

1 Modeling the impact of wild harvest on plant-disperser  
2 mutualisms

3 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;

37 Caughlin et al., 2015; Peres et al., 2016). The loss of the largest animal-dispersed trees and  
38 important vertebrate dispersers can have significant consequences for carbon sequestration  
39 (Osuri et al., 2016; Peres et al., 2016), forest tree composition (Markl et al., 2012), and  
40 predator-prey interactions (Terborgh et al., 2001). Furthermore, products derived from  
41 wildlife can be a critical source of nutrients and income generation, particularly for poor  
42 and remote communities with limited access to alternatives (Fa et al., 2002; Nielsen et al.,  
43 2018). Thus, understanding the circumstances under which wildlife and plant harvests are  
44 sustainable is of paramount importance to balance the needs of people and wildlife.

45 Stakeholders concerned with managing natural resources ultimately need to understand  
46 the sustainability of harvest practices. Assessing sustainability is challenging and methods  
47 and models have been developed to deal with differing quality and availability of data on the  
48 harvest system (Weinbaum et al., 2013; Young et al., 2016). Where sustainability models  
49 have been applied, they have often focused solely on either the animal harvest (Damania  
50 et al., 2003; Rowcliffe et al., 2004; Sirén et al., 2004; Levi et al., 2011) or that of plant  
51 products (e.g. fruit, bark, or roots) (Ticktin, 2004; Gaoue and Ticktin, 2010; García et al.,  
52 2016).

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

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

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

- 80 1. What is the impact of different hunting and harvest regimes (denoting animal hunting  
81 and plant NTFP harvest) on long-run plant-disperser pair population sizes?
- 82 2. For a specific set of biological life history parameters, how could managers identify a  
83 sustainable harvest level for both species?
- 84 3. For a given harvest regime, how does the interaction strength between the pair affect  
85 long-run population size?
- 86 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.

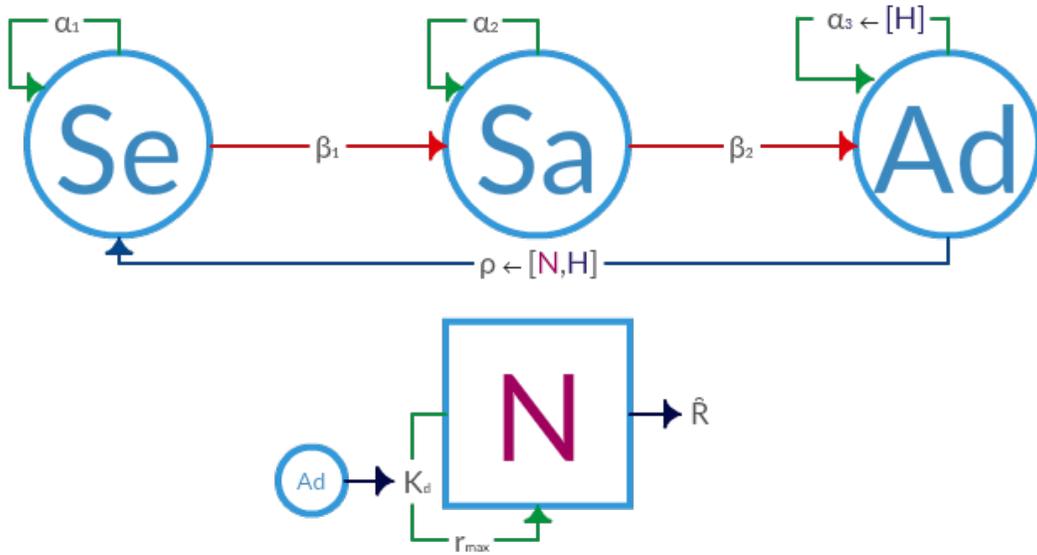


Figure 1: Population dynamics of plants and their seed dispersers in a harvesting regime. Compartments represent life stages (Se = seedlings, Sa = saplings and Ad = adult plants that contain both fruit/seed producing and non-producing mature plants). The  $\alpha_i$  are the stage specific survival probabilities,  $\beta_i$  are the transition probabilities between stages and  $\rho_j$  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

