Modeling the impact of wild harvest on plant-disperser mutualisms

Plant and disperser co-harvest model

Kevin De Angeli
The Bredesen Center
University of Tennessee, Knoxville
kevindeangeli@utk.edu

Eeman Abbasi
Department of Biological Sciences
University of Pennsylvania, Philadelphia
eabbasi@sas.upenn.edu

Alan Gan
Department of Mathematics
University of Tennessee, Knoxville
a@utk.edu

Daniel J. Ingram
African Forest Ecology Group
Biological and Environmental Sciences
University of Stirling
Stirling, FK9 4LA, UK
daniel.ingram@stir.ac.uk

Xingli Giam
Department of Ecology & Evolutionary Biology
University of Tennessee, Knoxville
xgiam@utk.edu

Charlotte H. Chang
Environmental Analysis Program
Department of Biology
Pomona College
Claremont, CA, 91711
chchang@pomona.edu

December 4, 2020

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;

1

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 maximas*, Sekar and Sukumar 2013), and *Beilschmiedia assamica* and hornbills (e.g. *Aceros nipalensis*, Velho

2

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.
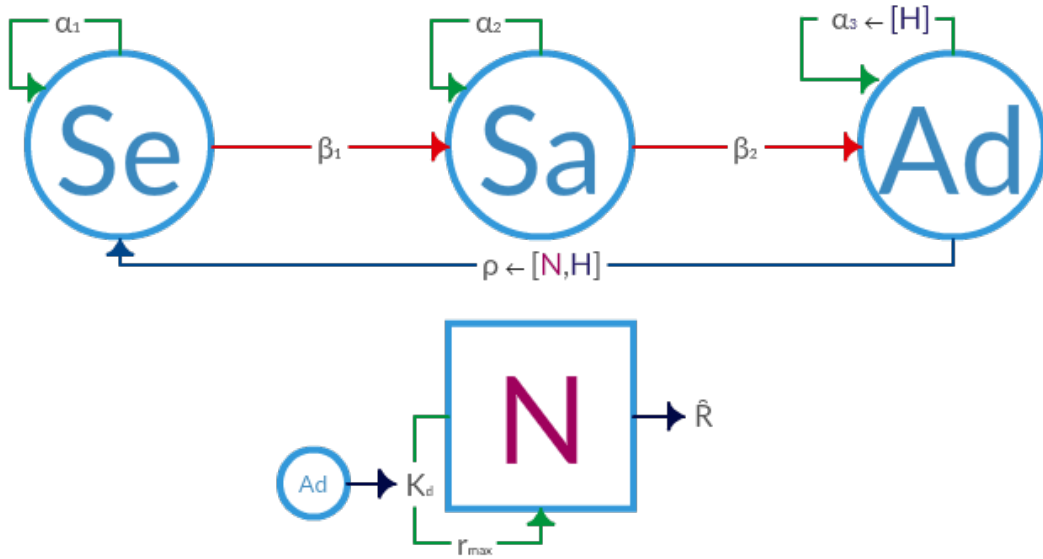

Figure 1: Population dynamics of plants and their seed dispersers in a harvesting regime. Compartments represent life stages (Se = seedlings, Sa = saplings and Ad = adult plants that contain both fruit/seed producing and non-producing mature plants). The α_i are the stage specific survival probabilities,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

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

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

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 $G_t, S_t \to 1$, then the system's maximal germination and/or adult survival rate is attained; conversely, when $G_t, S_t \to 0$, 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).

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

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

$$f(\mathbf{v_{a,t}}) \tag{3}$$

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

2.1 Functional forms relating plant-disperser interactions

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

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

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

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

6

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 δ 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. δ 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 δ terms to describe the impact of the plant population on the disperser

and that of the disperser on the plant. $\delta_{d \to p}$ represents the reliance of the plant on the seed disperser, and $\delta_{p \to d}$ 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).

