

Modeling the impact of wild harvest on plant-disperser mutualisms

Plant and disperser co-harvest model

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Abstract

Across the tropics, millions of rural families rely on non-timber forest products for protein, subsistence, and other financial or cultural uses. Often, communities exploit biotically dispersed trees and their mammalian or avian seed disperser. Empirical findings have indicated that many plant and animal resources are overexploited, presenting challenges for biodiversity conservation and sustainable rural livelihoods. However, there has been limited research investigating the impacts of harvest that targets both seed dispersers and zoochoric trees. We formulated a discrete-time model for interacting seed dispersers and plants under harvest. We found that the more dependent species will dictate the sustainable threshold level of harvest, and that higher levels of dependence could drive the species pair to local extinction. We illustrated the application of sensitivity analysis to our modeling framework in order to facilitate future analyses and applications using this approach.

Keywords: quantitative ecology; conservation science; tropical forest; coupled human natural systems; harvesting model

1 Introduction

Wild plants and animals are harvested across the world, and in many cases provide an important source of food and livelihood (Gaoue, 2016; Nielsen et al., 2018; FAO, 2019). Yet there are widespread challenges to sustainable harvest, presenting grave consequences for biodiversity conservation (Peres et al., 2016; Benítez-López et al., 2017), ecosystem function (Young et al., 2016), and livelihoods (Fa et al., 2002; Golden et al., 2011). These challenges are particularly notable in the tropics and sub-tropics where reliance upon wild resources is highest (Milner-Gulland and Bennett, 2003; Nielsen et al., 2018). One key challenge facing managers is the absence of a framework to model and anticipate the impacts of harvesting that exploits both seed dispersers and plants (Morales et al., 2003; Soulé et al., 2005).

Harvested species often include vertebrate seed dispersers as well as long-lived tropical tree species that play critical roles in ecosystem function (Schmidt et al., 2011; Bello et al., 2015;

Caughlin et al., 2015; Peres et al., 2016). The loss of the largest animal-dispersed trees and important vertebrate dispersers can have significant consequences for carbon sequestration (Osuri et al., 2016; Peres et al., 2016), forest tree composition (Markl et al., 2012), and predator-prey interactions (Terborgh et al., 2001). Furthermore, products derived from wildlife can be a critical source of nutrients and income generation, particularly for poor and remote communities with limited access to alternatives (Fa et al., 2002; Nielsen et al., 2018). Thus, understanding the circumstances under which wildlife and plant harvests are sustainable is of paramount importance to balance the needs of people and wildlife.

Stakeholders concerned with managing natural resources ultimately need to understand the sustainability of harvest practices. Assessing sustainability is challenging and methods and models have been developed to deal with differing quality and availability of data on the harvest system (Weinbaum et al., 2013; Young et al., 2016). Where sustainability models have been applied, they have often focused solely on either the animal harvest (Damania et al., 2003; Rowcliffe et al., 2004; Sirén et al., 2004; Levi et al., 2011) or that of plant products (e.g. fruit, bark, or roots) (Ticktin, 2004; Gaoue and Ticktin, 2010; García et al., 2016).

Yet in many tropical regions, communities often harvest both fruiting trees and their disperser populations (hereafter referred to as a “plant-disperser pair”) in tandem. We model a two-species non-timber forest product (NTFP) harvest where components of a zoochoric plant are harvested and the plant’s animal disperser is hunted. Examples of plant NTFPs include the removal of foliage or bark for medicinal uses and fruit and nut harvest; the term NTFP distinguishes this form of foliage, bark, and fruit harvest from timber extraction by logging. Notable examples of important harvested plant-disperser pairs include the Brazil nut (*Bertholletia excelsa*) and agouti (*Dasyprocta* spp., Mori and Prance 1990; Haugaasen et al. 2010), Atlantic palm (*Astrocaryum aculeatissimum*) and toucans (*Ramphastos* spp., Galetti et al. 2006), Chulta (*Dillenia indica*) and elephants (*Elephas maximus*, Sekar and Sukumar 2013), and *Beilschmiedia assamica* and hornbills (e.g. *Aceros nipalensis*, Velho

et al. 2009). Given the mutualistic relationship between a plant-disperser pair, overharvesting leading to defaunation of the seed disperser may have cascading detrimental effects on the availability and dispersal of the plant (Muller-Landau, 2007; Beaune et al., 2013). Models focused exclusively on animal harvest neglect the impact that reduced plant food or shelter resources may exert on disperser populations (Peres et al., 2003). Conversely, models of plant harvest may fail to capture germination failure as disperser populations collapse (Caughlin et al., 2015; Granados et al., 2017). To that end, we modeled the harvesting and hunting dynamics of plants and their seed dispersers. Specifically, we formulated a discrete-time population model of co-harvested plant-disperser pairs.

A more holistic representation of the interactive effects of harvest on plant-disperser pairs would provide greater insight for conservation management. Indeed, such an approach would yield insights that a single species model may fail to produce. An integrated framework would benefit conservation by anticipating and identifying species co-management thresholds; beyond these thresholds, both species could be driven to deterministic extinction. Using our model, we examine the following questions using the Brazil nut-agouti plant-disperser pair as an illustrative example:

1. What is the impact of different hunting and harvest regimes (denoting animal hunting and plant NTFP harvest) on long-run plant-disperser pair population sizes?
2. For a specific set of biological life history parameters, how could managers identify a sustainable harvest level for both species?
3. For a given harvest regime, how does the interaction strength between the pair affect long-run population size?
4. In this modeling framework, which parameters exhibit the greatest importance?