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

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

102

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

103 We represent plant harvesting as (a) reduced germination or fecundity rates (e.g. from  
 104 the removal of fruits), (b) reduced survivorship probability for the adult plant (e.g. damage  
 105 sustained from bark harvest), or (c) a combination of both. Thus, plant harvest is represented  
 106 by the multipliers  $G_t$  (fecundity multiplier) and  $S_t$  (survivorship multiplier). When  $G_t, S_t \rightarrow$   
 107 1, then the system's maximal germination and/or adult survival rate is attained; conversely,  
 108 when  $G_t, S_t \rightarrow 0$ , these rates fall to 0. Moreover, we also model the effect of the seed  
 109 disperser on fecundity with another scalar,  $g(N_t)$ . For all three multipliers, note that  
 110  $0 \leq G_t, S_t, g(N_t) \leq 1$ . We also extend this framework to incorporate plant density  
 111 dependence (Allen, 1989) (see SI Section 1.1 for the model and analyses).

112 The disperser's population dynamics are given by discrete-time logistic growth (Equa-  
 113 tion 2). Hunting enters as a rate removing a proportion of the population ( $\hat{R}_t$ ), which  
 114 corresponds to how hunting rates are often quantified using interview data. We then as-  
 115 sume that plants affect faunal population dynamics by modifying their carrying capacity  
 116 (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

137  $[0, 1]$ . That is, when there are no more seed dispersers ( $N \sim 0$ ), then there would be no more  
 138 germination ( $f(x = N) \sim 0$ ). On the other hand, if the population of seed dispersers was at  
 139 its carrying capacity ( $N \sim K$ ) then germination would be at its maximum ( $f(x = N) \sim 1$ ).

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

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

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

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

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

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

155 We used separate  $\delta$  terms to describe the impact of the plant population on the disperser

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

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

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

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

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

## 167 2.2 Case study description and parameter estimation

168 The Brazil nut and agouti disperser-pair are an excellent focal example to illustrate the  
 169 model and its application for conservation management and sustainable use. The Brazil nut  
 170 is a long-lived tropical tree that produces large seeds encased in a hard, woody capsule that  
 171 is extremely difficult to extract (Pires, 1984; Mori and Prance, 1990). Without a disperser to  
 172 crack open the seed case, the Brazil nut seed experiences severely compromised germination  
 173 rates (Peres et al., 2003). The agouti, and in particular, the red-rumped agouti (*Dasyprocta*  
 174 *leporina*), is one of the most effective dispersal agents for the Brazil nut (Scoles and Gribel,  
 175 2012). Peres and Baider (1997) found that in the absence of agoutis, the mortality rate  
 176 for Brazil nut seeds was 100%. Both Brazil nuts and agoutis are harvested extensively,

177 contributing to local food intake and livelihoods. In the Brazilian Amazon, where the Brazil  
178 nut and the agouti are widely distributed, up to 8 million rural people may consume wild  
179 animals, and agoutis are among the most intensely exploited species (Peres, 2000; Thomas  
180 et al., 2015). Brazil nut harvests are also important to rural communities, contributing 14-  
181 43% of total household income for harvesters, measured in 12 communities in Bolivia and  
182 Brazil (Duchelle et al., 2011).

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

### 196 **2.3 Sensitivity Analysis**

197 Oftentimes, tropical systems where plants and animals are both harvested exhibit extreme  
198 data paucity and uncertainty. To evaluate the sensitivity of the model to its parameters,  
199 we performed global sensitivity analysis using the Fourier amplitude sensitivity test (FAST)  
200 method to estimate Sobol indices for the model parameters (Saltelli et al., 1999; Nossent  
201 et al., 2011). The Sobol index quantifies the contribution that any given parameter has on  
202 the variance of long-run plant and animal populations; that is, it quantifies how important  
203 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)
<b>P</b>	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 <sup>2</sup> )	Silvius and Fragoso (2003)
$K_a$	Maximum adult Brazil nut population size	20-150 (indiv/km <sup>2</sup> )	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.

