

Towards a mechanistic understanding of the synergistic effects of harvesting timber and non-timber forest products

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Summary

1. Classic theories of resource harvest assume logistic growth and incorporate harvest through an additional loss term. This methodology has been applied successfully in forest products harvesting such as timber logging. However, modelling harvest through a loss term is not appropriate for non-timber forest products (NTFP) since harvesting in this case does not always require the complete removal of individual plants.
2. Empirical evidence suggest that NTFP harvest affects plant population growth rates. Additionally, timber and NTFP harvest can have synergistic effects on population dynamics. We develop and analyse a simple model that incorporates non-lethal harvest implicitly through the population growth rate of plants and lethal harvest explicitly through permanent removal of whole plants, with additional synergistic effects on population growth rate. To capture transient dynamics, we model the growth rate of plants explicitly as a dynamic variable affected by harvesting.
3. Transient dynamics results indicate that populations have delayed response to discrete harvesting. We demonstrate exactly how the sustainability of lethal harvest, non-lethal harvest or both types of harvests depends on the demographic effect of each type of harvest on the population growth rate.
4. Finally, we identify a threshold parameter \mathcal{R} , such that combined lethal and non-lethal harvest results in plant population sustainability when $\mathcal{R} > 1$ and extinction when $\mathcal{R} \leq 1$.

Key-words: harvest model, logistic growth, non-lethal demographic cost, non-timber forest products, sustainability threshold, sustainable resource exploitation

Introduction

Understanding how to harvest renewable resources such as forest products or wild plants in a sustainable way is a topic of great interest in conservation biology. These forest products include timber as well as non-timber forest products (NTFP) such as fruits, foliage, bark and roots which serve, among other, as medicine, food and source of income for local communities. Harvesting forest products is often carried out by multiple user groups with competing interests. The quality and quantity of harvestable non-timber forest products are constrained by what is left after timber logging. Logging is often carried out by small to big companies, and the effects of logging on the structure of forests depend on the scale of the operation. Recent discussions on the sustainability of wild plant harvest have focused on the possibility of harvesting the same species of plant for timber, for example through logging, as well as for non-timber products, for example fruits, leaves, resin and barks (Guariguata *et al.* 2008; Klimas *et al.* 2012;

Rist *et al.* 2012). Timber harvest is lethal since it results in the complete removal of individual plants, while NTFP harvest is mostly non-lethal. For example, harvesting fruits from *Sclerocarya birrea* in Southern Africa (Emanuel, Shackleton & Baxter 2005), or bark and foliage from *Khaya senegalensis* in West Africa (Gaoue & Ticktin 2007), does not kill harvested plants directly. However, the cumulative effects of non-lethal harvest can result in reduced population growth rate, for example, through delayed reproduction (Endress, Gorchov & Berry 2006; Gaoue, Horvitz & Ticktin 2011; Lopez *et al.* 2012; Gaoue *et al.* 2013).

Some forms of NTFP harvest lead to individual plant death. For example, harvesting bark from *Prunus africana* in Cameroon involves girdling, which can lead to tree death shortly after harvest (Cunningham & Mbenkum 1993; Stewart 2009). Some plant species experience both lethal and non-lethal NTFP harvesting. For example, the harvesting of amla fruits from large *Phyllanthus emblica* in India may involve felling the plant, while smaller plants may be harvested simply by bending them (Sinha & Bawa 2002; Ticktin *et al.* 2012). The biological cost associated with harvesting depends on the

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type of organ that is harvested (Ticktin 2004). For example, harvesting bark can disrupt phloem and increase insect attacks (Guedje *et al.* 2007; Delvaux *et al.* 2009). Partially harvesting roots, as is the case with some populations of American ginseng (Farrington *et al.* 2009), can inflict more damage to plants than harvesting flowers or fruits.

Several plant species that are harvested for NTFP are also harvested for timber (Guariguata *et al.* 2008; Klimas *et al.* 2012). Harvesting often takes place in a context where species are already subject to multiple stressors such as frequent fire, habitat fragmentation, soil erosion and drought (Gaoue & Ticktin 2007; Mandle & Ticktin 2012; Schmidt & Ticktin 2012; Ticktin *et al.* 2012). The removal of individual plants from a system, for example, through logging or lethal NTFP harvest, might impose indirect negative effects on the harvested plants in addition to the direct effects of removal. The removal of individual plants, as well as logging in forest management, is expected to reduce intraspecific competition. However, if the rate of individual removal is high, this will negatively affect population dynamics by limiting various facilitative functions. For example, reduced density can improve individual growth through release from competition, but it can also decrease flower visitation and pollination rates (Bosch & Waser 1999), and population resistance to physical damage by wind (Everham & Brokaw 1996). Human-induced disturbances such as forest fragmentation can result in landscape mosaics, which may affect the population dynamics of the remaining species (Faria *et al.* 2009). Accounting for the synergistic effects of individual removal on the dynamics of plant populations harvested for NTFP is rare. Yet, understanding species resilience to harvest in a context of multiple stressors is critical to our global understanding of sustainable management of extractive reserves.

