, with the unexpected outcome of low initial biomasses resulting in high productivity, is likely due to interactions between these species and the cocoa pest. The common trait in maintaining high productivity was a lack of pests in the system, whereas pests were always present when productivity was low (figure 5). It is likely that if cocoa biomass is initially very low, the pests will very quickly go locally extinct and allow for cocoa trees to grow to carrying capacity in the absence of consumers. If cocoa biomass starts very high, the pest biomass will likely rapidly increase, followed closely by increased biomasses of the consumers of pests (gleaner predators and

carnivorous arthropods), which will in turn consume the pests until they once again go locally extinct. Similar system behaviours may explain the shade canopy trees bifurcation. At high initial biomasses, the shade trees support a rapid increase in the groups that consume them – aerial and vegetation arthropods. These arthropods are in turn preyed upon by carnivorous arthropods and gleaner predators, which are also consumers of the cocoa pest. Thus, by supporting high biomasses of pest predators through the complex and dynamic food web interactions, pests may be consumed until local extinction occurs. Alternatively, if there is an exceptionally low initial biomass of shade trees, their prey may quickly go locally extinct, resulting in the carnivorous arthropods consuming exclusively pests to extinction. Based on these findings, management guidelines for this study system should concentrate on pest exclusion, as this appears to be the principal commonality leading to high productivity. Natural biocontrol methods could focus on managing a high abundance of shade trees to support the persistence of pest predators.

## **Limitations and Further Work**

### *Inference Methods*

The behaviours that emerge from a food web with dynamic interactions are intricate and often unpredictable. Curtsdotter et al (2011) demonstrate that both bottom-up and top-down trophic cascades lead to non-random secondary extinctions in dynamic food webs, with potentially extensive impacts rippling through the web over time. Despite this, Dunne et al (2002) detail that robustness to perturbations, such as extinctions, increases with increasing food web connectivity. While this complexity is clearly important to capture when making recommendations for ecosystem-wide management, disentangling the causes and effects between initial conditions and system outcomes becomes a difficult task.

Identification of important species interactions and system behaviours is made more difficult within the framework since multiple behaviour trajectories can produce the same state outcomes. This phenomenon arises for two reasons. First, I look at transient dynamics, not equilibrium states, since agricultural land is constantly perturbed and not allowed to reach an equilibrium. Systems in any given state may only temporarily be in that region of state-space before being drawn elsewhere due to state-space fields of attraction. Scheffer

et al (2001) provide a detailed explanation of this concept. Briefly, if multiple states exist in state-space, each with its own field of attraction, small changes in system conditions can move the system from the attraction field of one state to the field of another. Therefore, two iterations of the model that are at the same state after 20 years may have arrived there from different system behaviours and are only temporarily sharing the same state-space. Second, several of the identified states are composed of more than one hotspot (figure 2D), due to our pooling by low, mid, or high biodiversity. The conditions that result in hotspots being in only marginally different areas of state-space may be hugely variable.

These two reasons mean that, although I was able to provide some biological plausible theories regarding the behaviours leading to high productivity states, this insight has limited analytical support within this thesis. Determining the precise behaviours that result in specific states of interest will require more comprehensive analyses. Future methods may look to quantify the average behavioural trajectories of systems arriving in a given state, or investigate the temporal trends in extinction cascades. A further line of inquiry might be to identify the most important connections for retaining biodiversity within a food web. One suggestion to identify important species or connections could be to adapt the method outlined by Sahasrabudhe & Motter (2011) which systematically identifies species extinctions that lead to the most secondary extinctions. Although direct inference has remained elusive at this initial stage of development, there are many potential methods that future studies can apply to the results produced using this modelling framework.