2 Methods

We now introduce our general modelling framework which can be used to simulate population dynamics of any interacting plant-disperser pair in harvesting and hunting regimes. We model the plant-disperser harvest system using the population dynamics of the plant and its disperser, and we introduce terms that represent both harvest rates. We only consider animals mature enough to disperse seeds. Figure 1 presents an overview of the modeling framework that we used. We chose to model a plant-disperser harvesting system in discrete time (time step: one year). Our chosen time step corresponds to standard tropical plant monitoring protocols and existing plant projection matrices. Thus our approach can accommodate the vast majority of existing plant projection matrices.

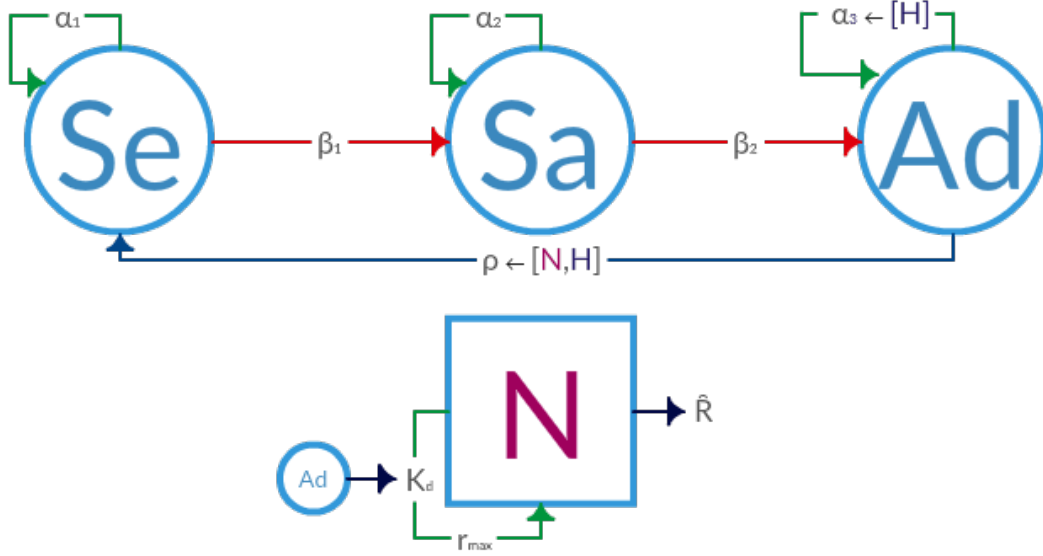


Figure 1: Population dynamics of plants and their seed dispersers in a harvesting regime. Compartments represent life stages (Se = seedlings, Sa = saplings and Ad = adult plants that contain both fruit/seed producing and non-producing mature plants). The α_i are the stage specific survival probabilities, β_i are the transition probabilities between stages and ρ_j is the fecundity probability - new seedlings produced per adult plant. The N represents the disperser population, hunting is depicted as \hat{R}_t , and harvest of the adult plants and/or plant products as H. K_d is the disperser carrying capacity and r_{max} is the maximum intrinsic growth rate of the disperser.

The plant dynamics (\mathbf{P} , Equation 1) are given by a discrete-time population projection

matrix. In this matrix, α_i represents the probability of survival within the same stage, β_i is the probability of transitioning to the next stage, and ρ_i is the number of seedlings (stage 1) produced by each adult tree from stage i . We incorporate the impact of seed dispersers, denoted as N_t , on the plant population (\mathbf{v}_t) by including them as a parameter in \mathbf{P}_t .

$$\mathbf{v}_{t+1} = \mathbf{P}_t(N_t) \mathbf{v}_t \quad (1)$$

$$\mathbf{P}_t = \begin{bmatrix} \alpha_1 & 0 & \dots & \rho_i G_t g(N_t) & \rho_n G_t g(N_t) \\ \beta_1 & \alpha_2 & 0 & \dots & 0 \\ 0 & \beta_2 & \ddots & 0 & \vdots \\ \vdots & 0 & \ddots & \alpha_i S_t & 0 \\ 0 & \dots & 0 & \beta_i & \alpha_n S_t \end{bmatrix}$$

We represent plant harvesting as (a) reduced germination or fecundity rates (e.g. from the removal of fruits), (b) reduced survivorship probability for the adult plant (e.g. damage sustained from bark harvest), or (c) a combination of both. Thus, plant harvest is represented by the multipliers G_t (fecundity multiplier) and S_t (survivorship multiplier). When $G_t, S_t \rightarrow 1$, then the system's maximal germination and/or adult survival rate is attained; conversely, when $G_t, S_t \rightarrow 0$, these rates fall to 0. Moreover, we also model the effect of the seed disperser on fecundity with another scalar, $g(N_t)$. For all three multipliers, note that $0 \leq G_t, S_t, g(N_t) \leq 1$. We also extend this framework to incorporate plant density dependence (Allen, 1989) (see SI Section 1.1 for the model and analyses).

