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ORIGINAL PAPER

Optimal harvesting strategies for timber and non-timber forest products in tropical ecosystems

Orou G. Gaoue[1,2] · Jiang Jiang[3] · Wandi Ding[4] · Folashade B. Agusto[5] · Suzanne Lenhart[3]

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Abstract Harvesting wild plants for non-timber forest products (NTFPs) can be ecologically sustainable–without long-term consequences to the dynamics of targeted and associated species–but it may not be economically satisfying because it fails to provide enough revenues for local people over time. In several cases, the same species can be harvested for NTFP and also logged for timber. Three decades of studies on the sustainability of NTFP harvest for local people's livelihood have failed to successfully integrate these socio-economic and ecological factors. We apply optimal control theory to investigate optimal strategies for the combinations of non-lethal (e.g., NTFP) and lethal (e.g., timber) harvest that minimize the cost of harvesting while maximizing the benefits (revenue) that accrue to harvesters and the conservation value of harvested ecosystems. Optimal harvesting strategies include starting with non-lethal NTFP harvest and postponing lethal timber harvesting to begin after a few years. We clearly demonstrate that slow growth species have lower optimal harvesting rates, objective functional values and profits than fast growth species. However, contrary to expectation, the effect of species lifespan on optimal harvesting rates was weak suggesting that life history is a better indicator of species resilience to harvest than lifespan. Overall, lethal or nonlethal harvest rates must be <40 % to ensure optimality. This optimal rate is lower than commonly reported sustainable harvest rates for non-timber forest products.

Keywords Differential equations model · Harvest model · Life history · Lifespan · Non-timber forest products · Optimal control theory · Sustainable timber harvest

Introduction

Identifying sustainable harvest limits for renewable resources and how these limits are constrained by socio-economic and environmental factors represent some of the most debated issues in conservation biology. Non-timber forest products (NTFPs) such as fruits, leaves, and resins are increasingly harvested from wild populations as source of food and medicine to local people worldwide and are part of a growing interest from pharmaceutical firms (Bawa et al. 2004). Harvesting NTFP provides a range of benefits for local people and can contribute to poverty alleviation (Shackleton and Shackleton 2004; Shackleton et al. 2011). In developing countries, more than 80 % of the population relies on medicinal plants for primary healthcare (Hamilton 2004), and 72,000 species of medicinal plants are used regularly by local people with 3000 species as part of the international trade (Schippmann et al. 2003, 2006). During the dry season when agricultural products are scarce and herbaceous pasture burned, several fruits are harvested for

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✉ Orou G. Gaoue
ogaoue@hawaii.edu

[1] Department of Botany, University of Hawaii at Manoa, Honolulu, HI 96822, USA

[2] Universite de Parakou, 123, Parakou, Benin

[3] National Institute for Mathematical and Biological Synthesis, University of Tennessee, Knoxville, TN 37996, USA

[4] Department of Mathematical Sciences and Computational Science Program, Middle Tennessee State University, Murfreesboro, TN 37132, USA

[5] Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

direct consumption, and tree foliage is harvested to feed cattle (Emanuel et al. 2005; Avocevou Ayisso et al. 2009; Gaoue and Ticktin 2010). The NTFP market is estimated at more than US$90 billion (Pimentel et al. 1997). From an economic perspective, NTFP harvesting provides revenue to families who collect these products directly from the forest, and even higher net margins for bundlers and industries at the top of the value chain. However, harvesting comes with a huge ecological cost in some cases (Schmidt et al. 2011; Ticktin 2015).

Several plant species are harvested too frequently and at very high intensity such that they are threatened with extinction (Hall and Bawa 1993; Peres et al. 2003; Silvertown 2004; Potts and Vincent 2008; van Andel and Havinga 2008). For example, *Prunus africana* is a tree whose bark is harvested in Central and Southern Africa to treat prostatic hypertrophy. As a consequence of overharvesting, multiple populations of this tropical tree are extinct (Cunningham and Mbenkum 1993). Brazil nuts have been harvested for decades (Silvertown 2004) and in some parts of South America, populations of *Bertholletia excelsa* are declining as a result of chronic fruit harvest (Peres et al. 2003). Recent reviews of the ecological impact of NTFP harvest suggest that most species are facing decline as a consequence of harvesting (Schmidt et al. 2011; Ticktin 2004). In most cases, harvesting NTFP (non-lethal) does not lead to the death of harvested individuals. For several NTFP plants, local people remove fruits, bark, and leaves from standing plants. For example, harvesting Brazil nuts (Zuidema and Boot 2002) or fruits from *Sclerocarya birrea* (Emanuel et al. 2005) does not involve cutting down harvested trees. However, for some NTFP harvesting such as Amla fruits from *Phyllantus emblica* in India (Ticktin et al. 2012), or Gaharu, a fragrant resinous wood, from *Aquilaria* spp. in Indonesia (Soehartono and Newton 2001), individuals plants could be cut down prior to harvesting these NTFP. For *P. africana*, some harvesters girdle trees to maximize the amount of bark they harvest from each trees and this leads to the death of individual trees (Stewart 2009). Nearly 28 % of the 188 medicinal plants species surveyed in Suriname were harvested lethally (van Andel and Havinga 2008).