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

## 211 3 Results

### 212 3.1 Population persistence under varying harvest and hunting regimes

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

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

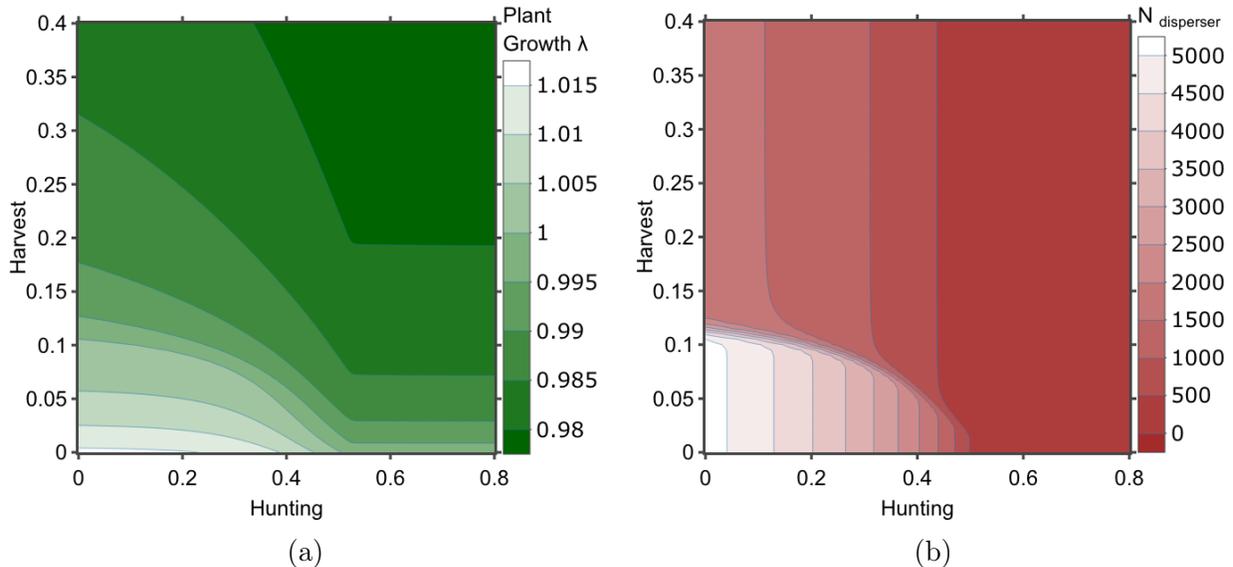


Figure 2: Agouti population size ( $N_{\text{disperser}}$ ) and the stochastic growth rate of Brazil nut (plant;  $\lambda$ ) under varying levels of harvesting and hunting. The simulation was run with the parameters in Table 1 as well as  $\delta_{d \rightarrow p} = 1$  and  $\delta_{p \rightarrow d} = 0.7$ . 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.

### 227 3.2 Sustainable Harvest-Hunting threshold level for plant-disperser 228 pair

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

238 We also observe a region of high sensitivity in the disperser population graph around  
239 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 ( $\lambda$ ) is  $\geq 1$ , 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).