The disperser's population dynamics are given by discrete-time logistic growth (Equation 2). Hunting enters as a rate removing a proportion of the population (\hat{R}_t), which corresponds to how hunting rates are often quantified using interview data. We then assume that plants affect faunal population dynamics by modifying their carrying capacity (Equation 3, Sibly and Hone 2002).

$$N_{t+1} = \begin{cases} \left[r_{max} N_t \left(1 - \frac{N_t}{K_d f(\mathbf{v}_{a,t})} \right) + N_t \right] (1 - \hat{R}_t) \\ 0 \text{ if } N_t + \Delta N_t < 0 \end{cases} \quad (2)$$

117 We represent the impact of adult plants on disperser carrying capacity using the multiplier
118 function

$$f(\mathbf{v}_{a,t}) \quad (3)$$

119 where $\mathbf{v}_{a,t}$ denotes the population of adult plants. We restrict the multiplier to be $0 \leq$
120 $f(\mathbf{v}_{a,t}) \leq 1$. So when $f(\mathbf{v}_{a,t}) \sim 1$, the carrying capacity of the seed disperser is at maximum,
121 and when $f(\mathbf{v}_{a,t}) \sim 0$, the carrying capacity is severely limited.

122 2.1 Functional forms relating plant-disperser interactions

123 In general, empirical data that could be used to specify functional forms for $g(N_t)$, the
124 impact of the disperser on plant germination rates, and $f(\mathbf{v}_{a,t})$, the impact of the adult plant
125 population on disperser carrying capacity do not exist (Muller-Landau, 2007; Caughlin et al.,
126 2015). Thus, we specified functional forms to represent $g(N_t)$ and $f(\mathbf{v}_{a,t})$ that accounted
127 for (1) abundance-function relationships and (2) species interactions. As both $g(N_t)$ and
128 $f(\mathbf{v}_{a,t}) \in [0, 1]$, we used a sigmoid functional form, denoted by $f(x)$, as it is bound to the
129 interval of 0 and 1 (Equation 4).

$$f(x) = \frac{1}{1 + e^{-q(x-x_0)}} \quad (4)$$

130 For both $g(N_t)$ and $f(\mathbf{v}_{a,t})$, the terms x_0 and q denote the midpoint of the sigmoid function
131 and its steepness, respectively. For $g(N_t)$, we specified that the midpoint of this function (x_0)
132 would be half of the disperser's carrying capacity based on the assumption that germination
133 would fall to half when the disperser is at $\frac{K}{2}$. Note that in Equation 4, q represents the
134 steepness of the curve. When q is large, a small change in x (here, the disperser population
135 size, N_t) would result in excessively large changes to $f(x)$.

136 We chose a value for q that would make Equation 4 roughly map the interval $[0, K]$ to

[0, 1]. That is, when there are no more seed dispersers ($N \sim 0$), then there would be no more germination ($f(x = N) \sim 0$). On the other hand, if the population of seed dispersers was at its carrying capacity ($N \sim K$) then germination would be at its maximum ($f(x = N) \sim 1$).

To determine a suitable value of q , we imposed the condition that $f(m \cdot K) = m$ for some $m \in (0, 1)$. This condition is equivalent to saying that if the animal population were at m proportion of its carrying capacity, then germination would be at m proportion of its maximum. Thus,

$$f(m \cdot K) = m \tag{5}$$

$$\implies m = \frac{1}{1 + e^{-q(mK - \frac{K}{2})}} \tag{6}$$

$$\implies q = -\frac{\log(1-m) - \log(m)}{(m - \frac{1}{2})K} \tag{7}$$

We included a term denoting the interaction strength ($\delta \in [0, 1]$) between the disperser and plant. In ecology, the term “interaction strength” connotes the degree to which one or more species is affected by changes in the abundance of other species with which it interacts; such relationships are often quantified from time series data evaluating changes to population abundance or other functional outcomes (Wootton and Emmerson, 2005). A δ value of 0 indicates no dependence between the plant and the disperser, perhaps corresponding to a pair of generalist species that do not rely on each other for long-term persistence. Conversely, $\delta \sim 1$ represents strong dependence, which could correspond to specialist species that rely on a unique set of resources. δ could be estimated from studies quantifying diet breadth or other metrics of ecological interaction between species. By including the term $(1 - \delta)$ in Equation 4, $f(x)$ thus lies between $1 - \delta$ and 1.

$$f(x) = \frac{\delta}{1 + e^{-q(x-x_0)}} + (1 - \delta) \tag{8}$$

We used separate δ terms to describe the impact of the plant population on the disperser

and that of the disperser on the plant. $\delta_{d \rightarrow p}$ represents the reliance of the plant on the seed disperser, and $\delta_{p \rightarrow d}$ the seed disperser's reliance on the plant for resources such as food or shelter. Incorporating these components produces the functional forms $g(N_t)$ (the dispersers' effect on plant fecundity) and $f(\mathbf{v}_{a,t})$ (the effect of plants on disperser carrying capacity).

$$g(N_t) = \frac{\delta_{d \rightarrow p}}{1 + e^{-q_p(N_t - \frac{K_d}{2})}} + (1 - \delta_{d \rightarrow p}) \quad (9)$$

$$f(\mathbf{v}_{a,t}) = \frac{\delta_{p \rightarrow d}}{1 + e^{-q_d(\mathbf{v}_{a,t} - \frac{K_a}{2})}} + (1 - \delta_{p \rightarrow d}) \quad (10)$$

$$\text{where } q_i = -\frac{\log(1-m) - \log(m)}{(m - \frac{1}{2})K_i} \quad (11)$$

where K_d denotes the carrying capacity of the disperser and K_a the equilibrium maximum population size of adult plants. Regarding the parameter m , in Figure 5, we observe that m generally has negligible effect on the long-run behavior of the plant-disperser system as long as m is within the interval $[0.01, 0.1]$. Within this interval, the sigmoid curve appears reasonable, and outside the interval, the sigmoid becomes too steep. Thus, we chose a roughly midpoint value of 0.05 for m , though it may not necessarily be better than other values of m in that interval.