Although most studies on the sustainability of forest resources harvest considered either NTFP or timber harvesting, in reality, several species in tropical ecosystems are often harvested both for timber and non-timber forest products (van Andel and Havinga 2008; Guariguata et al. 2009, 2010; Klimas et al. 2012b; Rist et al. 2012; Grogan et al. 2014). Guariguata et al. (2010) in an extensive review provides evidence for several cases of combined timber and non-timber forest products harvest on the same species or the same forest. For example, more than half of the main timber species harvested in Cameroon (e.g., *Triplochiton scleroxylon*, *Entandrophragma cylindricum* and *Milicia excelsa*) are also harvested for medicinal and food purposes (Ndoye and Tieguhong 2004). Similarly, in Benin, most of the fodder tree species (e.g., *Khaya senegalensis*, *Afzelia africana*, *Pterocarpus erinaceus*) whose foliage are repeatedly harvested by local people to feed cattle during the dry season are also the main timber tree species (Gaoue and Ticktin 2007, 2009). In Brazil, *Carapa guianensis* is valuable for its NTFP (for its seeds which produce prized oils) and also for its timber (Klimas et al. 2012a).

Studies on the sustainability of NTFP or timber harvest have developed independently, and even within the literature on NTFP harvest, there are two parallel sets of studies. While NTFP harvest studies are rarely concerned with optimal harvesting strategies, early studies on timber harvest focused on determining the optimal harvesting rotation or age (Hardie et al. 1984; Plantinga 1998; Chang 1998), and on the effects of price fluctuation on optimal harvesting strategies (Newman et al. 1985; Brazee and Mendelsohn 1988). On the other hand, studies on the sustainability of NTFP harvest have historically been divided into two categories. A first set of studies focus on the socio-economic sustainability of harvesting. There is an extensive body of work on the role that NTFP harvesting plays in alleviating (or not) poverty (Cosyns et al. 2011; Shackleton and Pandey 2014; Shackleton and Shackleton 2004), on the value of NTFP and on the average revenues that accrue to local collectors of NTFP (Klimas et al. 2012b; Godoy et al. 2000; Gopalakrishnan et al. 2005; Vodouhê et al. 2009). A second set of studies focus on ecological sustainability of harvest and use matrix projection models (Caswell 2001) to estimate the long-term population growth rate, λ, (the dominant eigenvalue) and used simulations to identify sustainable NTFP harvesting thresholds (Bernal 1998; Ticktin et al. 2002, 2012; Zuidema et al. 2007; Gaoue et al. 2011; Mondragon and Ticktin 2011; Klimas et al. 2012a). Unfortunately, these two lines of research on the sustainability of NTFP exploitation by local people have also evolved independently and understanding the socio-economic and ecological sustainability of such activities remains elusive (for a broader discussion see Armsworth et al. 2010). Hernandez Barrios et al. (2015), in an attempt to combine both ecological and economic data to define sustainable leaf harvest, focused on maximizing the economic profit under the constraint that survival and growth of individuals are not significantly reduced. Macpherson et al. (2012) also utilized a similar approach, where economic data are used to update the outcome from an ecological model. Although these approaches are valid, they fail to directly integrate costs and benefits with the conservation value of the remaining stands.

Here, we use for the first time, optimal control theory to investigate sustainable harvest strategies for non-timber as well as timber forest product species. Optimal control theory for differential equations gives a way to choose time-dependent management actions (controls) to achieve a goal (Pontryagin et al. 1962), and this has been used for different types of management strategies (Fister et al. 1998; Miller Neilan et al. 2010; Clark 2010). We investigate how species lifespan, life history, and targeted conservation goals affect optimal harvesting strategies over a management time period. We ask if combined timber and NTFP harvest is economically and ecologically sustainable and when should harvesting start? We hypothesize that slow growth and long-lived species would have lower optimal harvest intensity for both timber and NTFP than fast growth or short-lived species.

Model and optimal control analysis

Model

Gaoue et al. (2015) developed and studied a new harvest model, which incorporates constant non-lethal and lethal harvesting efforts with additional synergistic effects on plant population growth rate. They demonstrated that the sustainability of lethal and non-lethal harvest depends on the demographic cost of each type of harvest on population growth rate. Our system of ordinary differential equations has two states, $x(t)$, the density of a plant species and $r(t)$, the intrinsic growth rate of the plant. The plant species x has logistic growth with a carrying capacity K. The model incorporates both non-lethal and lethal effects of harvesting. In addition to the direct effects of plant removal caused by lethal harvest, we assume that both lethal, $h_L(t)$, and non-lethal harvest, $h_N(t)$, would alter (indirect effects) the growth rate of the remaining individuals. To account for the direct and indirect effects of harvesting, we model the intrinsic growth rate $r(t)$, as a function of both non-lethal $h_N(t)$ and lethal harvest $h_L(t)$. The dynamics of $r(t)$ occurs at a time scale that is different from that of the population density, because effects of harvest on population growth rate require a generation to affect offspring. We add a parameter τ that represents the average lifespan of the plant species; for example, $\tau = 1$ is for annual plants.

$$\frac{dx(t)}{dt} = r(t)x(t)\left(1 - \frac{x(t)}{K}\right) - h_L(t)x(t), \tag{1}$$

$$\tau\frac{dr(t)}{dt} = r_e - r(t) - (\alpha h_N(t) + \beta h_L(t)), \tag{2}$$

with initial conditions

$$x(0) = x_0,\ r(0) = r_e, \tag{3}$$

where r_e is the maximum growth rate (under given environmental conditions) in the absence of harvest and competition between individuals, α accounts for the rate of population decay due to non-lethal harvest (e.g., harvest of foliage, fruits, bark), and β is the rate of population decay due to lethal harvest (e.g., logging). The model parameters are defined in Table 1. Gaoue et al. (2015) showed that when $\mathcal{R} > 1$, where $\mathcal{R} = \frac{r_e}{\alpha h_N + (1+\beta)h_L}$, the system (1–2) with constant harvest rates has a globally and asymptotically stable non-trivial positive equilibrium solution,

$$x^* = \frac{K(\alpha h_N + (1+\beta)h_L)}{r_e - \alpha h_N - \beta h_L}(\mathcal{R} - 1),\ r^* = r_e.$$

In contrast, when $\mathcal{R} \le 1$, only a trivial equilibrium exists and it is globally and asymptotically stable.