Classical harvest models show that proportional harvest strategies are more sustainable than constant yield harvest and that stochastic harvesting or harvesting of fluctuating populations leads to reduced maximum sustainable yield (Beddington & May 1977; May *et al.* 1978; Lande, Engen & Saether 1994; Jonzén, Ripa & Lundberg 2002; Wikström, Ripa & Jonzén 2012). This modelling framework can be readily applied to sustainable game hunting and timber logging where individuals are directly removed from the population (Fryxell *et al.* 2001; Boyce, Baxter & Possingham 2012). This classical modelling approach relies on accounting for harvesting through an additional loss term in a logistic growth-type framework (Pöysä 2004). Although this framework is suitable for modelling populations that can be harvested through complete removal, it cannot be applied directly in modelling NTFPs, where plant harvest does not always result in complete removal of harvested plants from the population. These classical harvest models fail to capture the indirect cost of harvesting.

Modelling the ecological impacts of NTFP harvest has been carried out using stage-structured matrix models (Schmidt *et al.* 2011), rather than logistic growth harvest models. These stage-structured models are based on projection matrices (Caswell 2001) that are built using data, typically collected over a period of 2–4 years. These models summarize the

size-dependent transition rates (e.g. growth, reproduction) from one life stage to another. Separate transition matrices are developed for populations with different levels of NTFP harvest rates (often 2–3 levels), and the dominant eigenvalues of these matrices, which represent the long-term population growth rates, are compared (Schmidt *et al.* 2011). If the dominant eigenvalue for harvested populations is greater than unity, then harvesting is assumed to be sustainable on the grounds that these populations are projected to increase under the current harvesting scenario. Although these models can quantify the influence of different life stages on plant population dynamics, they do not include harvest intensity explicitly, which poses a challenge in quantifying the influence of harvest intensity on each stage transition. Additionally, matrix models have more parameters than classical logistic growth models and may be difficult to link with well-developed harvest theories based on logistic growth models.

Here, we follow the proportional harvest logistic growth framework and develop a novel harvest model, which integrates the non-lethal effects of NTFP harvest and accounts for the lethal effects of some types of NTFP harvest, as well as direct death of individual plants from timber logging for plant species that are harvested for multiple purposes. To our knowledge, this is the first continuous theoretical model on NTFP harvesting. Although non-lethal NTFP harvest does not lead to direct plant mortality or removal, it may reduce reproduction and plant growth significantly (Gaoue & Ticktin 2008), which in turn affect long-term population demography (Ghimire *et al.* 2008; Gaoue, Horvitz & Ticktin 2011). Our model captures lethal harvesting effects as an additional loss term, similarly to classical harvest models, and non-lethal harvest effects through a second differential equation, which captures the effects of harvest on the intrinsic plant population growth rate. This model is general enough to be applied to timber, NTFP and to both timber and non-timber forest products harvest problems and allows us to gain a mechanistic understanding of these effects on plant population dynamics. We show that combined harvest of timber and NTFP is possible under specific conditions defined by the demographic effects of harvest on the plants. We also show how one can use parameter values retrieved from the literature to calibrate our model and gain insights into the sustainability of combined harvest. Compared with the matrix projection models often used in this field, our model requires fewer parameters, is easier to use and yields more conservative estimates of sustainable harvest limits.

Model and analysis

The underlying assumption of our model is that the plant population grows according to a logistic function with r being the intrinsic growth rate and k the carrying capacity of the environment. The model is adjusted for lethal harvest through a loss term with rate h_l and includes a second type of harvesting (non-lethal) that does not lead to the death of harvested individuals with rate h_n . We assume that lethal harvest, in addition to removing individuals from the system, has indirect effects on the remaining population. For example, logging may

reduced intraspecific competition within remaining stand or limit intraspecific facilitative effects. To account for these direct (non-lethal harvest) and indirect (lethal harvest) effects of harvesting, we modelled the intrinsic growth rate r , as function of both the non-lethal, h_n , and lethal h_l , harvest rates. Because the dynamics of r occur at a time scale that is different from the time scale at which the population-level dynamics occur, we added a correcting term τ that represents the average lifespan of the plant species, such that the rate of change of r per lifespan $\frac{dr}{dT} = \tau \frac{dr}{dt}$. For example, if we assume an annual time scale for population dynamics, τ would be the average lifespan of the plant in terms of years, with $\tau = 1$ for annual plants. The dynamics of the plant population, x , and the population growth rate of the plant are governed by the following system:

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{k}\right) - h_l x, \\ \tau \frac{dr}{dt} &= r_e - \alpha h_n - \beta h_l - r, \end{aligned} \tag{eqn 1}$$

where r_e is the maximum growth rate (under given environmental conditions) in the absence of harvesting and competition between individuals, α is a parameter to account for the demographic cost of non-lethal harvest of NTFP (e.g. harvest of foliage, fruits and bark), and β is a parameter to account for indirect effects of lethal harvest. We assume that removing individuals would alter the growth rate of remaining individuals.