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

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

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

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 14-43% 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 ($\delta_{d\to p}$, $\delta_{p\to d}$). Given our understanding of the high dependence of the Brazil nut trees on the agouti as the primary seed disperser, we assign $\delta_{d\to p} = 1$. However, the agouti is known to be a generalist seed disperser which can consume multiple food resources including Brazil nuts; thus we set $\delta_{p\to d} = 0.5$. 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)
$\delta_{p \to d}$	Reliance of agouti on Brazil nut	0.5 (or $\in [0, 1]$)	Peres et al. (1997)
$\delta_{d \to p}$	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.
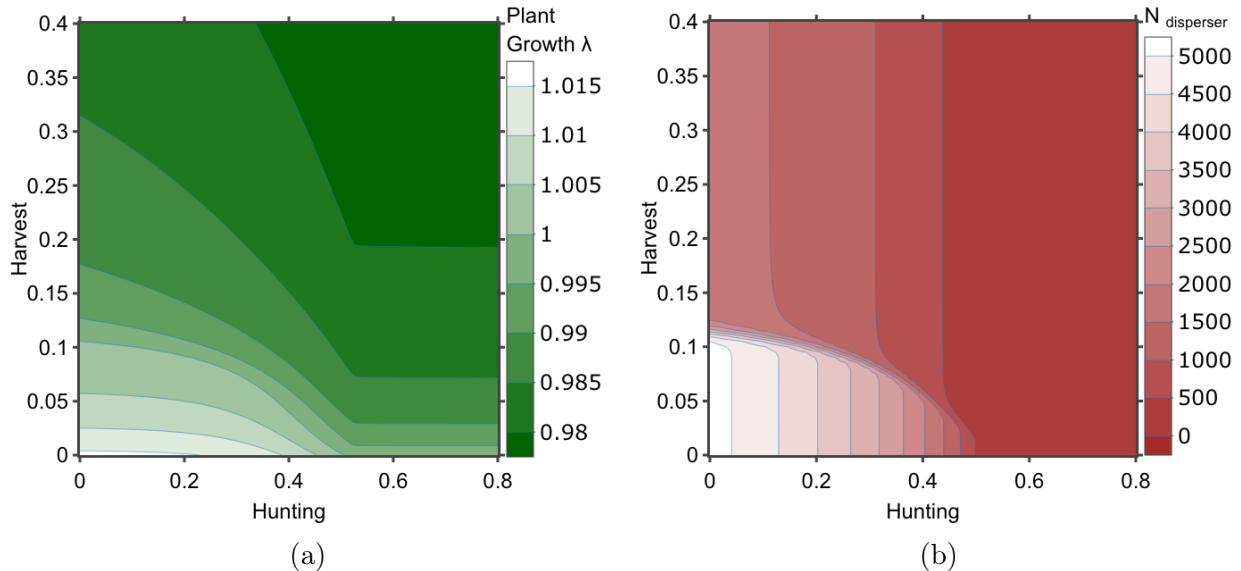
11

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 $\delta_{d \to p} = 1$ and $\delta_{p \to d} = 0.7$. 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

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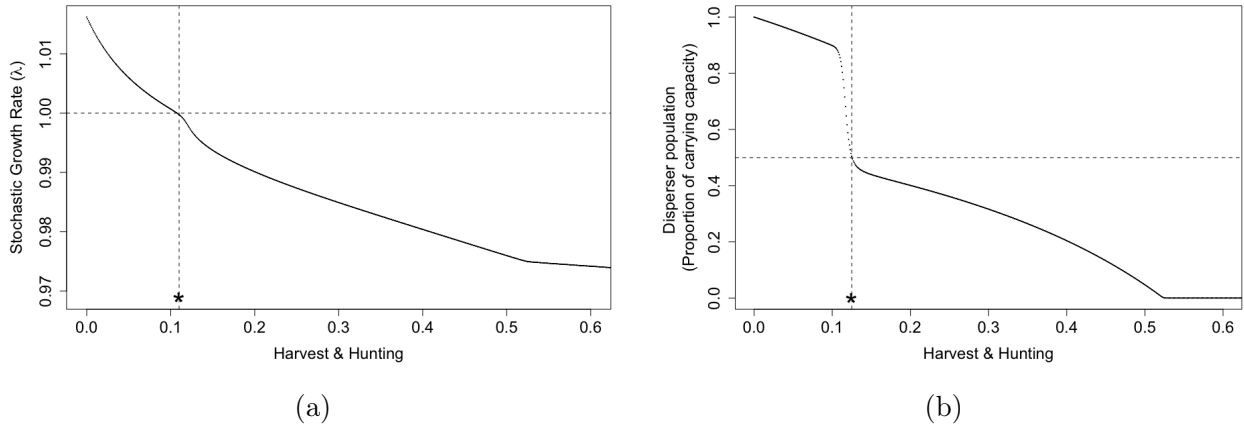