2.2 Case study description and parameter estimation

The Brazil nut and agouti disperser-pair are an excellent focal example to illustrate the model and its application for conservation management and sustainable use. The Brazil nut is a long-lived tropical tree that produces large seeds encased in a hard, woody capsule that is extremely difficult to extract (Pires, 1984; Mori and Prance, 1990). Without a disperser to crack open the seed case, the Brazil nut seed experiences severely compromised germination rates (Peres et al., 2003). The agouti, and in particular, the red-rumped agouti (*Dasyprocta leporina*), is one of the most effective dispersal agents for the Brazil nut (Scoles and Gribel, 2012). Peres and Baider (1997) found that in the absence of agoutis, the mortality rate for Brazil nut seeds was 100%. Both Brazil nuts and agoutis are harvested extensively,

contributing to local food intake and livelihoods. In the Brazilian Amazon, where the Brazil nut and the agouti are widely distributed, up to 8 million rural people may consume wild animals, and agoutis are among the most intensely exploited species (Peres, 2000; Thomas et al., 2015). Brazil nut harvests are also important to rural communities, contributing 43% of total household income for harvesters, measured in 12 communities in Bolivia and Brazil (Duchelle et al., 2011).

To model this system, we obtained a life history projection matrix \mathbf{P} (Zuidema, 2000) and field-realistic model parameter values (e.g. harvest rates) for the Brazil nut and agouti from several sources (Table 1). Currently there exists no experimental approach to explicitly determine the dependence parameters of our model ($\delta_{d \rightarrow p}$, $\delta_{p \rightarrow d}$). Given our understanding of the high dependence of the Brazil nut trees on the agouti as the primary seed disperser, we assign $\delta_{d \rightarrow p} = 1$. However, the agouti is known to be a generalist seed disperser which can consume multiple food resources including Brazil nuts; thus we set $\delta_{p \rightarrow d} = 0.5$. Furthermore, while there is limited evidence that traditional forms of Brazil nut harvest (e.g. collecting fallen fruits from the forest floor) are highly deleterious to adult trees, for other zoochoric trees with valuable fruits or nuts, harvesters sometimes cause reduced adult survivorship from damage associated with bark removal or other intensive activities (Guedje et al., 2007; Gaoue and Ticktin, 2007). Hence, we assume a high adult survival rate for the Brazil nut tree in our model.

2.3 Sensitivity Analysis

Oftentimes, tropical systems where plants and animals are both harvested exhibit extreme data paucity and uncertainty. To evaluate the sensitivity of the model to its parameters, we performed global sensitivity analysis using the Fourier amplitude sensitivity test (FAST) method to estimate Sobol indices for the model parameters (Saltelli et al., 1999; Nossent et al., 2011). The Sobol index quantifies the contribution that any given parameter has on the variance of long-run plant and animal populations; that is, it quantifies how important the parameter is to the persistence of the plant or animal.

Parameter	Description	Value	Source
r_{max}	Agouti population growth rate	0.67-1.1	Robinson and Redford (1986); Robinson and Bennett (2000)
P	Brazil nut projection matrix	17x17 Matrix	Zuidema (2000)
$\delta_{p \rightarrow d}$	Reliance of agouti on Brazil nut	0.5 (or $\in [0, 1]$)	Peres et al. (1997)
$\delta_{d \rightarrow p}$	Reliance of Brazil nut on agouti	1 (or $\in [0, 1]$)	Peres and Baider (1997)
K_d	Agouti carrying capacity	5200 (indiv/km ²)	Silvius and Fragoso (2003)
K_a	Maximum adult Brazil nut population size	20-150 (indiv/km ²)	Zuidema (2000)
$\hat{R}(t)$	Agouti hunting removal rate	0.037-0.57	Hill and Padwe (2000)
S_t	Brazil nut adult survival multiplier	1.00-0.90	Zuidema (2000)
G_t	Brazil nut germination multiplier	1.00-0.85	Zuidema (2000)
m	Steepness of sigmoid functions	[0.01, 0.1]	Author decision

Table 1: Life history and model parameters for Brazil nut and agouti plant-disperser pair.

More specifically, the FAST method calculates first-order and total-order sensitivity indices. The first order indices show how the long-run plant and disperser populations would change when perturbing one parameter at a time, while the total-order indices indicate the sensitivity when perturbing all the parameters at once and thus considers interaction effects with other parameters. We used the `fast99` function from the R package `sensitivity` (Saltelli et al. 1999; Iooss and Lemaître 2015; Iooss and Janon 2019) to vary each parameter within its estimated range and generate the Sobol indices.

3 Results

3.1 Population persistence under varying harvest and hunting regimes

We initially varied the harvest and hunting regime, holding all other parameter values constant. The term “harvest regime” or “hunting regime” denotes the combination of multipliers ($\in [0, 1]$) that scaled plant survivorship and germination rates as well as a hunting rate which removed a proportion of the disperser population.

We found that high rates of harvesting drove the Brazil nut-agouti pair to extinction (Figure 2). Given that the Brazil nut is highly reliant on the agouti for seed dispersal, we observed that even modest rates of plant harvest (e.g., Harvest = 0.1), and extensive rates of hunting (e.g., Hunting = 0.5) could drive the Brazil nut to deterministic extinction ($\lambda < 1$). On the other hand, the agouti population persisted even under a moderate rate of plant harvest. Our model indicated critical thresholds where the impact of the harvesting regime exhibited a discontinuity in its impact on the Brazil nut and agouti populations. We observed that under low harvesting and hunting rates, the plant and disperser contour lines were non-linear, indicating the importance of both parameters on long-run species pair dynamics.