### Ecological Realism

The inherent complexity within the model is only one reason that we cannot confidently inform management solutions. A second limitation is that the model lacks ecological realism. I parameterised the model system using biological first principals and expert opinion, and made several assumptions regarding consumption rates and the shape of functional responses. This suggests that whereas the model makes reasonable biological sense, it does not represent realistic ecological interactions. To enhance ecological realism, the model needs to be fit to data. However, a principal goal in developing this framework was to minimise reliance on field data and maximise generalisability. Therefore, it is important to identify the parameters that are most sensitive to small changes, and would

therefore benefit most from investing limited resources in collecting data to inform them. To that end, I found that the maximum consumption rate used to inform the multi-species functional response can have significant impacts on the model outcome. However, before investing resources in data collection it would be best to assess which parameters are particularly sensitive. One can explore the impact of a given parameter by systematically changing it while keeping all other parameters, as well as the initial conditions, constant. The number of different system outcomes that arise from the systematically changing each parameter could then act as an indicator of sensitivity, and we could then determine the most sensitive parameter(s).

Beyond parameterisation, an additional issue that decreases ecological realism is that I have not yet considered spatial processes. I have assumed that the cocoa plantations are isolated and do not occur in any meta-population system, and have therefore excluded any possibility of species re-colonisation after local extinction. Firstly, this assumption is unaligned with a fundamental inspiration for this project; low-intensity agriculture promotes decreased habitat fragmentation, allowing for species to move more easily across landscapes and, thus, re-colonise land (Tschardt et al., 2008). Additionally, Holt (2002) demonstrates that immigration can have profound and counterintuitive impacts on population sizes through processes such as time-lagged density-dependence. Furthermore, perturbations such as species immigration can push a system from one system state to an alternative state (Fukami & Nakajima, 2011). By not explicitly allowing this important spatial process, ecological realism has been decreased, and thus limited the usefulness of the inference. In particular, immigration is likely to have major impacts on the common local extinctions of the cocoa pest, which I speculate drive the high frequency of high productivity states. Therefore, the next step in developing the model should be accounting spatial processes, firstly by incorporating stochastic re-introductions of all species groups after local extinction.

## Biodiversity Quantification

The third major limitation in the framework is a limited quantification of biodiversity. In most food web papers, biodiversity is described as species richness (e.g. Brännström, Loeuille, Loreau, & Dieckmann, 2011; Thebault & Loreau, 2003). However, species abundances are also important in quantifying biodiversity in multi-trophic systems (Soliveres et al., 2016). The Simpson diversity measure is commonly used to assess both species richness and abundance in single trophic levels (Magurran, 2004). Since it is calculated using biomasses of the different species present, a bias is introduced when the taxa involved have inherently very different biomasses, such as in my multi-trophic food web where trees are approximately 1000 times more massive. To account for this bias, I developed a weighted Simpson diversity measure as described in the methods that adjusts based on the inherent biomass bias present between trophic levels and the species richness contained within each species group. This weighting appears to flatten the bias that arises from the vegetation groups (figure 2C). However, since outcomes are notoriously sensitive to the biodiversity measure used (Magurran, 2004), and we look to use these outcomes to identify optimal states and inform management decisions, a thorough exploration of sensitivity to the measure used should be conducted. Other methods of quantifying diversity might include functional diversity (Huang & O. Luukkanen, S. Johanson, V. Kaarakka, S. Räisänen, 2002; Montoya et al., 2015) or structural properties of food webs, such as connectance (Dunne et al., 2002).

## CONCLUSIONS

This study is the first to identify multiple transient states in a complex and dynamic system through the development of a food web model, with a multi-species functional response, and the application of the model to a novel methodological framework. While there is still progress to be made, my model and framework are certainly a viable approach to overcome the restrictions of small-scale observational studies which can only observe one possible state. Additionally, in taking a holistic ecosystem approach, I have highlighted the intricate behavioural interactions that can produce unpredictable outcomes. These intricacies are indiscernible in traditional observational studies concentrating on the responses of a single trophic level or taxa, further supporting the adoption of this food web modelling framework.