Optimal control formulation

In this section, we consider optimal control of the system (1–2). The cost associated with non-timber forest products harvesting by indigenous people is often negligible, but does include their time spent on this work and the cost of small equipment such as machetes, hoes, and baskets to carry the products. Our goal is to maximize both the revenue benefits that accrue to local population and also the conservation benefit of maintaining the size of the plant population, while minimizing the nonlinear cost of harvesting for timber and non-timber forest products. The control functions h_L and h_N represent lethal and non-lethal harvesting. Our goal is to find an optimal control pair, h_L and h_N, in order to maximize the objective functional J where

$$\begin{aligned} J(h_L, h_N) = A_T x(T) + \int_0^T e^{-\delta t}\Big(Ax(t) + B_1 h_L(t)x(t) \\ + B_2 h_N(t)x(t) - C_1 h_L^2(t) - C_2 h_N^2(t)\Big)\,dt. \end{aligned} \tag{4}$$

The coefficients B_1 and B_2 represent prices from the two types of harvest, and thus terms with $B_1 h_L(t)x(t) + B_2 h_N(t)x(t)$ give the corresponding revenue. The weight coefficient A balances the relative importance of conservation of species x. To account for the conservation value of the plants at the end of the harvest, a term $A_T x(T)$ is also considered. The quadratic terms with the controls give the costs of harvesting, which is expected to be nonlinear. We used the quadratic form for simplicity. The coefficient $e^{-\delta t}$ is the discount factor. The overall profit from harvesting is $P = \int_0^T e^{-\delta t}[B_1 h_L(t)x(t) + B_2 h_N(t)x(t) - C_1 h_L^2(t) - C_2 h_N^2(t)]$. The control set of bounded Lebesque measurable functions is

$$\mathcal{U} = \{(h_L, h_N) \in (L^\infty(0,T))^2 : 0 \le h_L \le M_1,\\ 0 \le h_N \le M_2,\ 0 \le t \le T\},$$

with M_1, M_2 being the upper bounds of the harvesting rates. This state system, with Lebesque measurable coefficients, has a unique non-negative bounded solution on the finite

Table 1 Notation for the model and optimal control

	Values	Definition
$x(t)$	–	Density of plant species at time t
x_0	80	Initial population density at $t = 0$
$r(t)$	–	Intrinsic rate of $x(t)$ at time t
K	100	Carrying capacity for the plant
$h_N(t)$	–	Rate of non-lethal harvest at time t
$h_L(t)$	–	Rate of lethal harvest at time t
r_e	0.03, 0.25	Maximum growth rate without harvest
τ	1, 20	Average lifespan of the plant in years
α	0.4	Growth decay rate for nonlethal harvest
β	0.23	Growth decay rate due to lethal harvest
A	–	Weight for the value of conservation
δ	0.05	Discount rate
B_1	0.3	Benefit from non-lethal harvest
B_2	0.15	Benefit from lethal harvest
C_1	15	Cost coefficient of non-lethal harvest
C_2	15	Cost coefficient of lethal harvesting
M_1	1	Upper bound for nonlethal harvest rate
M_2	0.7	Upper bound for lethal harvest rate

time interval $[0, T]$ (Lukes 1982). Note for this system, the control set and the objective functional have the appropriate compactness and convexity assumptions to guarantee the existence of an optimal control pair and the corresponding states (Lenhart and Workman 2007; Fleming and Rishel 1975). Having the existence of an optimal control, we can now apply Pontryagin's Maximum Principle to obtain a characterization of the optimal control (Pontryagin et al. 1962). To construct the necessary conditions that an optimal control pair must satisfy, we use the Hamiltonian H:

$$\begin{aligned} H &= e^{-\delta t}\Big[Ax(t) + B_1 h_L(t)x(t) + B_2 h_N(t)x(t) \\ &\quad - \left(C_1 h_L^2(t) + C_2 h_N^2(t)\right)\Big] \\ &\quad + \lambda_x \left[r(t)x(t)\left(1 - \frac{x(t)}{K}\right) - h_L(t)x(t)\right] \\ &\quad + \frac{\lambda_r}{\tau}\left[r_e - r(t) - (\alpha h_N(t) + \beta h_L(t))\right]. \end{aligned}$$