(a)

(b)

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, $\delta_{d \to p} = 1$, $\delta_{p \to d} = 0.5$. * represents the sustainable harvesting and hunting regimes corresponding to a persistent population.

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

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

13

254 a deleterious impact on both the Brazil nut λ and the long-run agouti abundance (N_{disp}),

255 even when $\delta_{p \to d}$ values were low. The effect of $\delta_{p \to d}$ on the agouti population was more

256 pronounced at moderate $\delta_{d \to p}$ values.

257   Conversely, the Brazil nut exhibited different dynamics based on its reliance on the agouti.

258 Under low levels of $\delta_{d \to p}$, the Brazil nut's growth rate remained relatively constant and high

259 across a wide range of interaction strengths (specifically, $\delta_{p \to d} \in [0, 1]$ when $\delta_{d \to p} \le 0.4$).

260 However, as $\delta_{d \to p}$ increased, we began to see interacting effects between $\delta_{p \to d}$ and $\delta_{d \to p}$ on

261 the population growth rate of the Brazil nut.

262   The plant growth rate was primarily affected by $\delta_{d \to p}$, with $\delta_{p \to d}$ mostly impacting plant

263 growth during high values of $\delta_{d \to p}$. This was not the case for the seed disperser's population

264 which showed a more non-linear pattern. The combined effect of $\delta_{d \to p}$ and $\delta_{p \to d}$ 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 $\delta_{d \to p}$ 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).

3.4 Quantifying the impact of parameter uncertainty and parameter 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), $\delta_{d \to p}$ (reliance of the Brazil nut

279 on the agouti), and $\hat{R}_t$ (the agouti hunting rate). For the agouti, while the hunting rate

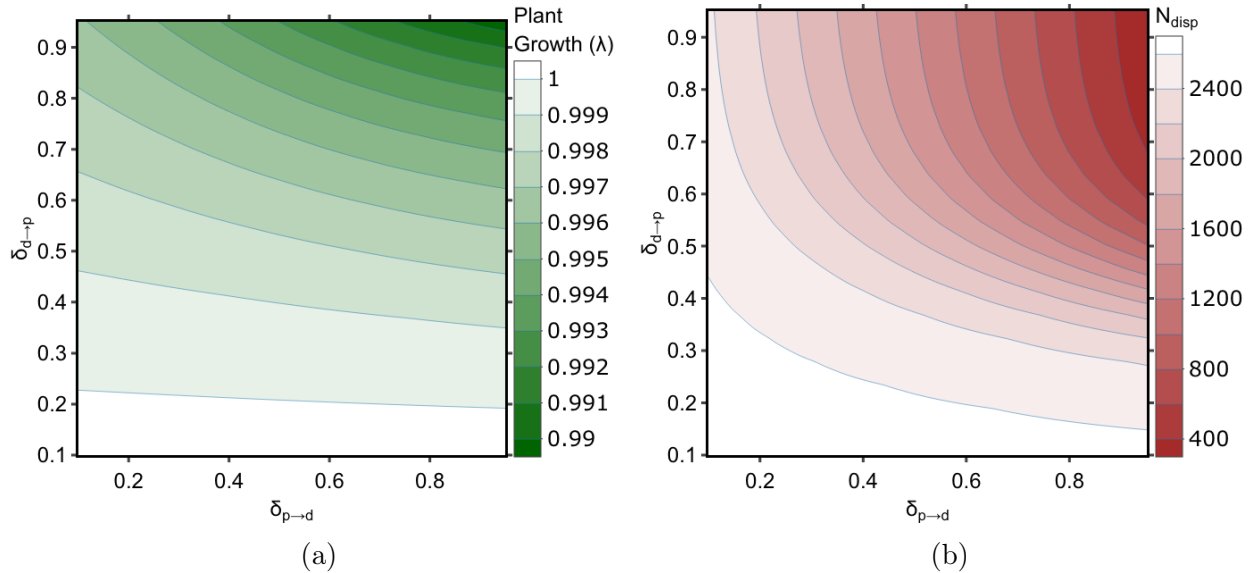280 ($\hat{R}_t$) was generally the most critical variable, the reliance of the agouti on the Brazil nut