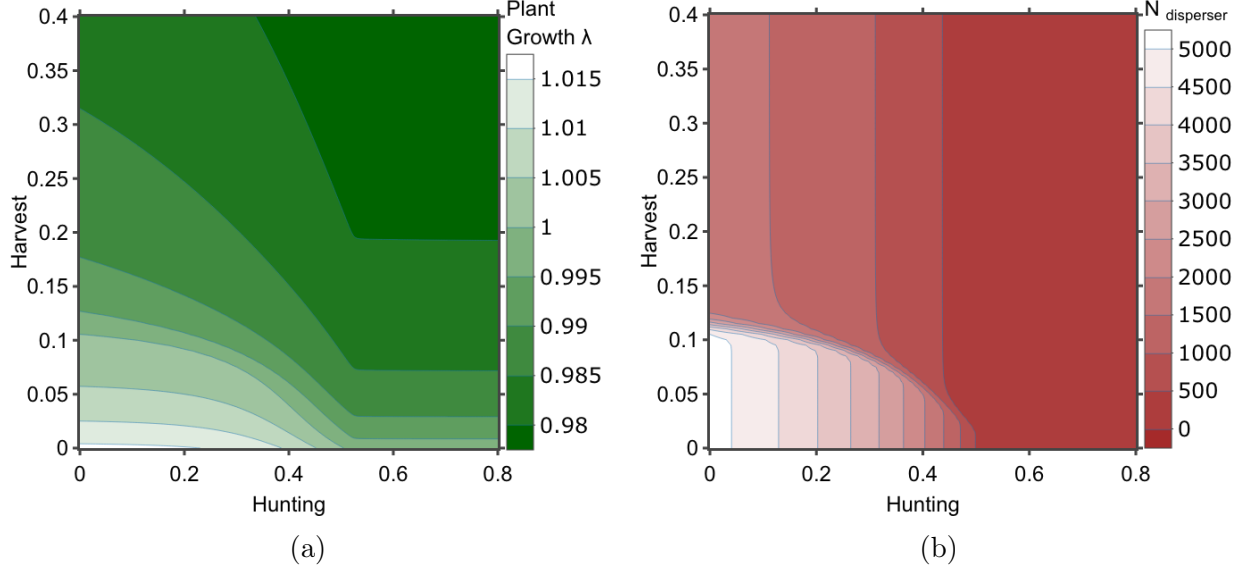


Figure 2: Agouti population size ($N_{\text{disperser}}$) and the stochastic growth rate of Brazil nut (plant; λ) under varying levels of harvesting and hunting. The simulation was run with the parameters in Table 1 as well as $\delta_{d \rightarrow p} = 1$ and $\delta_{p \rightarrow d} = 0.7$. Each simulation was run for a time length of 500 years and the outputs represent either the average plant population growth rate or the equilibrium animal population size.

3.2 Sustainable Harvest-Hunting threshold level for plant-disperser pair

We used our model to estimate sustainable upper limits for harvesting regimes (plant harvest and hunting rates); below this threshold, given the model dynamics, the plant-disperser pair should persist (Figure 3). Our model indicated that the Brazil nut's sustainable harvest regime threshold was lower than the agouti's $\frac{K_d}{2}$ threshold, given its complete dependence on agoutis for germination. We observed distinct shifts in the sustainable threshold levels when altering harvest and hunting levels independently and when considering their combined effect on the persistence of the Brazil nut and agouti population (for more details, see the Supplementary Figure S9). In general, the model indicated that lower levels of inter-dependence would correspond to higher limits for the sustainable harvest regime.

We also observe a region of high sensitivity in the disperser population graph around the harvest/hunting value of 0.11 where small changes in harvest/hunting result in large

240 changes in long-run disperser population (Figure 3). This corresponds to the threshold level
 241 of harvest/hunting from the plant graph at which the average population growth rate is
 242 stable and not declining (Figure 3a). When the average growth rate (λ) is ≥ 1 , then in our
 243 modelling framework, the Brazil nut population could support a large agouti population.
 244 However, when $\lambda < 1$, then the Brazil nut would exponentially decay to 0, which would
 245 permit only a fraction of the agouti population to persist based on $\delta_{p \rightarrow d} = 0.5$ (Figure 3b).