LONG-TERM SUSTAINABILITY OF HARVEST

Case 1: Combined lethal and non-lethal harvest

At the long-term time scale, we assume the dynamics of r are at a quasi-steady state, in which $r = r_e - \alpha h_n - \beta h_l$, and $\frac{r_e}{\alpha h_n + \beta h_l} > 1$. We use this to reduce system (1) into the following single equation:

$$\frac{dx}{dt} = (r_e - \alpha h_n - \beta h_l)x \left(1 - \frac{x}{k}\right) - h_l x, \tag{eqn 2}$$

which is the logistic growth model adjusted for lethal and non-lethal harvest. To complete the definition of the model, we require an initial condition of the form $x(0) = x_0$. Using standard techniques described in Jordan & Smith (1999), it is easy to verify that equation (2) has a unique solution that depends continuously on x_0 . Therefore, our model is well-posed from a mathematical and ecological stand-point. Using solution techniques for first order ordinary differential equations, we obtain the solution of equation (2) with initial condition $x(0) = x_0$ as

$$x(t) = \frac{kx_0(\alpha h_n + (1 + \beta)h_l)(\mathcal{R} - 1)}{x_0(r_e - \alpha h_n - \beta h_l) + ((k - x_0)(r_e - \alpha h_n - \beta h_l) - h_l k)e^{-(\alpha h_n + (1 + \beta)h_l)(\mathcal{R} - 1)t}} \tag{eqn 3}$$

which is non-zero and positive when $\mathcal{R} = \frac{r_e}{\alpha h_n + (1 + \beta)h_l} > 1$. The non-trivial equilibrium population density is $x^* = \frac{k(r_e - \alpha h_n - (1 + \beta)h_l)}{r_e - \alpha h_n - \beta h_l} = \frac{k(\alpha h_n + (1 + \beta)h_l)}{r_e - \alpha h_n - \beta h_l} (\mathcal{R} - 1)$. Observe that $x(t) \rightarrow x^* > 0$ as $t \rightarrow \infty$ when $\mathcal{R} > 1$. Therefore, when

$\mathcal{R} > 1$, equation (2) has a globally and asymptotically stable non-trivial positive equilibrium solution x^* , indicating that even with lethal and non-lethal harvest, the plant population can still be sustained. On the other hand, when $\mathcal{R} \leq 1$, only a trivial equilibrium solution ($x^* = 0$), which is globally and asymptotically stable, exists. This represents the situation in which harvest leads to the extinction of the plant population. Therefore, the threshold parameter \mathcal{R} is essential in determining whether the plant population is sustained or eradicated in the presence of lethal and non-lethal harvesting. The threshold parameter \mathcal{R} is the equivalent of the vectorial and basic reproduction numbers in vector and epidemiological models (Van den Driessche & Watmough 2002; Ngonghala, Ngwa & Teboh-Ewungkem 2012; Ngonghala, Teboh-Ewungkem & Ngwa 2014a; Ngonghala *et al.* 2014b). Note that the equilibrium solutions of equation (2) can also be obtained by setting the right-hand side of the equation to zero and solving for x .

Case 2: Non-lethal harvest only

In the absence of lethal harvest, equation (2) reduces to

$$\frac{dx}{dt} = (r_e - \alpha h_n)x \left(1 - \frac{x}{k}\right), \tag{eqn 4}$$

whose solution is $x(t) = \frac{kx_0}{x_0 + (k - x_0)e^{-(r_e - \alpha h_n)t}}$. Again, x is globally and asymptotically stable. Clearly, in the absence of lethal harvest, the population goes to its environmental carrying capacity k , that is $x(t) \rightarrow k$ as $t \rightarrow \infty$, provided $\frac{r_e}{\alpha h_n} > 1$. When $\frac{r_e}{\alpha h_n} \leq 1$, the plant population declines and will be driven to extinction if harvesting continues at the same level.

Case 3: Lethal harvest only

In the absence of non-lethal harvest, equation (2) reduces to the classic harvest model with slight adjustments to account for the indirect cost of lethal harvest:

$$\frac{dx}{dt} = (r_e - \beta h_l)x \left(1 - \frac{x}{k}\right) - h_l x, \tag{eqn 5}$$

with solution $x(t) = \frac{kx_0(r_e - (1 + \beta)h_l)}{x_0(r_e - \beta h_l) + ((k - x_0)(r_e - \beta h_l) - h_l k)e^{-(r_e - (1 + \beta)h_l)t}}$.

Here, $x(t) \rightarrow \frac{k(1 + \beta)h_l}{r_e - \beta h_l} \left(\frac{r_e}{(1 + \beta)h_l} - 1\right) > 0$ as $t \rightarrow \infty$. The plant population is sustained ($x > 0$) even when there is lethal harvest when $\frac{r_e}{(1 + \beta)h_l} > 1$ and will be driven to extinction provided that $\frac{r_e}{(1 + \beta)h_l} \leq 1$.

Figure 1 depicts the long-term dynamics of equation (2). As expected, Fig. 1(a) confirms the fact that non-lethal harvest, if

not exceptionally high, is preferred to lethal or both lethal and non-lethal harvest for plant sustainability. Figure 2 illustrates that the system is stable and sustainable if combined lethal and non-lethal harvest fall below the threshold line

$h_n = \frac{r_c}{\alpha} - \frac{1+\beta}{\alpha} h_l$ at which $\mathcal{R} = 1$. Furthermore, even in the absence of lethal harvesting, non-lethal harvest affects the growth rate and can drive the population to an unstable state and ultimately to extinction, when $h_n > \frac{r_c}{\alpha}$. In practice, although the system is stable when harvest occurs just below the threshold line, harvest activities would drag the population density to unrealistically low values, as indicated by the light shaded region (Fig. 2). To acquire further insights into the qualitative behaviour of the system, we conducted local sensitivity analyses of the threshold parameter \mathcal{R} and the population equilibrium density x^* to perturbation of model parameters.

