

## Original Research Article

# Modeling the effects of size-dependent harvesting strategies on the population dynamics of tropical trees

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## ABSTRACT

Several forest plant species are harvested both lethally for their timber and non-lethally for their non-timber forest products by the local people for cultural and economic reasons. To maximize yield, harvesters target various life stages of these species including both adults and juveniles particularly when the number of harvestable adults decline. The demographic consequences of harvesting various plant sizes differ based on what life stage is targeted. In this paper, we develop a size-structured, seasonal system of difference equations and corresponding matrix model with time-varying harvest to model the effects of size-dependent harvesting strategies on the population dynamics of tropical trees. We illustrate numerically our work specifically on African mahogany, *Khaya senegalensis*, a tropical tree in Benin. Novel applications and combinations of previously established matrix compression algorithms are presented to determine certain rates in our model, with other rates coming from the use of generalized linear modeling and ordinary least squares estimation incorporating observed population data. Harvesting rates for two types of populations are estimated, one with simulated harvest and the other experiencing natural harvest. Eigenvalue analysis suggests that for the populations in our study, harvesting may not have a drastic effect on the long-term persistence of the population. However, this should be taken with caution given that our model does not account for stochastic environmental variations that can interactively reduce population growth rates.

## 1. Introduction

Understanding how local people can sustainably use the environmental resources on which they depend for their livelihood is critical for biodiversity conservation and future human population dynamics. Addressing this question has equally interested mathematical biologists [1–4] as well as empirical and theoretical ecologists [5–10]. The approach used to investigate sustainable harvest limits markedly differs between these two disciplines and can lead to different outcomes [3]. While most mathematical models focus on the dynamics of harvested species [11–13], applied ecologists are directly interested in the detailed influence of various harvesting strategies [14–17]. Models often failed to account for the multi-purpose harvest of plants in tropical forests given that most classical harvest models focus on hunting and logging [4,16,18,19], ignoring that non-lethal harvesting of plants is a widespread endeavour [17,20]. A more complex harvesting scheme often faced in tropical systems combines both lethal harvesting such as logging with non-lethal harvest of non-timber forest products [3,6,21].

In addition, the amount of biomass or fruit quality or concentration of secondary chemicals which confer medicinal values to plants tend to be size dependent. Therefore, it is critical to understand how size dependent harvest can impact the population dynamics of targeted species while accounting for the combined lethal versus non-lethal harvest. In this study, we explore different harvesting strategies and the corresponding impact on tree population dynamics. This work advances our overall understanding of the ecological processes that occur simultaneously when populations experience harvest, which may influence management strategies in the short-term or long-term.

In tropical regions, several plant species are harvested heterogeneously for timber (whole plant removal) and/or just partially by removing branches, leaves, or reproductive organs [6]. Non-lethal harvesting does not directly kill the tree, but results in a reduction in reproduction and thus the population growth rate [7]. Lethal harvesting does directly kill the tree and also affects the growth rate of the population [6]. Classical harvest models incorporate only the direct removal of individuals from the population, but do not account for the indirect

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effects of non-lethal harvesting [3]. Moreover, most stage-structured projection matrix models [22] do not explicitly include harvesting intensities, and therefore identifying how harvest directly affects specific stage transitions is challenging. The population dynamics consequences of stage specific vital rate changes can be evaluated using life table response experiment [23]. However, this approach limits our ability to examine the response of harvested systems to perturbation rates that are beyond the boundaries of rates empirically observed in nature.

Previous models incorporate non-lethal harvest to better explore the indirect effects on the population dynamics [7,17,21,24,25] but rarely include the effect of lethal harvest. However, failure to account for both lethal and non-lethal harvest can limit management options in terms of when to initiate each type of harvesting and what optimal harvesting intensity to allocate to each [6]. Recent work [3,6] includes the development of a general model to investigate the role of both lethal and non-lethal harvesting on plant population dynamics with application to timber and non-timber forest products harvest. An application of optimal control theory was used to determine optimal time-dependent non-lethal and lethal harvesting strategies, with the goal of maximizing conservation and benefits of harvesters, while minimizing cost [6]. The results in [6] illustrate the need for distinguishing between non-lethal and lethal harvesting effects on population levels and costs of harvesting. The different ‘optimal’ intensity levels of the two harvesting types were shown. However, these models failed to account for the size-dependent variation in harvest intensity over time.