Given an optimal control pair $(h_L^*(t), h_N^*(t))$ and the corresponding states x^*, r^*, Pontryagin's Maximum Principle (Pontryagin et al. 1962) gives the system satisfied by the adjoint functions λ_x, λ_r:

$$\begin{aligned} \lambda_x' = -\frac{\partial H}{\partial x} &= -e^{-\delta t}\left(A + B_1 h_L^*(t) + B_2 h_N^*(t)\right) \\ &\quad -\lambda_x\left[r^*(t) - \frac{2r^*(t)x^*(t)}{K} - h_L^*(t)\right], \qquad (5) \\ \lambda_r' = -\frac{\partial H}{\partial r} &= -\lambda_x x^*(t)\left(1 - \frac{x^*(t)}{K}\right) + \frac{\lambda_r}{\tau}. \qquad (6) \end{aligned}$$

where

$$\lambda_x(T) = A_T,\ \lambda_r(T) = 0 \qquad (7)$$

are the transversality conditions. The characterization of an optimal control pair $(h_L^*(t), h_N^*(t))$ was derived by solving $\partial H/\partial h_L = 0$, and $\partial H/\partial h_N = 0$ on the interior of the control set:

$$\begin{aligned} h_L^* &= \frac{B_1 x^*(t) - \left(\lambda_x x^*(t) + \beta\frac{\lambda_r}{\tau}\right)e^{\delta t}}{2C_1} \\ h_N^* &= \frac{B_2 x^*(t) - \alpha\frac{\lambda_r}{\tau}e^{\delta t}}{2C_2}. \end{aligned}$$

Considering the upper and lower bounds of the controls, our characterization of the optimal control pairs becomes

$$h_L^*(t) = \min\left\{M_1, \max\left\{0, \frac{B_1 x^*(t) - \left(\lambda_x x^*(t) + \beta\frac{\lambda_r}{\tau}\right)e^{\delta t}}{2C_1}\right\}\right\}, \qquad (8)$$

$$h_N^*(t) = \min\left\{M_2, \max\left\{0, \frac{B_2 x^*(t) - \alpha\frac{\lambda_r}{\tau}e^{\delta t}}{2C_2}\right\}\right\}. \qquad (9)$$

Numerical simulations

The goal of this study is to investigate optimal harvesting strategies for the combined harvesting of non-timber (non-lethal) and timber (lethal) forest products. To illustrate various scenarios, we solved the optimality system (the state system (1–2), adjoint system (5–6) and optimal control pair characterization (8–9) with corresponding initial (3) and final time conditions (7)) by using an iterative method known as the Forward-Backward sweep approach from Lenhart and Workman (2007). We note that uniqueness of the optimal control pair can be proved for the restriction of small final time T (Fister et al. 1998), and we did not see any evidence of non-uniqueness of optimal control pairs in our simulations for $T = 5$.

To understand how species life history would affect optimal harvesting strategies, we ran scenarios for fast growth species ($r_e = 0.25$) and slow growth species ($r_e = 0.03$). Previous studies showed that variation in economic discounting rate can affect the optimality of harvest (see for details Lande et al. 1994, Potts and Vincent 2008, and Armsworth et al. 2011). However, to simplify our scenarios, we assumed a typical 5 % discounting rate ($\delta = 0.05$) and ran simulations for 5 years ($T = 5$). We also assumed that plant population carrying capacity is limited to 100 individuals ($K = 100$), which is a reasonable assumption based on previous studies on NTFP harvesting ecology (see Gaoue and Ticktin 2007). In a previous work, we showed that the sustainability of harvest is dependent upon the demographic damage to growth inflicted by harvesting on the plant (Gaoue et al. 2015). We use median values for the demographic damage rates of lethal (timber) ($\beta = 0.23$) and non-lethal (non-timber) forest product ($\alpha = 0.4$) harvesting; these values are taken from Ticktin et al. (2002) for *Aechmea magdalenae*. We assumed that the cost of harvesting timber and non-timber forest products is similar and therefore used the same cost coefficients ($C_1 = C_2$) in our model. To test how plant lifespan affects optimal harvest strategy, we compared short- and long-lived plant species with $\tau = 5$ and $\tau = 20$, respectively. We also investigated how the weight coefficient on the conservation term during control period (A) and at the end of harvest (A_T) change the optimal strategy in our harvested system. We used partial rank correlation coefficient (PRCC) to calculate sensitivity of the objective functional value J and profit P at the optimum with respect to each parameter (Marino et al. 2008).

Results

In the absence of any harvesting activity, as expected, population density increased gradually while population intrinsic growth rate was constant at maximum growth rate over time (Fig. 1). Under that strategy, the objective functional value equals conservation value (baseline value) and it was $J = 3874.5$ with no profit ($P = 0$) to harvesters. To maximize the economic and ecological benefits from combined harvesting, lethal harvest must be delayed to start nearly 4 years after the start of NTFP harvest. As timber harvest rate increases, one needs to gradually decrease NTFP harvest intensity to maintain optimality. Under such strategy, population density only decreased by 5–10 % of its initial density, the objective functional value, and profit both increased ($J = 5306.6$, $P = 1516.8$).

Optimal harvesting rate was consistently higher for fast growth species than for slow growth species (Fig. 2). For slow growth species, lethal harvest must be delayed a few months and nonlethal harvest must start at very low rate (close to 0) to ensure optimality. Regardless of life history, increase in lethal harvest intensity clearly decreased population density (Fig. 2a, c). However, over the first 5 years of combined harvest, the decrease in population density was modest for fast growth (7 % decrease) as compared to that of slow growth (15 % decrease from initial density) species (Fig. 2a). Slow growth plants had lower objective functional value ($J = 4608.2$) and profit ($P = 1059.0$) than fast growth plants ($J = 5328.8$, $P = 1525.2$). This indicates that for fast growth species, combined timber and NTFP harvest may be possible.