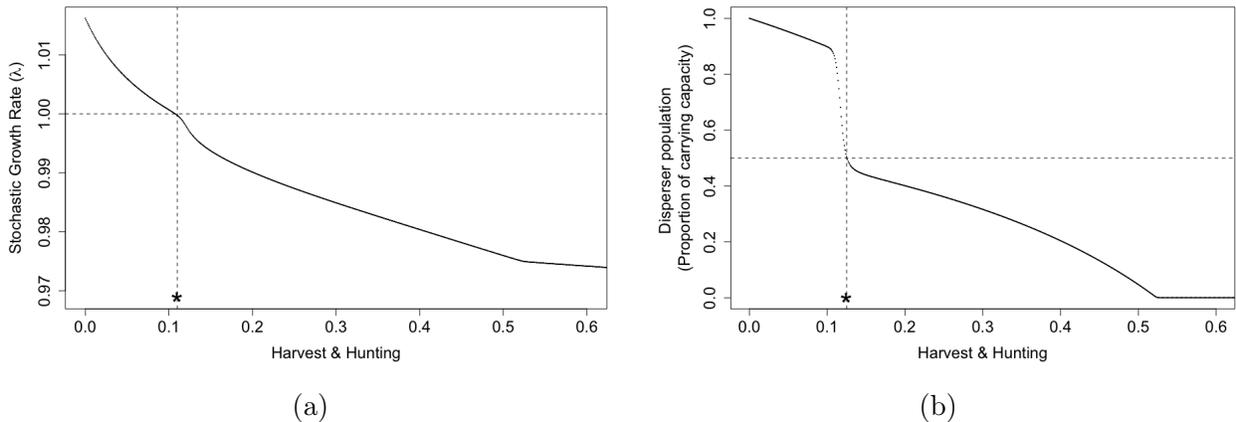


Figure 3: The impact of harvesting regimes (plant harvest and disperser hunting) on Brazil nut (a) and agouti populations (b). The x-axis on both graphs represents the harvest and hunting values: for the disperser,  $x$  is the proportion of animals taken, and for the plant,  $(1-x)$  is multiplied with 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

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

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

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

### 272 **3.4 Quantifying the impact of parameter uncertainty and parame-** 273 **ter importance**

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

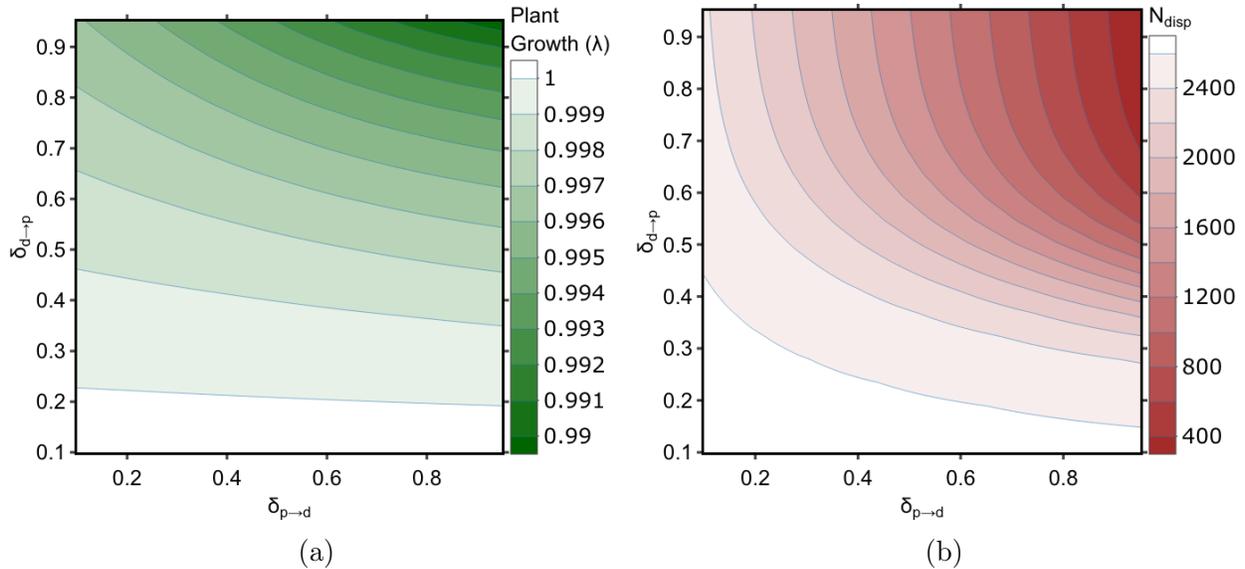


Figure 4: Stochastic growth rate of Brazil nut ( $\lambda$ ) and Agouti abundance ( $N_{\text{disp}}$ ) under varying strengths of coupling (represented by  $\delta_{d \rightarrow p}$ , reliance of Brazil nut on agouti, and  $\delta_{p \rightarrow d}$ , the impact of the Brazil nut on the agouti). The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