Figure 4: Stochastic growth rate of Brazil nut(λ) and Agouti abundance (N_{disp}) under varying strengths of coupling (represented by $\delta_{d\to p}$, reliance of Brazil nut on agouti, and $\delta_{p\to d}$, 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 $\hat{R}_t = 0.35$.

281 $(\delta_{p\to d})$ 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 $(\delta_{d\to p})$ were impor-

286 tant factors. We observed that $\delta_{d\to p}$ 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 $\delta_{d\to p}$ have a much greater effect on long-run plant population when coupled with

289 changes in all other parameters, indicating that $\delta_{d\to p}$ interacts strongly with other parame-
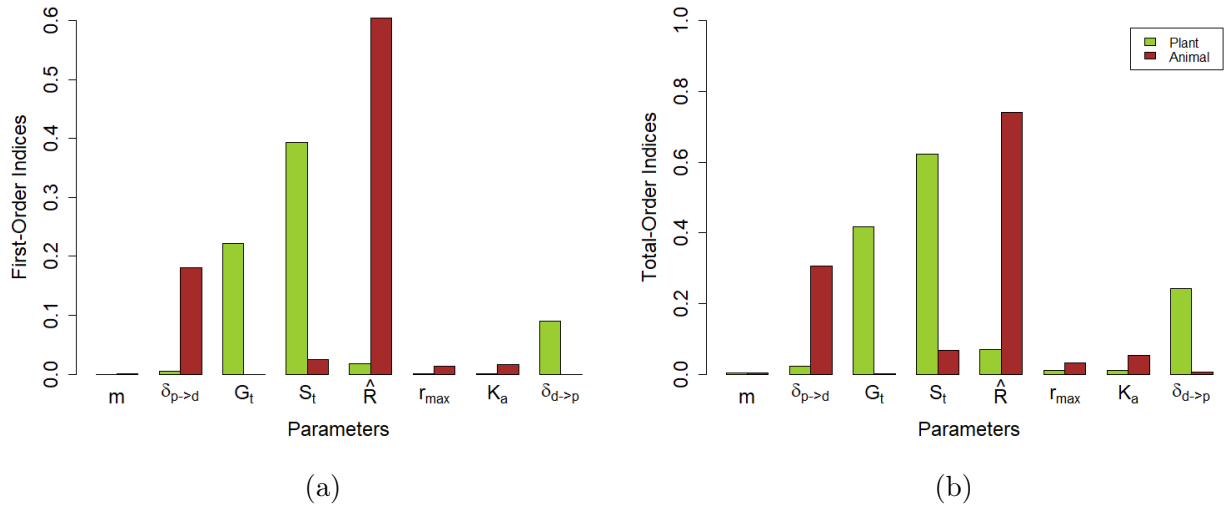
290 ters. (Figure 5; total-order index).

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.

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

17

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.

5   Acknowledgments

Wiggins for helpful comments and guidance.

6 Competing Interests

The authors declare no conflicts of interest.

7 Code Availability

Github - `https://github.com/TheAlanGan/HuntHarvest`

References

Allen, L. J. (1989). A density-dependent leslie matrix model. *Mathematical Biosciences*, 95(2):179 – 187.

Baskett, M. L., Micheli, F., and Levin, S. A. (2007). Designing marine reserves for interacting species: insights from theory. *Biological conservation*, 137(2):163–179.

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., and Fruth, B. (2013). Seed dispersal strategies and the threat of defaunation in a congo forest. *Biodiversity and Conservation*, 22(1):225–238.