SENSITIVITY OF \mathcal{R} TO HARVEST

We compute the sensitivity and elasticity indices of the threshold parameter, \mathcal{R} , and plant population size at equilibrium, x^* , to perturbation of the parameters h_l and h_n (see Appendix S1). Elasticity indices measure relative quantitative changes in model outputs and threshold parameters with respect to changes in input model parameters. In Fig. 3, we illustrate three ‘regimes’ of the elasticity indices under different harvest levels h_l and h_n . When non-lethal harvest is high and lethal harvest is low, the threshold parameter, \mathcal{R} , and the non-trivial equilibrium plant population density, x^* , are both more sensitive to non-lethal harvest (Fig. 3, regime *a*). As expected, both are also highly sensitive to lethal harvest (see Fig. 3, regime *b*). However, in the case of both low lethal and non-lethal harvest, \mathcal{R} is more sensitive to non-lethal harvesting (h_n), that is the stability of the system would be more sensitive to non-lethal harvest, while the equilibrium plant population, x^* , is more sensitive to lethal harvesting intensity (h_l) (Fig. 3, regime *c*). Note that the sizes of the three regions in Fig. 3 depend on the respective effects of non-lethal (α) and lethal harvest (β). For example, when the effect of harvesting organs is high, that is, when α is large, the $h_n = \frac{r_c}{2\alpha}$ line is lowered and in this case, the

sustainable population size will be more sensitive to non-lethal harvest than lethal harvest, although the stability of the system will still depend on lethal harvest rate. The diagonal line $h_n = \frac{(1+\beta)}{\alpha} h_l$ encapsulates the parameter combinations for which \mathcal{R} is equally sensitive to both types of harvest.

TRANSIENT DYNAMICS OF HARVESTED SYSTEMS

Apart from the long-term or asymptotic dynamics of system (1) studied above, transient dynamics are also important (Hastings 2004), especially since harvest can alter the equilibrium growth rate at a different time scale than the dynamics of the plant population density. We first use the full system (1) to investigate the transient dynamics when lethal and non-lethal harvest are carried out on an undisturbed forest population, which is at its carrying capacity. As long as $h_n < \frac{r_c}{\alpha}$, non-lethal harvest alone does not change the long-term population dynamics, with population density remaining at carrying capacity if undisturbed, and returning to carrying capacity if disturbed (Fig. 4). In this case, non-lethal harvest may nonetheless hinder population recovery following disturbance. However, for $h_n > \frac{r_c}{\alpha}$, non-lethal harvest eventually leads to population collapse, even though the transient dynamics may initially show the population following a recovery path after disturbance before it goes to extinction (Fig. 4a).

To further explore the transient dynamics of the system, we set up a simulation with discrete periods of non-lethal harvest, at intervals of 40 years in a population in which plants have 20 years of lifespans. That is, during the first 40 years, the population is harvested at a high level. This is followed by 40 years of forest closure to allow the population to recover, and then, the cycle is repeated. Population dynamics show delayed responses to harvest and closure periods (Fig. 4b). Although the forest was closed at year 40 for recovery, the population continued to decline due to damage caused during the first

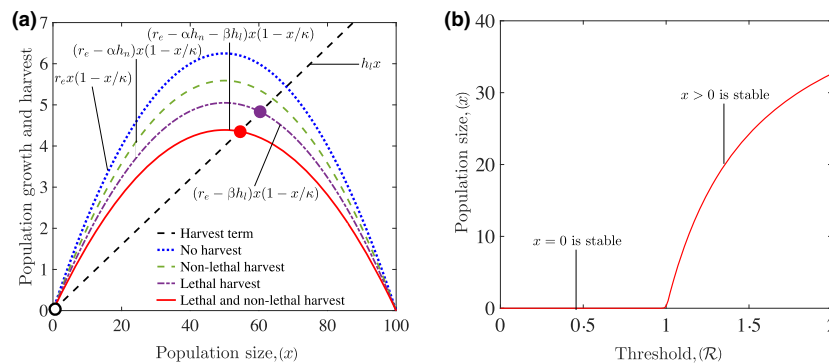


Fig. 1. (a) Dynamics of Equation 1 depicting example cases in which there is 1) no harvest (blue curve), 2) only non-lethal harvest (green curve), 3) only lethal harvest (purple curve) and 4) both lethal and non-lethal harvest (red curve) with parameters values $r_c = 0.25$, $k = 100$, $\alpha = 0.44$, $\beta = 0.6$, $h_n = 0.06$ and $h_l = 0.09$. The harvest term in Equation 1 is denoted by the black line. Non-trivial stable equilibria, that is, the point of intersection of the black straight line and the red curve for the lethal harvest model and the point of intersection of the black straight line and the magenta curves for the combined lethal and non-lethal harvest model are denoted by filled red and magenta circles, respectively, while the unstable trivial equilibrium at the origin is denoted by an open circle. The cost of non-lethal harvest on the growth rate is given by the region between the blue and the green curves, while the cost of both non-lethal and lethal harvest on the growth rate is given by the region between the blue and the magenta curves. (b) Bifurcation analysis of the combined lethal and non-lethal harvest model (Equation 2) for $0 \leq \mathcal{R} \leq \infty$ showing that harvest can lead to extinction when $\mathcal{R} \leq 1$ and sustenance when $\mathcal{R} > 1$.