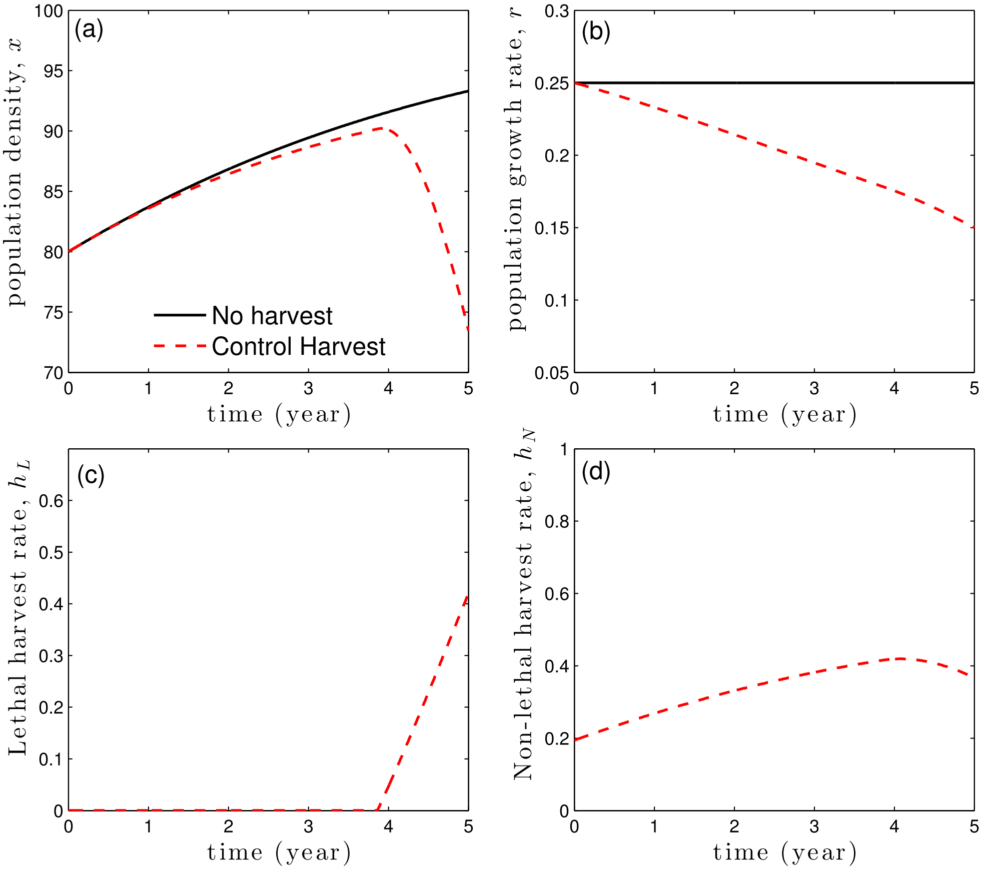


Fig. 1 Effect of optimal harvest on population density and growth rate for plants with fast growth and short lifespan. $r_e = 0.25$, $\tau = 5$, $A = 0.1$, $A_T = 0.1$, see Table 1 for other parameters