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A., Peres, C. A., Ovaskainen, O., and Jordano, P. (2015). Defaunation affects carbon storage in tropical forests. *Science advances*, 1(11):e1501105.

Benítez-López, A., Alkemade, R., Schipper, A. M., Ingram, D. J., Verweij, P. A., Eikelboom, J. A. J., and Huijbregts, M. A. J. (2017). The impact of hunting on tropical mammal and bird populations. *Science*, 356(6334):180–183.

Caughlin, T. T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S., and Levey, D. J. (2015). Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proceedings of the Royal Society B: Biological Sciences*, 282(1798):20142095.

Damania, R., Stringer, R., Karanth, K. U., and Stith, B. (2003). The economics of protecting tiger populations: linking household behavior to poaching and prey depletion. *Land Economics*, 79(2):198.

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345(6195):401–406.

Duchelle, A. E., Cronkleton, P., Kainer, K. A., Guanacoma, G., and Gezan, S. (2011). Resource theft in tropical forest communities: implications for non-timber management, livelihoods, and conservation. *Ecology and Society*, 16(1):4.

Fa, J. E., Peres, C. A., and Meeuwig, J. (2002). Bushmeat Exploitation in Tropical Forests: an Intercontinental Comparison. *Conservation Biology*, 16(1):232–237.

FAO (2019). The State of the World's Biodiversity for Food and Agriculture. Technical report.

Galetti, M., Donatti, C. I., Pires, A. S., Guimarães Jr, P. R., and Jordano, P. (2006). Seed survival and dispersal of an endemic atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society*, 151(1):141–149.

Gaoue, O., Horvitz, C., and Ticktin, T. (2011). Non-timber forest product harvest in variable environments: Modeling the effect of harvesting as a stochastic sequence. *Ecological Applications*, 21:1604–16.

Gaoue, O. G. (2016). Transient dynamics reveal the importance of early life survival to the response of a tropical tree to harvest. *Journal of Applied Ecology*, 53(1):112–119.

Gaoue, O. G. and Ticktin, T. (2007). Patterns of harvesting foliage and bark from the multipurpose tree khaya senegalensis in benin: variation across ecological regions and its impacts on population structure. *Biological conservation*, 137(3):424–436.

Gaoue, O. G. and Ticktin, T. (2010). Effects of harvest of nontimber forest products and ecological differences between sites on the demography of african mahogany. *Conservation Biology*, 24(2):605–614.

García, N., Zuidema, P. A., Galeano, G., and Bernal, R. (2016). Demography and sustainable management of two fiber-producing astrocaryum palms in Colombia. *Biotropica*, 48(5):598–607.

Golden, C. D., Fernald, L. C., Brashares, J. S., Rasolofoniaina, B. R., and Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proceedings of the National Academy of Sciences*, 108(49):19653–19656.

Granados, A., Brodie, J. F., Bernard, H., and O'Brien, M. J. (2017). Defaunation and habitat disturbance interact synergistically to alter seedling recruitment. *Ecological applications*, 27(7):2092–2101.

Guedje, N. M., Zuidema, P. A., During, H., Foahom, B., and Lejoly, J. (2007). Tree bark as a non-timber forest product: The effect of bark collection on population structure and dynamics of garcinia lucida vesque. *Forest ecology and management*, 240(1-3):1–12.

Haugaasen, J. M. T., Haugaasen, T., Peres, C. A., Gribel, R., and Wegge, P. (2010). Seed dispersal of the brazil nut tree (Bertholletia Excelsa) by scatter-hoarding rodents in a central amazonian forest. *Journal of Tropical Ecology*, 26(3):251–262.

Hill, K. and Padwe, J. (2000). Sustainability of Aché hunting in the Mbaracayu reserve, Paraguay. In Robinson, J. and Bennett, E. L., editors, *Hunting for sustainability in tropical forests*, chapter 5, pages 79–105. Columbia University Press, New York.

Iooss, B. and Janon, A. (2019). *sensitivity: Global Sensitivity Analysis of Model Outputs*. R package version 1.16.1.