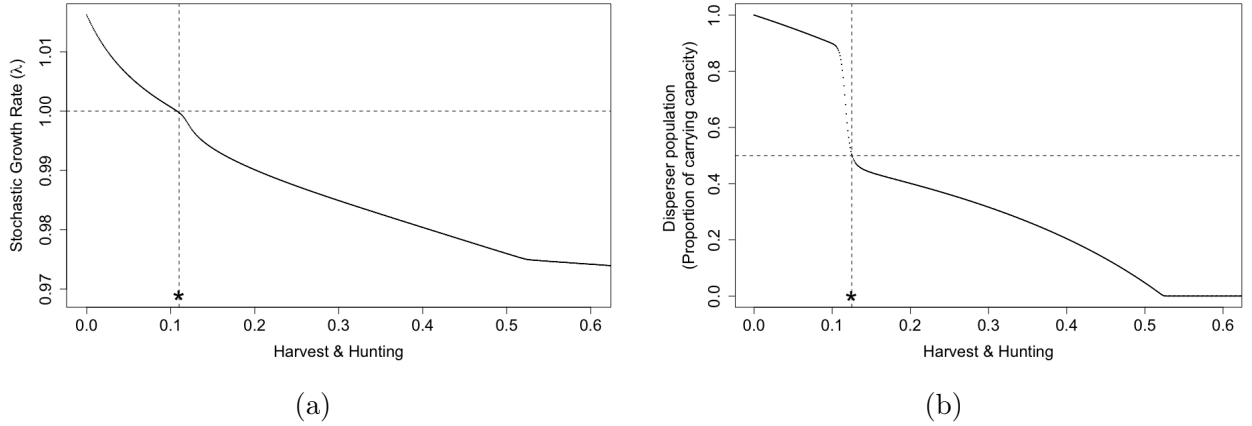


Figure 3: The impact of harvesting regimes (plant harvest and disperser hunting) on Brazil nut (a) and agouti populations (b). The x-axis on both graphs represents the harvest and hunting values: for the disperser, x is the proportion of animals taken, and for the plant, $(1-x)$ is multiplied with adult survival and germination in the projection matrix. Note also that in these simulations, $\delta_{d \rightarrow p} = 1$, $\delta_{p \rightarrow d} = 0.5$. * represents the sustainable harvesting and hunting regimes corresponding to a persistent population.

246 **3.3 The role of plant-disperser interaction strength on population** 247 **persistence**

248 We evaluated how the interaction strength between a plant-disperser pair would affect
 249 long-run population outcomes using a static set of values for the harvest regime (Figure 4).
 250 Given a specific harvest regime, a stronger species interaction was associated with more
 251 pronounced declines for the Brazil nut and agouti. The model indicated that when $\delta_{d \rightarrow p}$
 252 was low, the impact of $\delta_{p \rightarrow d}$ was less substantial, particularly for the Brazil nut population
 253 growth rate (Figures 4a, 4b). However, we observed that larger $\delta_{d \rightarrow p}$ values tended to exert

a deleterious impact on both the Brazil nut λ and the long-run agouti abundance (N_{disp}), even when $\delta_{p \rightarrow d}$ values were low. The effect of $\delta_{p \rightarrow d}$ on the agouti population was more pronounced at moderate $\delta_{d \rightarrow p}$ values.

Conversely, the Brazil nut exhibited different dynamics based on its reliance on the agouti. Under low levels of $\delta_{d \rightarrow p}$, the Brazil nut's growth rate remained relatively constant and high across a wide range of interaction strengths (specifically, $\delta_{p \rightarrow d} \in [0, 1]$ when $\delta_{d \rightarrow p} \leq 0.4$). However, as $\delta_{d \rightarrow p}$ increased, we began to see interacting effects between $\delta_{p \rightarrow d}$ and $\delta_{d \rightarrow p}$ on the population growth rate of the Brazil nut.

The plant growth rate was primarily affected by $\delta_{d \rightarrow p}$, with $\delta_{p \rightarrow d}$ mostly impacting plant growth during high values of $\delta_{d \rightarrow p}$. This was not the case for the seed disperser's population which showed a more non-linear pattern. The combined effect of $\delta_{d \rightarrow p}$ and $\delta_{p \rightarrow d}$ exhibited a stronger, interactive impact on the disperser population than on the stochastic growth rate of the Brazil nut. Nevertheless, when plant harvest rates were high, the model indicated that $\delta_{d \rightarrow p}$ did not significantly affect agouti equilibrium abundance (Supplementary Figure S8). Additionally, in comparing the impacts of harvesting Brazil nut fruits vs. reducing adult survival, we observed that fruit harvest, reflected in decreased germination, exhibited a much smaller effect on reducing long-run population growth rate (Supplementary Figure S10).

3.4 Quantifying the impact of parameter uncertainty and parameter importance

The Sobol variance-based global sensitivity analysis indicated that S_t (impact of harvest on adult Brazil nut tree survivorship) was the most important factor influencing the Brazil nut population, both as an individual parameter and one interacting with other parameters in the system (Figure 5, first- and total-order Sobol indices respectively). Subsequently, the next most important parameters were G_t (germination rate), $\delta_{d \rightarrow p}$ (reliance of the Brazil nut on the agouti), and \hat{R}_t (the agouti hunting rate). For the agouti, while the hunting rate (\hat{R}_t) was generally the most critical variable, the reliance of the agouti on the Brazil nut