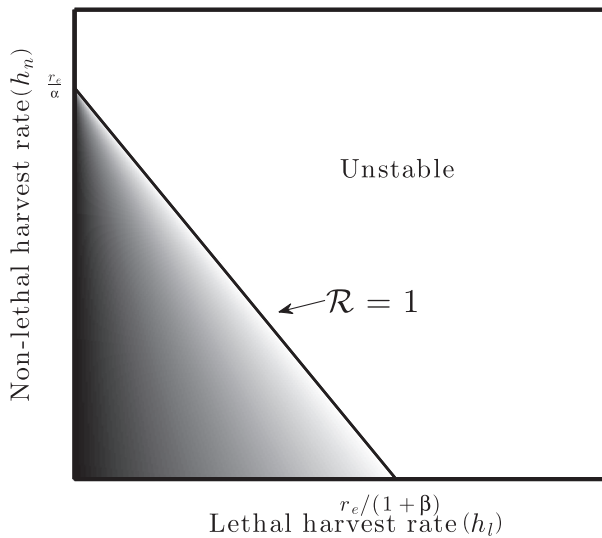


Fig. 2. Stability and density of plant population as a function of lethal (h_l) and non-lethal (h_n) harvest rates. In the shaded area, there is a positive stable equilibrium, meaning populations can sustainably be harvested at these levels. Darker shades represent higher stable population densities. Above the diagonal line, the only stable equilibrium is $x^* = 0$, meaning the population declines to extinction under harvest strategies represented by points in this region. Thus, the diagonal line $h_n = (r_e - (1 + \beta)h_l)/\alpha$ represents $\mathcal{R} = 1$ and defines the limits for sustainable harvest.

40 years. Population density began to recover only some years after the start of the closure period, and then continued through the end of the forest closure period and into the next harvest period. The delayed response of population dynamics to harvest depends on the lifespan of the plants, τ . For annual plants ($\tau = 1$), the transient phase is negligible (results not shown), since the population responds to harvest almost at the same time as observed in classic harvest models. However, natural forests are usually dominated by trees with long lifespans ($\tau > 20$), and for such systems, there is a delay in the response of population dynamics to harvest.

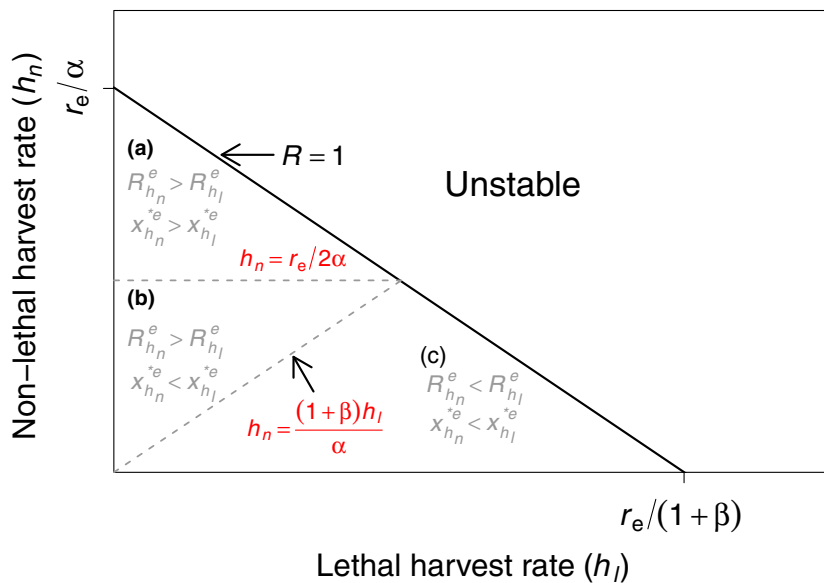


Fig. 3. Three ‘regimes’ of relative elasticity indices for the sustainable harvest threshold parameter, \mathcal{R} , and the equilibrium population size, x^* , to changes in non-lethal (h_n) and lethal (h_l) harvest. Above the $\mathcal{R} = 1$ line, population is unstable. When non-lethal harvest is relatively high, \mathcal{R} and x^* are more sensitive to non-lethal than lethal harvest (regime a). In contrast, when lethal harvest is relatively high, both are more sensitive to lethal harvest (regime c). There is also a region where \mathcal{R} is more sensitive to h_n while x^* is more sensitive to h_l (regime b).

Application to sustainable harvest

To test whether sustainable harvest predictions from our model are similar to those generated from matrix projection models often used in the literature (see Schmidt *et al.* 2011), we applied our model (Equation 1) to four case studies of lethal and non-lethal harvesting of wild plants with published results from matrix modelling. We selected these plant species to include various life forms and types of organs harvested (Table 1): a herb (*Nardostachys grandiflora*) harvested for its rhizomes (lethal harvest) in north-western Nepal, a tree (*Khaya senegalensis*) harvested for its foliage (non-lethal harvesting) in Benin, a Mexican Bromeliad (*Aechmea magdalenae*) harvested for its leaves (non-lethal harvest) and in some cases, the whole plant is harvested (lethal harvest) and an Asteraceae (*Saussurea medusa*) harvested for the whole plant (lethal harvesting) in China. For each species, the authors estimated the lethal (h_l) and non-lethal (h_n) harvesting rates at the population level (see data compiled in the appendix of Schmidt *et al.* 2011). The demography of each of these species was studied for 3–7 years and the authors used matrix projection models (Caswell 2001) to estimate sustainable harvest limits (see Ticktin *et al.* 2002; Law 2007; Ghimire *et al.* 2008; Gaoue & Ticktin 2010). We compared these estimates of harvest limits with results from our model.