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

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

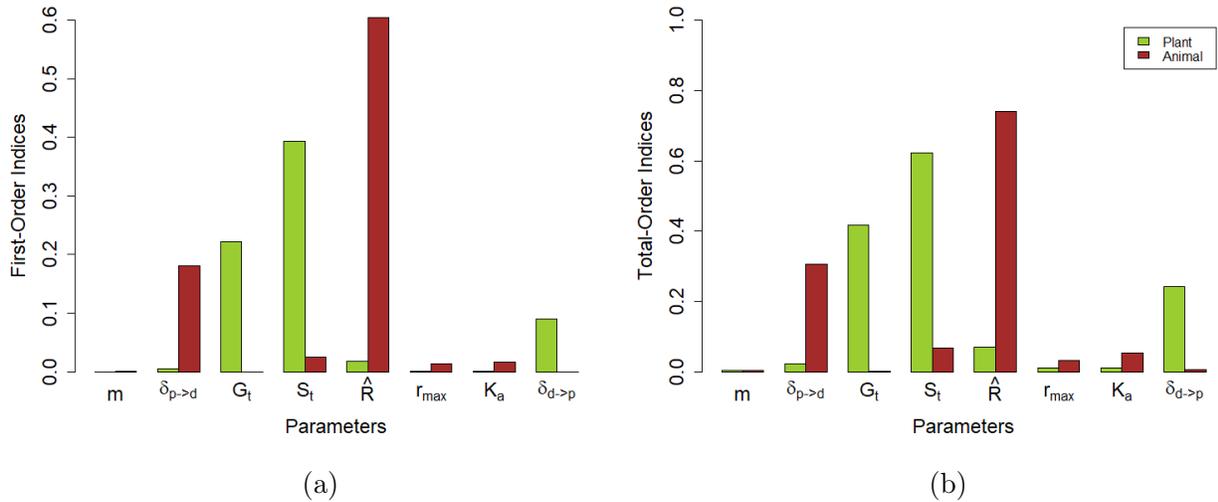


Figure 5: Sobol indices for each model parameter. Each bar shows the relative contribution of each parameter to the equilibrium Brazil nut and agouti population. The first order indices (a, left panel) indicate the impact of each parameter being varied when all other variables are held constant. The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

## 291 4 Discussion

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

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

304 on the agouti (Peres et al., 1997; Haugaasen et al., 2010). This prediction of our model aligns  
305 with empirical observations that suppressed agouti abundance due to hunting can severely  
306 disrupt Brazil nut recruitment and population persistence (Peres et al., 2003; Kainer et al.,  
307 2007). More generally, the loss of mammalian dispersers can cause recruitment failure and  
308 the collapse of biotically-dispersed tree populations (Jansen et al., 2012; Bello et al., 2015;  
309 Peres et al., 2016).

310 The global sensitivity analysis presented here can be used as a framework to determine  
311 the most sensitive parameters for prioritizing research and management effort. Our model  
312 indicates several key areas for future applied research on the Brazil nut and agouti. As  
313 adult survivorship under harvest and agouti hunting rate have the greatest impact on long-  
314 term sustainability, future researchers should carefully quantify these rates for prediction  
315 and management. Additionally, within any Brazil nut population, our model indicates that  
316 preserving adult trees should be a high priority, echoing previous findings (Peres et al., 2003;  
317 Kainer et al., 2007). Activities that substantially reduce adult survival, such as deep cuts  
318 in adult trees for harvesters to climb up and extract fruit, should be limited (Gaoue et al.,  
319 2011).

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

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

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

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

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

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

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

376 In conclusion, our model illustrates how to account for interacting species pairs when de-  
377 termining management decisions for harvested plants and dispersers in tropical systems. Our  
378 work shows that such an integrated approach identifies more conservative harvest thresholds  
379 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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