Iooss, B. and Lemaître, P. (2015). A review on global sensitivity analysis methods. In *Uncertainty management in simulation-optimization of complex systems*, pages 101–122. Springer.

Jansen, P. A., Hirsch, B. T., Emsens, W.-J., Zamora-Gutierrez, V., Wikelski, M., and Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences*, 109(31):12610–12615.

Kainer, K. A., Wadt, L. H., and Staudhammer, C. L. (2007). Explaining variation in brazil nut fruit production. *Forest Ecology and Management*, 250(3):244–255.

Kellner, J. B., Sanchirico, J. N., Hastings, A., and Mumby, P. J. (2011). Optimizing for multiple species and multiple values: tradeoffs inherent in ecosystem-based fisheries management. *Conservation Letters*, 4(1):21–30.

Levi, T., Shepard, G. H., Ohl-Schacherer, J., Wilmers, C. C., Peres, C. A., and Yu, D. W. (2011). Spatial tools for modeling the sustainability of subsistence hunting in tropical forests. *Ecological Applications*, 21(5):1802–1818.

Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., Wright,

S. J., and Böhning-Gaese, K. (2012). Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation biology*, 26(6):1072–1081.

Milner-Gulland, E. J. and Bennett, E. L. (2003). Wild meat: the bigger picture. *Trends in Ecology & Evolution*, 18(7):351–357.

Morales, M. A., Inouye, D. W., Leigh, M. J., and Lowe, G. (2003). *Considering Interactions: Incorporating Biotic Interactions into Viability Assessment*, pages 267–287. Springer Berlin Heidelberg, Berlin, Heidelberg.

Mori, S. and Prance, G. (1990). Taxonomy, ecology and economic botany of the Brazil nut (*Bertholletia Excelsa Humb.* & Bonpl.:Lecythidaceae). 8:130–150.

Muller-Landau, H. C. (2007). Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. *Biotropica*, 39(3):372–384.

Nielsen, M. R., Meilby, H., Smith-Hall, C., Pouliot, M., and Treue, T. (2018). The importance of wild meat in the global south. *Ecological economics*, 146:696–705.

Nossent, J., Elsen, P., and Bauwens, W. (2011). Sobol sensitivity analysis of a complex environmental model. *Environmental Modelling & Software*, 26(12):1515–1525.

Osuri, A. M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Astaiza, J. H., Bradford, M., Fletcher, C., Ndoundou-Hockemba, M., Jansen, P. A., Kenfack, D., et al. (2016). Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature communications*, 7:11351.

Peres, C., Schiesari, L., and Leme, C. (1997). Vertebrate predation of Brazil-nuts (*Bertholletia Excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: A test of the escape hypothesis. 13:69 – 79.

Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in amazonian forests. *Conservation Biology*, 14(1):240–253.

Peres, C. A. and Baider, C. (1997). Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia Excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology*, 13(4):595–616.

Peres, C. A., Baider, C., Zuidema, P. A., Wadt, L. H., Kainer, K. A., Gomes-Silva, D. A., Salomão, R. P., Simões, L. L., Franciosi, E. R., Valverde, F. C., et al. (2003). Demographic threats to the sustainability of brazil nut exploitation. *Science*, 302(5653):2112–2114.

Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J., and Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted amazonian forests. *Proceedings of the National Academy of Sciences*, 113(4):892–897.

Pires, J. (1984). The amazonian forest. in the amazon: limnology and landscape ecology of a mighty tropical river and its basin. pages 581–602.

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., and Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, (1):e1400103.

Robinson, J. and Bennett, E. (2000). Carrying capacity limits to sustainable hunting in tropical forests. In *Hunting for sustainability in tropical forests*, pages 13–30.

Robinson, J. G. and Redford, K. H. (1986). Body size, diet, and population density of neotropical forest mammals. *The American Naturalist*, 128(5):665–680.

Rowcliffe, J. M., de Merode, E., and Cowlishaw, G. (2004). Do wildlife laws work? Species protection and the application of a prey choice model to poaching decisions. *Proceedings of the Royal Society B Biological Sciences*, 271(1557):2631–2636.