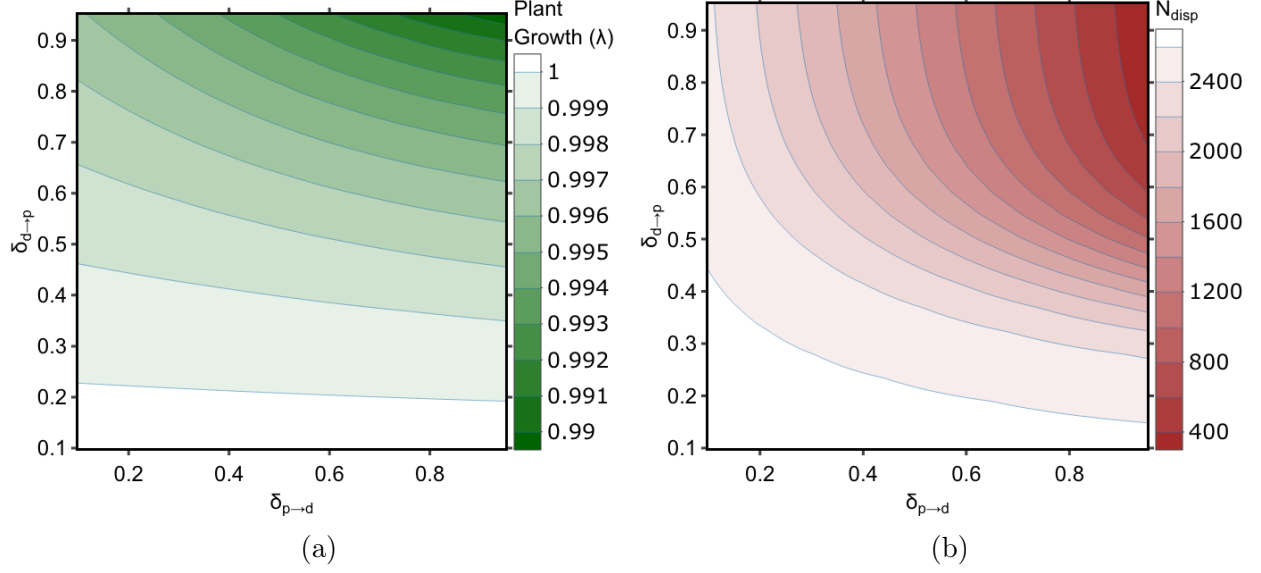


Figure 4: Stochastic growth rate of Brazil nut (λ) and Agouti abundance (N_{disp}) under varying strengths of coupling (represented by $\delta_{d \rightarrow p}$, reliance of Brazil nut on agouti, and $\delta_{p \rightarrow d}$, the impact of the Brazil nut on the agouti). The simulation was run with the following harvest regime: $G_t = 0.85$, $S_t = 0.9$ and $R_t = 0.35$.

($\delta_{p \rightarrow d}$) was also a prominent variable. Brazil nut adult survivorship and the intrinsic rate of increase for the agouti population were also critical to long-run agouti population size.

The total-order Sobol indices provide information on the relative importance of each parameter in concert with all of the other parameters. Under both the first- and total-order Sobol indices, hunting rate, S_t , and the reliance of Brazil nut on agouti ($\delta_{d \rightarrow p}$) were important factors. We observed that $\delta_{d \rightarrow p}$ had a greater contribution to the variation in long-run population dynamics in the total-order versus first-order Sobol indices. This highlights that changes in $\delta_{d \rightarrow p}$ have a much greater effect on long-run plant population when coupled with changes in all other parameters, indicating that $\delta_{d \rightarrow p}$ interacts strongly with other parameters. (Figure 5; total-order index).

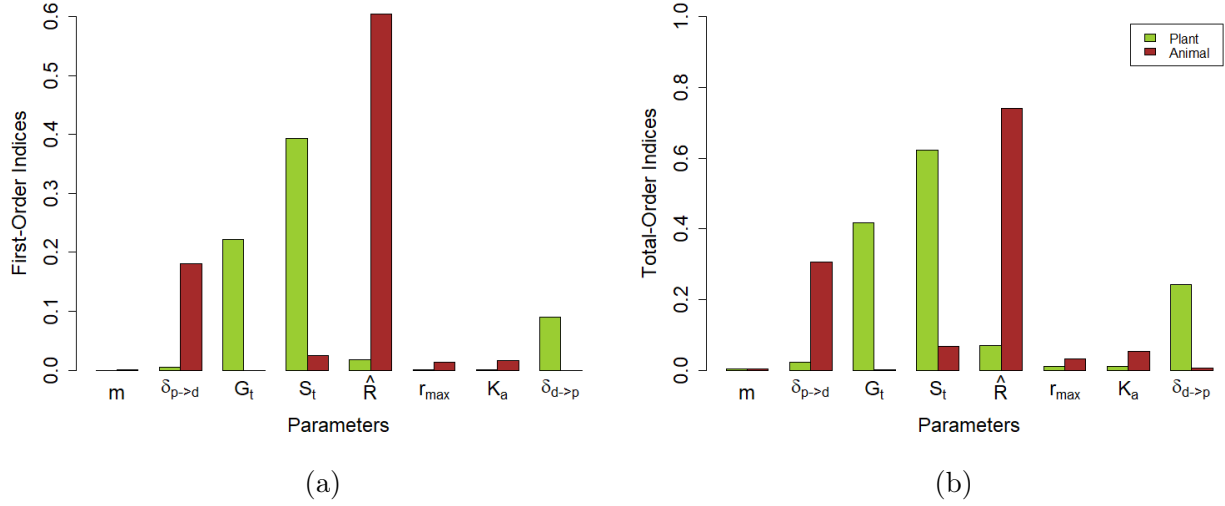


Figure 5: Sobol indices for each model parameter. Each bar shows the relative contribution of each parameter to the equilibrium Brazil nut and agouti population. The first order indices (a, left panel) indicate the impact of each parameter being varied when all other variables are held constant. The total-order indices (b, right panel) indicate the importance of each variable as it is manipulated in concert with all other variables.

4 Discussion

Our study presents a mathematical framework that combines the effect of sub-lethal plant harvest and hunting that targets animal seed dispersers. Using a case study of the Brazil nut and agouti, our model identified a sustainable rate of harvesting and hunting where both species could persist. We found that the impacts of a harvesting regime were more deleterious when species interaction strength was greater, all other things equal. Additionally, we illustrated how researchers and practitioners could use the Fourier amplitude sensitivity test to identify variable importance and estimate the effects of parameter uncertainty on long-run population dynamics.