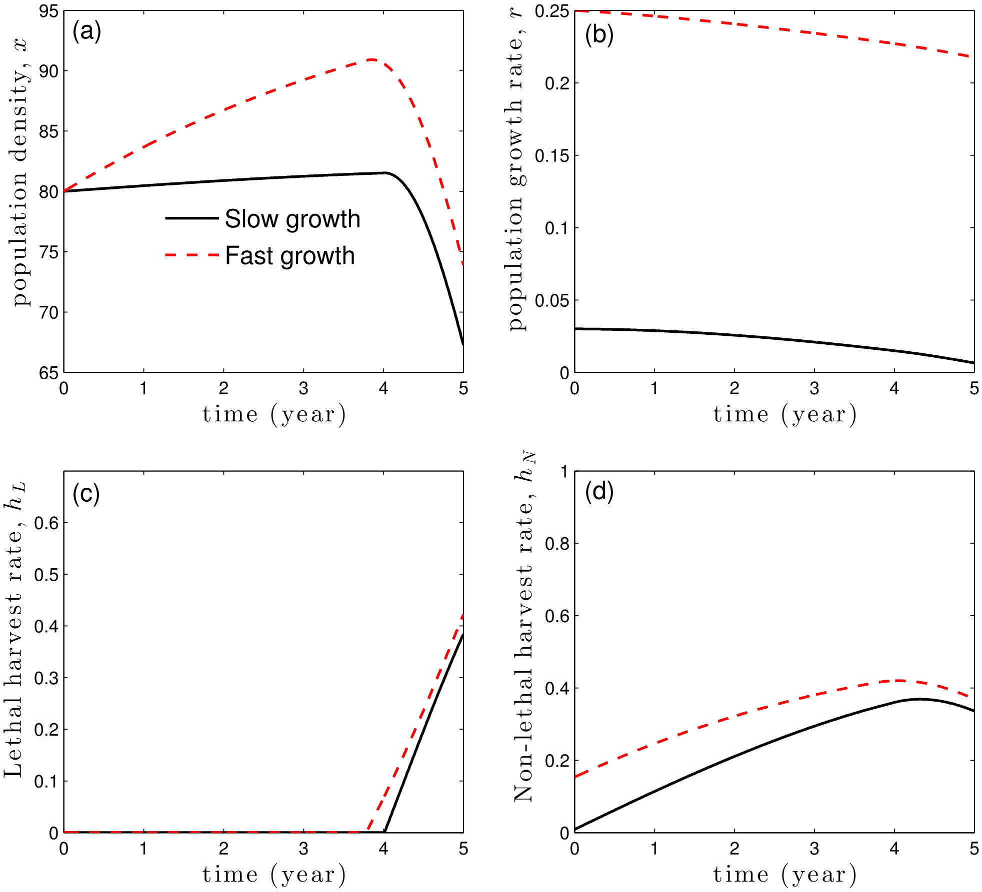


Fig. 2 Effect of species life history (slow: $r_e = 0.03$ versus fast growth: $r_e = 0.25$) on **a** population density and **b** growth rate, and optimal **c** lethal and **d** non-lethal harvesting strategies over a 5-year time period. $\tau = 20$, $A = 0.1$, $A_T = 0.1$, see Table 1 for other parameters

Contrary to the expectation that long-lived species often have slow growth and therefore both groups of species will respond similarly to combined harvest, we found that under optimal harvesting scenario, there was no difference in plant density between short- ($\tau = 5$) and long-lived species ($\tau = 20$; Fig. 3a). However, population intrinsic growth rate declined at a faster rate for short-lived than long-lived species under combined harvesting scenario (Fig. 3b). For example, at the end of the fifth year of harvesting, long-lived plant growth rate remained at $r = 0.23$ while growth rate decreased to nearly $r = 0.15$ for short-lived species. Nonetheless, this decline in intrinsic growth rate started early in the harvesting period, even in the absence of lethal harvest suggesting that nonlethal harvest alone can significantly reduce population growth in short-lived species. Obviously, the addition of lethal harvest at year 4 compounded this effect (Fig. 3d). Together, these results suggest that species response to combined lethal and non-lethal harvest may depend on plant life history, but independently on the lifespan.

When optimal harvest strategies emphasized a greater final ecological value for harvested stands (increasing A_T), plant density and growth rates were both higher than when the importance of remaining stands was accounted for (Fig. 4a, b, solid lines). Under the scenario that attributes greater importance to final stand ecological value, harvest rate must remain significantly lower during the harvest period. Typically, lethal harvest must start near the end of the harvest period for systems where both the initial (A) and final (A_T) stand values were high (Fig. 4c, red line). This makes it possible for nonlethal harvest to start early during that same period and can be maintained at higher intensity throughout the period than in a system where initial and final stand values were lower (Fig. 4d, red line).

Irrespective of harvest type, lifespan, life history, and ecological value attributed to stands, harvesting rates must be lower than 40 % of the population for lethal or nonlethal harvest (Figs. 3c, d and 4c, d). Using Latin Hypercube Sampling with PRCC (Marino et al. 2008), the objective functional value at the optimal control pair was more sensitive to changes in the conservation value during the control period (A), and to the benefit (B_2) and cost (C_2) associated with non-lethal harvest (Fig. 5a). This indicates that non-lethal harvest rate will drive the overall environmental and economic benefit one would gain from combined harvesting. Particularly, high cost of non-lethal harvest will decrease the objective functional value of the system. Similarly, the profit P was more sensitive to all of these parameters except