Nardostachys grandiflora is a medicinal herb harvested for its rhizome in the Himalayan mountains. Ghimire *et al.* (2008) experimentally harvested populations of *N. grandiflora* at rates of 10%, 25%, 50% and 75% and maintained one population unharvested to serve as a control. *Khaya senegalensis* is a tree whose leaves are harvested as a source of dry season fodder in West Africa. This is a widespread activity in the region and Gaoue & Ticktin (2010) showed that foliage harvest has negative effects on the population growth rates of *K. senegalensis* in Benin. They studied 12 populations of *K. senegalensis* in two ecological regions with half of the populations harvested. Harvested populations have more than 50% of their individuals

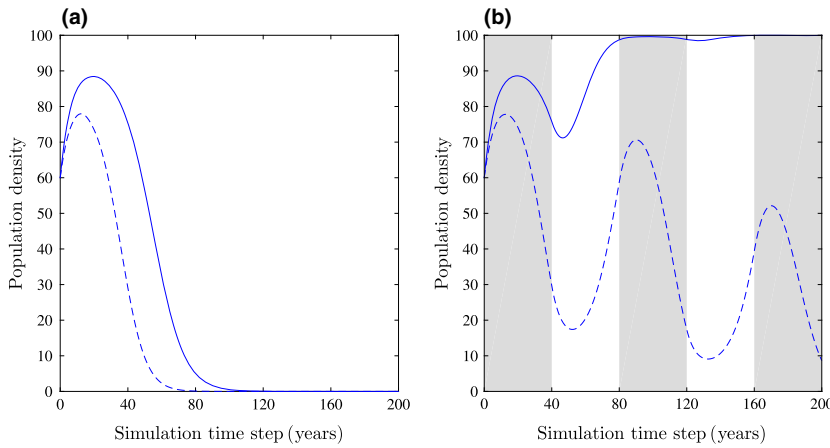


Fig. 4. Transient dynamics following a disturbance that depresses population densities 40% below carrying capacity for (a) continuous non-lethal harvest at $h_n = 0.8$ and (b) alternating 40-year periods with ($h_n = 0.8$) and without ($h_n = 0$) non-lethal harvest (shaded areas are harvest time periods) for intrinsic population growth rates of $r_e = 0.2$ (solid lines) and $r_e = 0.15$ (dashed lines). Dynamics follow Equation 1, with parameters $\tau = 20$, $\alpha = 0.4$, $k = 100$, $h_l = 0$, $\beta = 0$. The initial state was 60% of carrying capacity.

with no or few leaves left. Leaf harvesting targets adult trees and is non-lethal. We split the populations, as the authors did, according to whether the environment was dry or moist. *Aechmea magdalenae* is a forest bromeliad harvested by local people in Mexico to make a wide range of products including rope, fishing nets, clothing, mats and hammocks. Harvesters usually remove leaves (Valle Nacional system) but in a few cases, harvesters uproot the whole plant (Lalana system). Ticktin *et al.* (2002) studied populations of *Aechmea magdalenae* for 3 years to test the effect of both types of harvesting strategies on population growth rate. Finally, *Saussurea medusa* is a rare, slow-growing monocarpic plant with a long lifespan (>7 years) used for traditional medicine in the eastern Himalayas (Law & Salick 2005). The whole plant is harvested to treat high blood pressure, but it is less preferred by harvesters than its congener *Saussurea laniceps*. Harvesting takes place during the flowering period. Law (2007) collected 5 years (2002–2006) of demographic data on two populations of *S. medusa* found at 4200–4300 m elevations on the Meri mountains located at the north-eastern border of Yunnan and south-east Tibet. They conducted several pollination exclusion field experiments to test the effects of pollen limitation and harvest on population dynamics.

For these study species, we calculated the maximum growth rates r_e by discretizing the logistic growth equation without harvesting effect and obtained values for the carrying capacity k from the literature (see Ticktin *et al.* 2002; Law 2007; Ghimire *et al.* 2008; Gaoue & Ticktin 2010). Using a time series of population size $x(t)$ and $\frac{x(t+1)-x(t)}{x(t)}$, we estimated the intercept and slope from a linear regression:

$$\frac{x(t+1) - x(t)}{x(t)} = r_e - \frac{r_e}{k}x(t). \quad \text{eqn 6}$$

To calculate the demographic cost associated with each harvesting method, we used a two-step process. First, the time series data of population size in each site was used to estimate the growth rate, using the following equation:

$$\frac{x(t+1) - x(t)}{x(t)} = r - h_l - \frac{r_e}{k}x(t). \quad \text{eqn 7}$$

Here, r is the site-specific growth rate, which is affected by both lethal and non-lethal harvest, and h_l is also a site-specific