In this study, we develop a model to investigate the effect of size-dependent harvesting strategies on plant population dynamics while considering the influence of harvesting types. We used data for *K. senegalensis* (African Mahogany), a large tree species in Benin that is harvested lethally for its timber and non-lethally for both its leaves and bark [26,27]. The latter type of harvest of non-timber forest products (NTFP) holds economic and cultural significance; for instance, local Fulani cattle-herders defoliate the trees in the dry season to feed their livestock [28]. *K. senegalensis* is typically 30 meters high with a 3 meter diameter, and due to the risk of climbing for harvesting, Fulani maximize the amount of foliage they obtain per tree, with an estimated 80% of trees fully defoliated on average [27].

The African mahogany harvest system has been extensively studied including using linear matrix projection models to investigate the short and long term dynamics of the species under harvesting and climate variations [25,29] and the role of stochasticity in shaping species response [30]. Work in [25] showed that the effect of NTFP harvest was greater in the short-term compared to the long-term by looking at differences in growth rates between low and high harvest intensities, and that early stage survival was more important for transient dynamics than long-term dynamics from elasticity analysis. These results suggested that using only long-term growth rates to inform harvest management decisions can be misleading. This stage-structured model generalized harvest of adults as high or low to explore short and long-term population growth rates, but was not explicit with the amount of harvest for each size class, and harvest did not vary over time. In addition, this model did not include the non-lethal harvest of juveniles or the lethal harvest of adults, which is unrealistic. These features provide the basis for our model presented in this paper: a stage-structured, time-varying harvesting system of difference equations and a corresponding matrix model for a tropical tree population. We will provide an illustration of our model specifically to the *K. senegalensis* population, with our focus on one area of Benin where this tree species grows: the Sudanian northern dry region. In our work, applications of compression algorithms enable a set of baseline rates to be determined for specific populations, with other rates estimated through ordinary least squares. A reproduction function dependent on non-lethal harvesting is established, as well, and the combination of these rates provide a basis for eigenvalue analysis to determine the impact harvesting has on the populations.

In this paper, we first describe the seasons in Benin that are incorporated into our discrete-time model based on methodologies in [31] and

provide an explanation of the model. An overview is then given of how the matrix model from [25] is compressed from five classes to four, a novel application of matrix compression algorithms, in order to inform rates in our  $4 \times 4$  matrix in which all adults are in the same class. This compression result is then used to find two specific  $4 \times 4$  matrix models representing naturally unharvested and harvested populations. Next, the reproduction function, which is dependent on harvest, is established for the harvested population. The remaining unknown rates are estimated for the harvested population and simulated harvest is applied to the unharvested population to determine effective levels of harvest that would be required to closely match the harvested population observed data. Finally, eigenvalue analysis is performed to determine the long-term effects of harvesting on the tree populations, and we then present our conclusions.

## 2. Methods

### 2.1. Background on seasons in the study system

The model we formulate in the next section is informed by seasonal events for tropical trees and we specifically use the African Mahogany population to discuss these as we will ultimately use this population as an illustration of our model. The northern region of Benin, where African mahogany is naturally distributed, experiences a dryer season from October to April, and a rainy season from May to September. Table 10 in the Appendix displays a detailed monthly calendar for events that occur [32] which informs our model in Section 2.2. Data collection on *K. senegalensis* tree populations happened on a yearly basis in December [32].

In October, “early fire” is set in the savanna to burn vegetation before it is too dry, as this is when grass is at its maximum height but not fully dry ( Table 10). This prevents accidental burning later on in the year and also facilitates community-based hunting. Because most grass in the region are annual, they rarely resprout after fire [33], leaving only trees to serve as the main source of fodder for livestock. Thus, after the “early fire”, non-lethal fodder tree branch harvesting begins and lasts most of the dry season [27]. Lethal harvest also mostly occurs in the dry season since it is easier for the logging companies to transport logs out of the forest in that period than in the wet season. Tree growth primarily takes place in the wet season. For our model, we do not include fire explicitly but instead let it be the implicit reasoning behind when harvest occurs.

### 2.2. Model formulation

Gaoue [25] developed a stage-structured matrix projection model to measure the impact of only non-lethal harvesting of adults on population dynamics. This model consisted of five population classes based on size: seedlings, saplings, juveniles, small-reproductive adults, and large-reproductive adults. Both reproductive adult classes were non-lethally harvested. Data was gathered from six populations in the Sudanian dry region of Benin, three of which were experiencing high harvest and the remaining three experiencing low harvest, as well as six populations from the Sudano-Guinean moist region in Benin with the same split in harvesting levels [25,29]. Population matrices were built using average population structures and harvesting intensities over 4 years.