To reveal the full potential of these proposed methods, we need to overcome the identified limitations of both the model and the framework. Ecological realism in the model must be enhanced through the systematic identification of the parameters most sensitive to small changes, and then securing data to fit the model to. Additionally, spatial processes should be considered, principally through allowing re-colonisation of species after local extinctions. Furthermore, quantification of biodiversity requires additional exploration, either through further adapting a weighted measure or by considering alternative methods and indicators, such as food web topology. With more work, I have no doubt these two issues can be overcome. Once these limitations have been addressed, the identification of optimal biodiversity-productivity states can be robustly utilised to inform sustainable management practices. Developing a suite of analytical techniques to perform inference on the conditions and behaviours resulting in optimal states will be critical for effective management.

Through exploration of the potential biodiversity-productivity states realisable by a defined cocoa agroforest system, this study has provided unique insight into the drivers of the conflict over LIA effectiveness. I have demonstrated that starkly different productivity outcomes can be achieved by the same system when initialised with different state conditions. In addition, my framework allows us to address how particular outcomes of interest can be achieved by tracking the initial conditions and behaviours that allowed that outcome to arise. The ability to simultaneously identify and quantify biodiversity-

productivity states in a robust and efficient manor will be invaluable in the on-going effort to develop sustainable management guidelines in agriculture.

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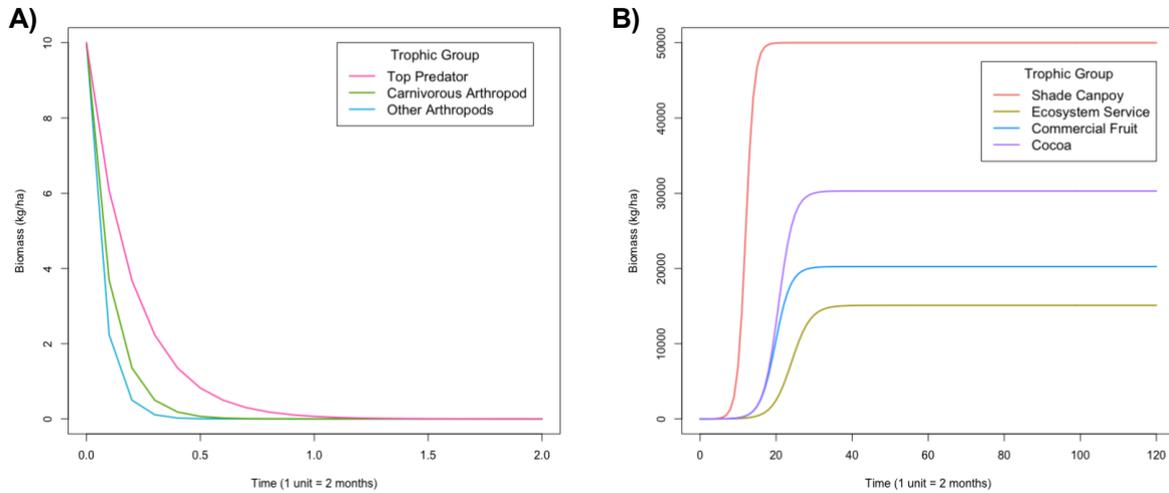
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# APPENDIX

## Appendix 1.



Appendix 1. Single species growth trajectories resulting from parameters in Table 1. A) Decay rates for animal groups. B) Logistic growth for vegetation groups.

## Appendix 2.

I assigned the inherent biomass bias to each trophic level in relation to the top predators. In final system states, arthropods were ~10 times more massive than top predators, while vegetation was ~1000 times more massive. Thus, the inherent bias was 1 for top predators, 10 for arthropods, and 1000 for vegetation.

Trophic group richness adjustments were assigned to represent differences in the species richness contained within each trophic species group. Cocoa trees and cocoa pests had a trophic richness of 1, while the other vegetation groups were given a richness adjustment of 5. All predator groups were assigned a richness of 20 and all arthropod groups (other than the pests) were given a richness of 100.