parameter obtained from the literature. Then, we used the estimated r and corresponding harvest intensity at each site to calculate α and β , using a linear regression:

$$r = r_e - \alpha h_n - \beta h_l. \quad \text{eqn 8}$$

Figure 5 provides the maximum values of non-lethal and lethal harvesting that are sustainable, that is, for which the population persists. Our simulations show that non-lethal and lethal harvest differentially impact the species depending upon the cost associated with each harvesting method and the growth rate r_e . For example, *N. grandiflora* and *K. senegalensis* are both highly sensitive to lethal harvesting, and therefore, these species can endure a high rate of non-lethal harvest only if the rate of lethal (logging) harvest remains low (Fig. 5). In contrast, combined lethal and non-lethal harvest can be implemented for *A. magdalenae* and *S. medusa*. For the specific harvesting rates we used in this simulation (see Table 1), none of the species is maintained when lethal harvesting rate is greater than 20%.

Discussion

The literature on modelling the effects of harvesting non-timber forest products to define sustainable management strategies has been based exclusively on matrix and integral projection models (e.g., Pinard 1993; Bernal 1998; Ticktin *et al.* 2002; Zuidema & Boot 2002; Endress, Gorchov & Noble 2004; Ghimire *et al.* 2008; Gaoue & Ticktin 2010; Baldauf *et al.* 2015; Mandle, Ticktin & Zuidema 2015). Matrix models are stage- or age- structured models developed using field data on life (st)age survival, growth and fertility to parametrize a set of difference equations that are simplified in a matrix form (Caswell 2001). Although there are standard tools for applying matrix models and this technique has been embraced by a number of NTFP studies (see Schmidt *et al.* 2011), this technique depends on extensive field data to estimate parameters for survival, growth and fecundity of each life stage. Our model suggests a general framework that allows us to assess the sustainability of harvest based on estimates of 2–3 parameters (r_e , α and β). Although this model is simple, it provides a mechanistic understanding of the population-level consequence of lethal and/or non-lethal forest products harvest.

Table 1. Parameter values used for numerical simulations of our model. For four plant species with different life histories, we estimated the population growth rates at equilibrium in the absence of harvesting (r_e), the demographic cost of non-lethal harvest (α) and lethal harvest (β), and the carrying capacity (k). k value for *Saussurea medusa* was provided by the author (W. Law, unpublished data). Some parameter values (italicized) were not available from the literature and for these parameters, reasonable values were chosen based on values from other species. ‘–’ indicates cases where α or β are not needed for species that are harvested only lethally, or only non-lethally.

Species	r_e	α	β	k	Part harvested	References
<i>Nardostachys grandiflora</i>	0.03	<i>0.03</i>	0.78	15 ind. m ⁻²	Rhizome	Ghimire <i>et al.</i> (2008)
<i>Khaya senegalensis</i> (Moist)	0.024	0.03	<i>0.70</i>	237 ind. ha ⁻¹	Bark, Leaf	Gaoue & Ticktin (2010)
<i>Khaya senegalensis</i> (Dry)	0.001	0.04	<i>0.70</i>	237 ind. ha ⁻¹	Bark, Leaf	Gaoue & Ticktin (2010)
<i>Aechmea magdalenae</i>	0.25	0.44	–	2.5 ind. m ⁻²	Leaf	Ticktin <i>et al.</i> (2002)
<i>Aechmea magdalenae</i>	0.25	–	0.23	2.5 ind. m ⁻²	Whole plant	Ticktin <i>et al.</i> (2002)
<i>Saussurea medusa</i>	0.22	<i>0.40</i>	0.47	4 ind. m ⁻²	Whole plant	Law (2007)

Compared to estimates of sustainable harvest limits obtained in the literature using matrix projection models (e.g., Ghimire *et al.* 2008; Gaoue & Ticktin 2010; Law, Salick & Knight 2010; Ticktin *et al.* 2012), our model yielded more conservative estimates. The upper bound of NTFP harvest intensity ($\leq 80\%$) in *K. senegalensis* found in our study is comparable to the sustainable harvesting limits suggested from stochastic matrix projection models (Gaoue & Ticktin 2010). However, in dry environmental conditions, our model for *K. senegalensis* provides more conservative sustainable harvesting limits for NTFP ($\leq 5\%$) and suggests that combined harvest of timber and NTFP is not sustainable. Law (2007) found that in the absence of envi-

ronmental stochasticity, harvesting $\leq 70\%$ of *S. medusa* individuals is sustainable if there is no pollen limitation. The sustainable harvesting limit decreases to $\leq 65\%$ when remaining individuals are pollen limited. Under a scenario where environmental stochasticity is taken into account, results are more conservative with sustainable harvesting limits ranging between 30 and 50% (Law, Salick & Knight 2010). These estimates are generous in comparison with the results from our theoretical model, which suggest that only $\leq 15\%$ of whole plant harvest would be sustainable for *S. medusa* in combination with $\leq 55\%$ of non-lethal harvest. These differences in sustainable harvest limits can be due to several factors, particularly in the way harvesting effects are modelled in Law (2007). The author models the effect of harvest by reducing plant fecundity given that individuals are harvested while they are flowering. Although this assumption is correct, whole plant removal has consequences beyond just the reduction of reproduction output. It results in a decrease in population size that can limit several positive density-dependent functions such as pollinator attraction and plant defence.