Saltelli, A., Tarantola, S., and Chan, K.-S. (1999). A quantitative model-independent method for global sensitivity analysis of model output. *Technometrics*, 41(1):39–56.

Samhouri, J. F., Stier, A. C., Hennessey, S. M., Novak, M., Halpern, B. S., and Levin, P. S. (2017). Rapid and direct recoveries of predators and prey through synchronized ecosystem management. *Nature ecology & evolution*, 1(4):0068.

Schmidt, I. B., Mandle, L., Ticktin, T., and Gaoue, O. G. (2011). What do matrix population models reveal about the sustainability of non-timber forest product harvest? *Journal of Applied Ecology*, 48(4):815–826.

Scoles, R. and Gribel, R. (2012). The regeneration of brazil nut trees in relation to nut harvest intensity in the trombetas river valley of northern amazonia, brazil. *Forest Ecology and Management*, 265:71–81.

Sekar, N. and Sukumar, R. (2013). Waiting for gajah: an elephant mutualist's contingency plan for an endangered megafaunal disperser. *Journal of Ecology*, 101(6):1379–1388.

Sibly, R. M. and Hone, J. (2002). Population growth rate and its determinants: an overview. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 357 1425:1153–70.

Silvius, K. M. and Fragoso, J. M. V. (2003). Red-rumped agouti (*Dasyprocta Leporina*) home range use in an amazonian forest: Implications for the aggregated distribution of forest trees. *Biotropica*, pages 74–83.

Sirén, A. H., Hamback, P., Machoa, J., Sirén, A., Hambäck, P., Machoa, J., Siren, A. H., Hamback, P., and Machoa, J. (2004). Including Spatial Heterogeneity and Animal Dispersal When Evaluating Hunting: a Model Analysis and an Empirical Assessment in an Amazonian Community. *Conservation Biology*, 18(5):1315–1329.

Soulé, M. E., Estes, J. A., Miller, B., and Honnold, D. L. (2005). Strongly Interacting Species: Conservation Policy, Management, and Ethics. *BioScience*, 55(2):168–176.

Terborgh, J., Lopez, L., Nuñez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D., et al. (2001). Ecological meltdown in predator-free forest fragments. *Science*, 294(5548):1923–1926.

Thomas, E., Alcázar Caicedo, C., McMichael, C. H., Corvera, R., and Loo, J. (2015). Uncovering spatial patterns in the natural and human history of Brazil nut (*Bertholletia Excelsa*) across the Amazon Basin. *Journal of Biogeography*, 42(8):1367–1382.

Ticktin, T. (2004). The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology*, 41(1):11–21.

Velho, N., Datta, A., and Isvaran, K. (2009). Effect of rodents on seed fate of five hornbill-

dispersed tree species in a tropical forest in north-east india. *Journal of Tropical Ecology*, 25(5):507–514.

Wacker, H. (1999). Optimal harvesting of mutualistic ecological systems. *Resource and Energy Economics*, 21(1):89–102.

Wadt, L., Kainer, K., Staudhammer, C., and Serrano, R. (2008). Sustainable forest use in Brazilian extractive reserves: natural regeneration of Brazil nut in exploited populations. *Biological Conservation*, 141(1):332–346.

Weinbaum, K. Z., Brashares, J. S., Golden, C. D., and Getz, W. M. (2013). Searching for sustainability: are assessments of wildlife harvests behind the times? *Ecology Letters*, 16(1):99–111.

Wootton, J. T. and Emmerson, M. (2005). Measurement of interaction strength in nature. *Annu. Rev. Ecol. Evol. Syst.*, 36:419–444.

Young, H. S., McCauley, D. J., Galetti, M., and Dirzo, R. (2016). Patterns, causes, and consequences of anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, 47(1):333–358.

Zuidema, P. A. (2000). *Demography of Exploited Tree Species in the Bolivian Amazon.* PhD thesis, Utrecht University and PROMAB, Department of Plant Ecology, Utrecht University, PO Box 80084, 3508 TB Utrecht, the Netherlands.

Zuidema, P. A. and Boot, R. G. (2002). Demography of the brazil nut tree (*Bertholletia Excelsa*) in the bolivian amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology*, 18(1):1–31.