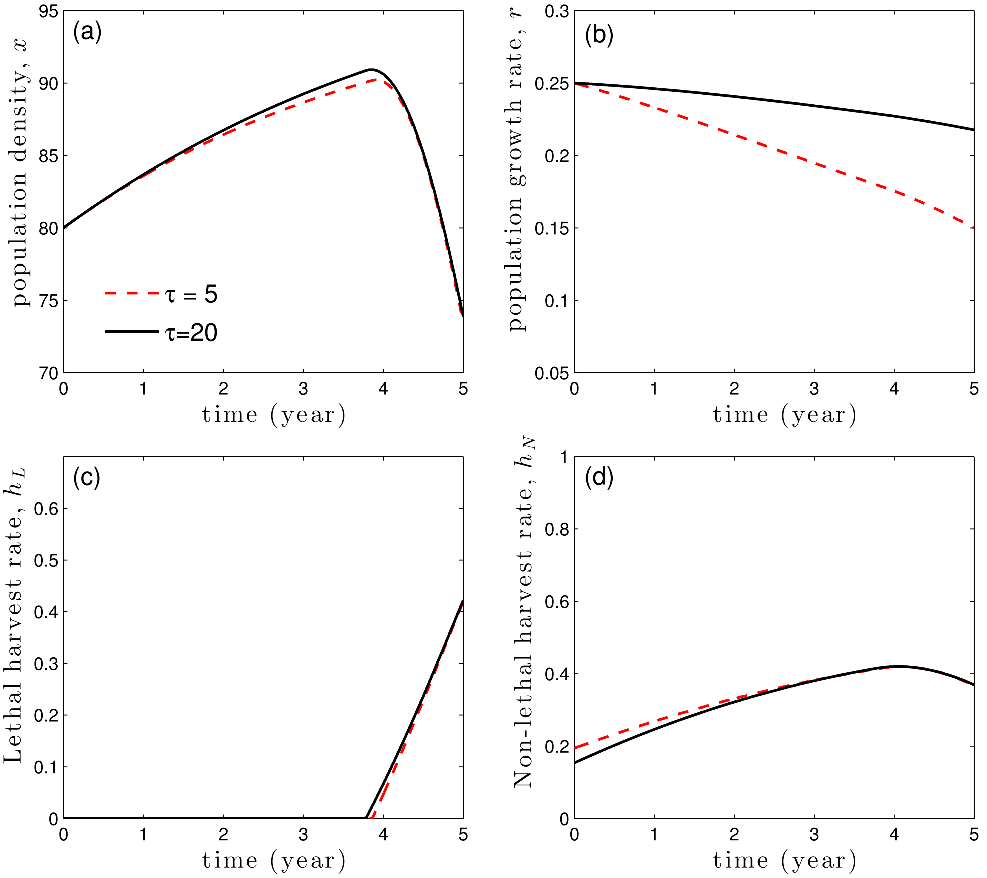


Fig. 3 Effect of species lifespan ($\tau = 5$ versus $\tau = 20$) on **a** population density and **b** growth rate, and optimal (**c**) lethal and **d** non-lethal harvesting strategies over a 5 years time period. $r_e = 0.25$, $A = 0.1$, $A_T = 0.1$ see Table 1 for other parameters

for the conservation value A, whose influence was greatly reduced (Fig. 5b).

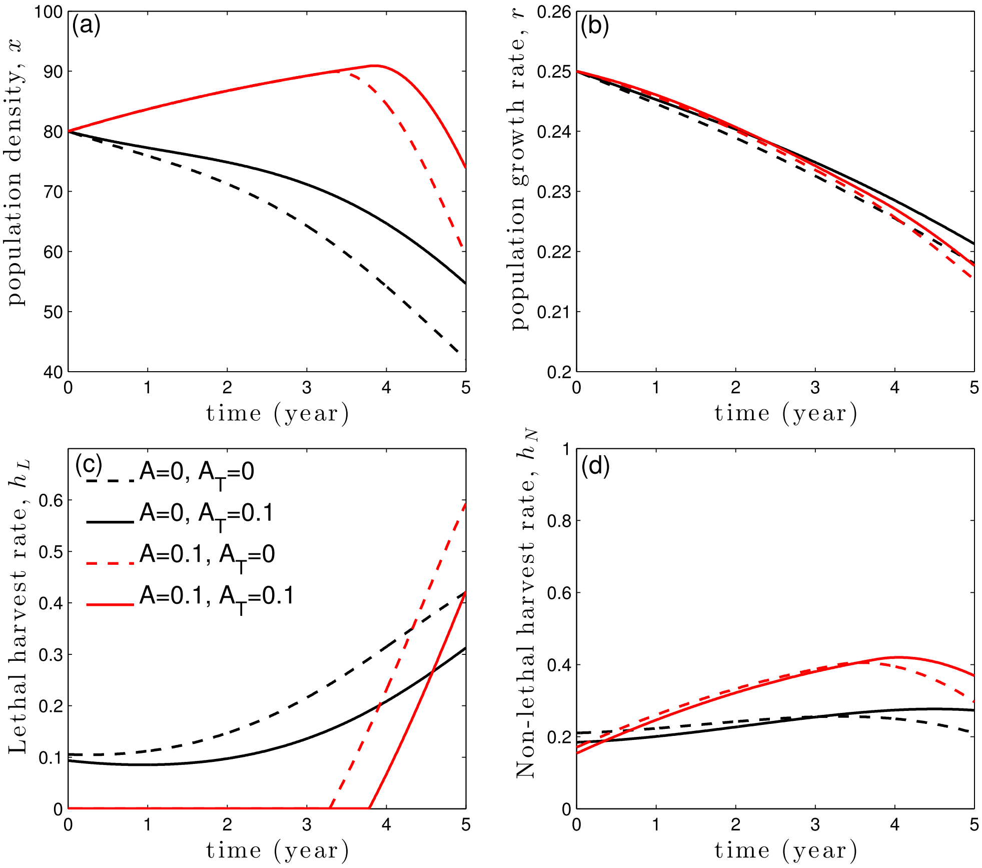
Discussion

Most studies on optimal forest resource management focused on timber harvest or logging. Fewer studies examined optimal control for NTFP harvesting and this is due to the expectation that harvesting this case has lower effect on forest structure and composition than logging (Peters 1994). However, recent studies provide evidence that NTFP could reduce population growth rate and therefore increase forest vulnerability (Gaoue et al. 2011; Peres et al. 2003). In addition, several types of NTFP harvest may lead to the death of harvested plants. Attempts to integrate economic and ecological data to define sustainable harvesting rate has been limited and often fail to account either for population short- or long-term dynamics or the cost-and-benefit analysis (Macpherson et al. 2012; Hernandez Barrios et al. 2015). In this study, we studied optimal harvesting strategies for the combination of timber and non-timber products which maximize the benefit that accrue to harvesters, ecological conservation, and persistence, while minimizing the cost of harvesting.

A combined timber and non-timber forest product harvest can be an economically viable approach to managing extractive reserves because it allows a continuous flow of income to stakeholders (Klimas et al. 2012b). However, the way in which to combine these two harvesting strategies over time and space will determine the global sustainability of these reserves. In this study, we show that optimal harvesting strategies include starting with non-lethal NTFP harvesting and postponing lethal timber harvesting to begin after a few years. Such delay in lethal harvesting will allow harvested stands to recover from previous lethal harvest and also reduce the population-level harvest-related stress. This is possible if the demographic effect of non-lethal harvest is low enough not to disrupt population recovery. Such a low rate of non-lethal harvest is sustainable for a wide range of NTFP harvested species (Emanuel et al. 2005; Guedje et al. 2007; Schmidt et al. 2011). In optimal fisheries literature, a similar approach has been advocated whereby harvested ecosystem can be partially or totally closed to harvest over limited or extended period (Joshi et al. 2009; Kasperski and Wieland 2009; Neubert and Herrera 2008). However, the optimality of delayed harvest is more complex (Armsworth et al. 2011).