We modified the model in [25] to develop a discrete harvesting model, specifically a Lefkovich matrix model derived from our system of difference equations outlined in this section [34]. The model is based on four size classes with units of number of trees:

- Seedlings ( $N$ ):  $0 \text{ cm} < \text{basal diameter} < 2 \text{ cm}$
- Saplings ( $S$ ):  $2 \text{ cm} \leq \text{basal diameter} < 5 \text{ cm}$
- Juveniles ( $J$ ):  $5 \text{ cm} \leq \text{diameter at breast height} < 20 \text{ cm}$
- Adults ( $A$ ):  $\text{diameter at breast height} \geq 20 \text{ cm}$ .

**Table 1**

Rates for our harvesting model with  $i = 1$  representing the seedling class,  $i = 2$  representing the sapling class,  $i = 3$  representing the juvenile class, and  $i = 4$  representing the adult class.

| Rate                     | Interpretation  |
|--------------------------|---|
| $\sigma_i$               | dry season, class $i$ survival probability  |
| $\sigma_{i+4}$           | wet season, class $i$ survival probability  |
| $\gamma_{ij}$            | class $i$ to class $j$ transition probability   |
| $\rho_{ij}$              | class $i$ to class $j$ shrinkage  |
| $h_N(k)$                 | time-dependent non-lethal adult harvest rate  |
| $h_L(k)$                 | time-dependent lethal adult harvest rate  |
| $h_J(k)$                 | time-dependent non-lethal juvenile harvest rate   |
| $\phi_A(h_N(k), h_L(k))$ | fertility rate of adult class; includes seedling survival in their first wet season (i.e. probability of establishment) |

We assume seedlings do not reproduce nor are harvested, juveniles do not reproduce but are able to be non-lethally harvested, and finally, adults are able to reproduce and are both non-lethally and lethally harvested [35]. We define reproduction as new seedlings that emerge as a result of adult trees dispersing seeds from the fruits they produce. In a practical sense, given that both the classes previously referred to as small adult and large adult in [25] are reproductive and both are non-lethally and lethally harvested, we have grouped them together into a single adult (A) class [32]. They are functionally the same with respect to harvest, so continuing the distinction of the classes would detract from the clarity of our model results. The compression of these classes in the model from [25] is discussed in detail in Section 2.3.

For our discrete-time model, we denote different events for the trees in Table 1 with  $i = 1$  representing the seedling class,  $i = 2$  the sapling class,  $i = 3$  the juvenile class, and  $i = 4$  the adult class (where  $k$  represents a year and  $k + 0.5$  represents the end of the dry season, discussed further below).

Harvesting can impose both direct and indirect effects on the tree population [6–8,17]. For example, human trampling of seedlings by harvesters and changes in adult canopy cover affect the survival rate of seedlings [26]. Although saplings are too far from adults to be affected by nonlethal harvesting and are also not affected by juvenile non-lethal harvesting, they are affected by the lethal harvest of adults due to the dragging of logs through the trees which damages them [32]. The two types of non-lethal harvest do not affect juveniles because they are too strong at that size to be affected. The lethal harvest of adults directly impacts adult tree survival and both the non-lethal and lethal harvest of adults affects its reproduction [6–8,17].

We formulate a model that starts in the dry season with positive initial conditions  $N(0) = N_0$ ,  $S(0) = S_0$ ,  $J(0) = J_0$ , and  $A(0) = A_0$  and then transitions to the wet season. We have  $k \geq 0$  denoting the time-step that represents a full year. Dry season dynamics are given by Eqs. (1)–(4) and run from time-step  $k$  to  $k + 0.5$ , while wet season dynamics are described by Eqs. (5)–(8), running from time-step  $k + 0.5$  to  $k + 1$ .