Due to the agouti's ability to exploit plant resources beyond the Brazil nut, it could persist—as long as the hunting rate was sufficiently low—even under high levels of plant harvest. However, our model indicated that if the agouti was overexploited, the Brazil nut could not persist, even under low plant harvest rates; this was driven by the Brazil nut's high reliance

on the agouti (Peres et al., 1997; Haugaasen et al., 2010). This prediction of our model aligns with empirical observations that suppressed agouti abundance due to hunting can severely disrupt Brazil nut recruitment and population persistence (Peres et al., 2003; Kainer et al., 2007). More generally, the loss of mammalian dispersers can cause recruitment failure and the collapse of biotically-dispersed tree populations (Jansen et al., 2012; Bello et al., 2015; Peres et al., 2016).

The global sensitivity analysis presented here can be used as a framework to determine the most sensitive parameters for prioritizing research and management effort. Our model indicates several key areas for future applied research on the Brazil nut and agouti. As adult survivorship under harvest and agouti hunting rate have the greatest impact on long-term sustainability, future researchers should carefully quantify these rates for prediction and management. Additionally, within any Brazil nut population, our model indicates that preserving adult trees should be a high priority, echoing previous findings (Peres et al., 2003; Kainer et al., 2007). Activities that substantially reduce adult survival, such as deep cuts in adult trees for harvesters to climb up and extract fruit, should be limited (Gaoue et al., 2011).

Harvesting the Brazil nut fruits had a much smaller effect (Supplementary Figure S10), indicating that the harvest of Brazil nuts could be sustainable if other factors, such as the agouti hunting rate, are controlled. More generally, our model predicted that under modest rates of hunting that did not completely remove the agouti, the Brazil nut population could persist under low to medium rates of harvest. This model finding aligns with research across the Amazon basin which has repeatedly found that Brazil nut populations can be sustainably harvested when agoutis are present (Zuidema and Boot, 2002; Wadt et al., 2008; Scoles and Gribel, 2012). Similar to recent findings on wild animal harvest, and based on our results, we suggest that managers should prioritize controlling the rate of offtake targeting the disperser (Dirzo et al., 2014; Ripple et al., 2015). Yet so long as the disperser has some degree of reliance on the harvested plant, ensuring a sustainable hunting rate alone is insufficient. The

plant harvest rate must also be below a specific threshold to ensure long-run persistence of both species.

The model highlights the importance of considering species interactions, as we found that greater interaction strength between the species pair tended to constrain the space of a sustainable harvesting-hunting regime. This finding reflects the mutualistic relationship between the seed disperser and plant that we considered (Wacker, 1999). In other contexts, such as terrestrial wildlife or fisheries management, researchers have shown that moving beyond individual species is necessary, as competitive, predatory, or other species interactions can dramatically affect the sustainable harvest level relative to a single-species model (Damania et al., 2003; Baskett et al., 2007). In fact, Samhouri et al. (2017) show that recovery plans for overharvested species are more efficient when managers account for the interaction structure between co-harvested species.

While our model provides a framework for understanding the impacts of harvested and hunted plant-disperser pairs, there are several limitations. One limitation of our model is that we do not specify a dynamic harvesting regime that responds to different control measures, such as penalties for over-harvest or incentives for certain behaviors (Damania et al., 2003; Rowcliffe et al., 2004; Nielsen et al., 2018). In the context of the Brazil nut and agouti, we caution that we used parameter values estimated across multiple sites, and that for several of the model variables, we were unable to find any estimates from the published or gray literatures. We also note that estimating species interaction strength is often extremely challenging (Wootton and Emmerson, 2005).

When the required data are available at a fine-grained site level, our model could be used to predict the impacts of harvesting and hunting plant-disperser pairs, allowing for more informed management decisions. However, under parameter uncertainty, future researchers and managers could interrogate parameter uncertainty using the sensitivity analysis approach that we illustrated with our case study. Finally, our model does not specify any density dependence for the plant species. Thus our model cannot be used to predict how

harvesters would respond to different incentives or penalties, which would in turn affect the harvesting and hunting offtake rates observed in the system. Recent findings in terrestrial harvesting highlights that harvester decision-making and gear choices are critical to dictating the outcome of harvest (Rowcliffe et al., 2004; Levi et al., 2011). Moreover, the values that harvesters hold, such as the monetary value of harvested goods or the cultural or spiritual significance of certain harvesting practices can affect the sustainable level of harvest in non-obvious ways (Kellner et al., 2011).

The results presented in this paper may serve as the basis for future work. We note the importance of comparing the results of our simulations with previous and current practices; to the best of our knowledge, the time series data required to facilitate this comparison does not exist at present for the Brazil nut and agouti. Future work may also include natural phenomena which has been left outside the scope of our research. For example, one could explore the impact of seed production variation across time and seed disperser satiation as a result of seed abundance. Additionally, our model is spatially implicit; in any specific setting, mismatches or alignment between seed disperser movements, harvester site selection, and seed germination rates as a function of distance to the parent tree can all influence the sustainability of multi-species harvest. One avenue for future work would be to extend our model to a multi-patch model to accommodate such dynamics.

In conclusion, our model illustrates how to account for interacting species pairs when determining management decisions for harvested plants and dispersers in tropical systems. Our work shows that such an integrated approach identifies more conservative harvest thresholds to ensure species persistence.

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386 **6 Competing Interests**

387 The authors declare no conflicts of interest.

388 **7 Code Availability**

389 Github - <https://github.com/TheAlanGan/HuntHarvest>

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