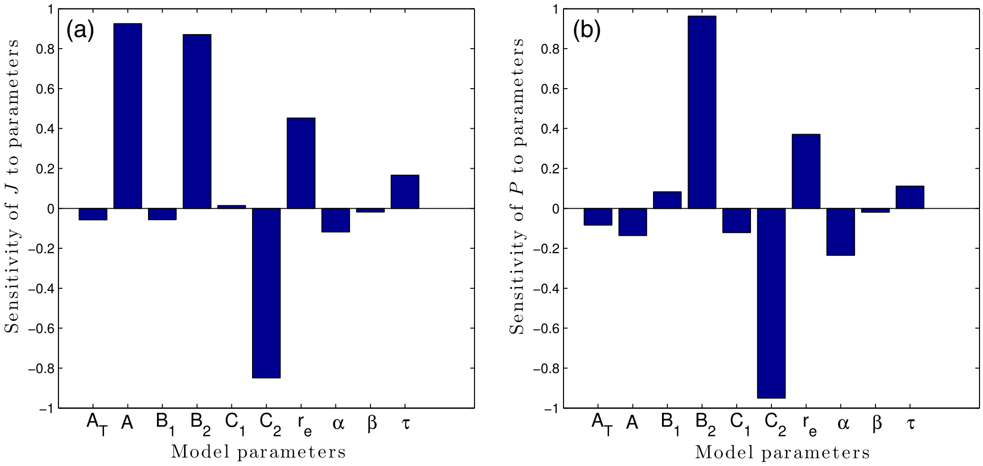
The sustainability of NTFP harvest depends on the organs that are harvested but also on the life history of

Fig. 4 Effect of conservation weight coefficient **a** population density and **b** growth rate, and optimal **c** lethal and **d** non-lethal harvesting strategies over a 5-year time period. *Black and red lines* represent $A = 0$ and $A = 0.1$, respectively. *Dash and solid lines* represent $A_T = 0$ and $A_T = 0.1$, respectively. $r_e = 0.25$, $\tau = 20$ see Table 1 for other parameters



harvested species (Hall and Bawa 1993; Ticktin 2004). Although this is often assumed in most studies (for discussion see Peters 1994; Ticktin 2015) and used in global NTFP management recommendations (SCBD 2001), the link between life history and plant resilience to harvest has not been previously tested. Here, we provide the first test for such hypothesis. We demonstrate that slow growth species have lower optimal harvest rates, objective functional values, and profits than fast growth species. Most timber species (trees) have slow growth, and our findings suggest that combined harvest may be possible mostly for fast growth species, which often do not have high wood density to be valuable timber species. Timber species may not withstand even short-term combined harvest. Instead, shrubs and other short-lived species that are expected to employ the live-fast-die-young life history strategy are potentially suitable for combined harvest. However, because these species are not timber producers, the form of lethal harvest in this

Fig. 5 Sensitivity analysis of the objective value J and profit P to the perturbation of final stand value A_T, the maximum equilibrium plant growth rate r_e, plant lifespan (τ), the effect of lethal (β) and non-lethal (α) harvest on intrinsic growth rate r, and to the benefits of lethal (B_1) and non-lethal (B_2) harvest and respective costs (C_1, and C_2)



case will include whole plant harvest for medicinal purpose (van Andel and Havinga 2008). Contrary to the expectation that long-lived species will have slow growth, and therefore species with any of the two traits will respond similarly to harvest, we found no effect of species lifespan on optimal harvesting rates. This result suggests that life history is a better indicator of species resilience to harvest than the lifespan.

Overall, our results indicate that to maintain a population with a decline of less than 10 % of its initial density, optimal lethal or nonlethal harvest rates should not exceed 40 % of total population density. This optimal rate is lower than commonly reported sustainable rates for NTFP (Ticktin 2004) but slightly higher than lethal harvest estimated for a few species using model (1) and (2) (Gaoue et al. 2015). A comprehensive review showed that most commonly reported sustainable harvest limits estimated by authors ranged from <5 % for whole plants or bark harvest to 80 % harvest rate for fruits (Ticktin 2004). These findings suggest that accounting for the economic and ecological constraints of harvesting NTFP can provide further insights into the global sustainability of NTFP harvest.

Although population density declined at the end of the control period, we found an optimal solution for which harvesting at a certain rate was possible at limited demographic cost while maximizing profit. Lethal harvest should be prohibited for almost 4 years out of a duration of total 5-year control period. Maintaining a low non-lethal harvest rate and increasing gradually is sustainable, especially for relatively fast growing species, is an optimal strategy. However, a drastic population reduction is caused by lethal harvest in all of our control scenarios. Although in our model simulations, the benefit from lethal harvest ($B_1 = 0.3$) is twice that of non-lethal harvest ($B_2 = 0.15$), the profit from non-lethal harvest ($J = 1136.6$) is three times that of lethal harvest ($J = 380.2$) over the 5 years. These results could be informative for local harvesters who may be shortsighted on short-term profit, and favor logging or lethal harvesting method for non-timber forest products.

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