Consistent with projections from published studies (see synthesis in Ticktin 2004), our model projects wide variation in sustainable harvest limits for non-timber forest products (2–98% harvest rate). Empirical evidence suggests that maximum harvest limits vary with the type of organ that is harvested. For example, it is expected that plants harvested for fruits can support harvest intensity of up to 80–90% (Ticktin 2004). Around 50% of total leaf biomass can be harvested without significant negative effects on population growth rates (Hernandez *et al.* 2015). For palm species, a set of studies have reported that regardless of harvest intensity, if harvesting is not too frequent, populations may slowly recover after leaf harvest even though growth or reproduction could be reduced (Hernandez *et al.* 2012; Lopez *et al.* 2012). Demographic studies on the impact of bark harvesting are rare. For *Garcinia lucida*, Guedje *et al.* (2007) reported that debarking is sustainable at current rates in Cameroon, while bark removal com-

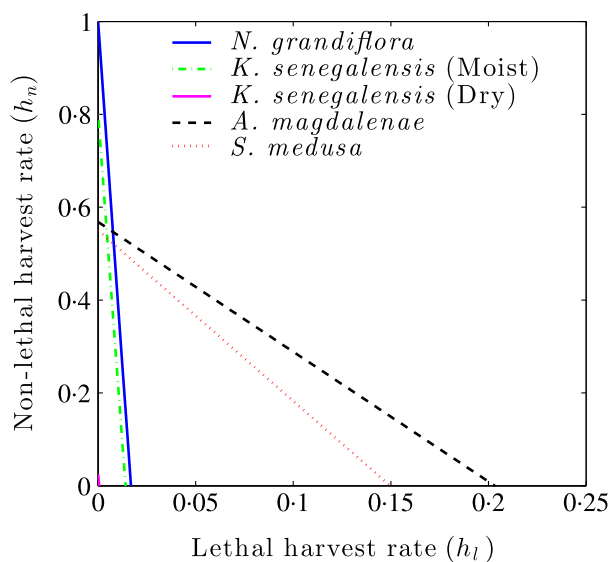


Fig. 5. Sustainable non-lethal (h_n), and lethal (h_l) harvesting rates for four plant species: (*Nardostachys grandiflora*, *Khaya senegalensis* in two ecological regions – dry and moist, *Aechmea magdalenae* and *Saussurea medusa*). The parameter space of h_l and h_n below each line defines the possible combinations of lethal and non-lethal forest product harvest rate that ensure the persistence of the plant species. The species goes extinct above the lines, which define the sustainable harvest rates.

bined with leaf harvesting in *Khaya senegalensis* leads to a significant reduction in population growth rates (Gaoue & Ticktin 2010). In general, lethal harvest such as whole plant or timber harvest has significantly more negative effects on population dynamics than does non-lethal harvest such as the removal of non-timber forest products. The application of our model to real-life data (Fig. 5) suggests that for a combined timber and NTFP harvest to be sustainable, lethal harvesting rate must be below 20%. For species with long lifespans such as trees (e.g. *Khaya senegalensis*), timber harvesting intensity must be below 2% for combined harvesting (leaf and timber) to be sustainable. Nonetheless, non-lethal harvesting can also significantly negatively impact population dynamics (see Schmidt *et al.* 2011) and strategies for sustainable resource use must consider both lethal and non-lethal harvests.

Our study provides new insights into classic harvest models and our new model can be readily applied to estimate sustainable harvest limits for lethal and non-lethal harvest of wild plants. We started with a classical harvest model which is often used to model the dynamics of harvested fisheries populations and timber harvesting. The novelty of our approach, however, resides in the fact that we are modelling two kinds of harvesting strategies, which have different impacts on population demographic processes. Lethal harvesting such as timber harvesting removes whole individuals from the population while non-lethal harvesting just removes part of the biomass while leaving individual units in the system, giving them the opportunity to contribute to population growth. The challenge was to find an appropriate way of modelling the effect of such non-lethal harvesting by introducing a second ordinary differential equation, which directly captures the impact of harvest on population growth rate. This modelling approach, unlike the classical harvest models, accounts for the indirect effects of harvest. We show that this novel approach yields more conservative estimates of sustainable harvest limits than most common modelling approaches used in non-timber forest product ecology (see for details Schmidt *et al.* 2011). Figure 2 particularly makes it easier to apply our method to determine real-life sustainable harvest limits for timber and/or non-lethal NTFP. By estimating the population growth rate for the species of interest in the absence of harvesting, r_c , and estimating the demographic costs of (lethal and/or non-lethal) NTFP or timber harvest (α and β) and computing r_c/α and $r_c/(1 + \beta)$, forest managers can determine combinations of sustainable harvesting rates. Future work on this problem can seek to incorporate structure (similarly to matrix projection models) and/or delay to account for different age groups and/or the time to maturity.

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Data accessibility

Data used in this manuscript are already publicly available from Ghimire *et al.* (2008), Gaoue & Ticktin (2010), Ticktin *et al.* (2002), Law (2007) and compiled in the appendix of Schmidt *et al.* (2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Equations for the sensitivity and elasticity analysis of \mathcal{R} and the nontrivial population equilibrium density x^* to lethal (h_l) and non-lethal harvesting (h_n).