$$N(k + 0.5) = (1 - h_N(k) - \alpha_1 h_L(k) - h_J(k))\sigma_1 N(k) + \rho_{21}(1 - \alpha_2 h_L(k))\sigma_2 S(k) \tag{1}$$

$$S(k + 0.5) = (1 - \rho_{21})(1 - \alpha_2 h_L(k))\sigma_2 S(k) \tag{2}$$

$$J(k + 0.5) = \sigma_3 J(k) \tag{3}$$

$$A(k + 0.5) = (1 - h_L(k))\sigma_4 A(k) \tag{4}$$

$$N(k + 1) = \phi_A(h_N(k), h_L(k))A(k + 0.5) + (1 - \gamma_{12})\sigma_5 N(k + 0.5) \tag{5}$$

$$S(k + 1) = \gamma_{12}\sigma_5 N(k + 0.5) + (1 - \gamma_{23})\sigma_6 S(k + 0.5) \tag{6}$$

$$J(k + 1) = \gamma_{23}\sigma_6 S(k + 0.5) + (1 - \gamma_{34})\sigma_7 J(k + 0.5) \tag{7}$$

$$A(k + 1) = \gamma_{34}\sigma_7 J(k + 0.5) + \sigma_8 A(k + 0.5). \tag{8}$$

The order of events for each season is summarized in Fig. 1 with details in Table 10 in Appendix. The dry season from October–April

begins at time step  $k$ , which is the end of the previous year’s wet season. In the dry season, we assume that: there is no diameter growth and therefore no transition to the next size (see [36,37] regarding minimal growth), both non-lethal and lethal harvesting occur, shrinkage of saplings to seedlings occurs caused by fires or drought [29,38], and no reproduction occurs. Although seed dispersal occurs in some dry season months (January and February), we consider reproduction to include both the fertility of adult trees, which is dependent on harvesting in the dry season, and the survival of seedlings throughout the wet season and therefore, is placed as an event in the wet season.

In Eq. (1), a proportion of the seedlings from the previous wet season survive ( $\sigma_1$ ) and is subsequently reduced by the indirect effects of all three types of harvest of juveniles and adults, leaving  $(1 - h_N(k) - \alpha_1 h_L(k) - h_J(k))\sigma_1 N(k)$  seedlings by the end of the dry season. Next, a proportion of the saplings from the previous dry season shrink  $[\rho_{21}(1 - \alpha_2 h_L(k))\sigma_2 S(k)]$ . In Eq. (2) a proportion of the saplings from the previous wet season survive ( $\sigma_2$ ), subsequently reduced by indirect effects of the lethal harvesting of adults ( $\alpha_2 h_L(k)$ ). Then, due to a proportion of the saplings that shrink and leave to go to the seedling class ( $\rho_{21}$ ), the remaining saplings by the end of the dry season are represented by  $((1 - \rho_{21})(1 - \alpha_2 h_L(k))\sigma_2 S(k))$ . For the juvenile Eq. (3), a proportion of the juveniles from the previous wet season survive ( $\sigma_3$ ) to the end of the dry season. Finally, in Eq. (4), a proportion of the adults from the previous wet season survive ( $\sigma_4$ ), and then are brought down by the lethal harvesting of adults ( $h_L(k)$ ) leaving  $((1 - h_L(k))\sigma_4 A(k))$  adults by the end of the dry season.

The wet season from May–September starts at time step  $k + 0.5$ , which is the end of the dry season in year  $k$ , and is shown in Eqs. (5)–(8). In the wet season, we assume that there is transition to the next size classes, no non-lethal or lethal harvesting, and no shrinkage of saplings. Reproduction of seedlings from adult trees occurs at the beginning of the season after the adults from the dry season have been harvested. Growth is about 1 cm per year for first 5 years, then slower after that. Since there is essentially no growth happening in the dry season, at the end of the second wet season seedlings will transition to saplings (i.e. after 1.5 years instead of 2 full years) [32]. At this point, seedlings are at a size large enough to survive fire in the upcoming dry season and so are considered saplings [26,39].

For seedling Eq. (5), first a proportion of the seedlings from the previous dry season survive ( $\sigma_5$ ), and due to a proportion ( $\gamma_{12}$ ) of those that transition out to the sapling class, the remaining seedlings by the end of the wet season are represented by  $((1 - \gamma_{12})\sigma_5 N(k + 0.5))$ . Next, seeds are dropped based on the number of adults from the previous dry season, and a proportion of these germinate to become seedlings by the end of the wet season,  $(\phi_A(h_N(k), h_L(k))A(k + 0.5))$ . We note that  $\phi_A(h_N(k), h_L(k))$  includes both the reproduction/fertility rate of the adults, which relies on the non-lethal and lethal harvesting rates of adults in the previous dry season, and the survival of these seedlings in the wet season.

In Eq. (6), a proportion of the saplings from the previous dry season survive first ( $\sigma_6$ ), and due to a proportion of those that transition out to the juvenile class ( $\gamma_{23}$ ), the remaining saplings by the end of the wet season is represented by  $((1 - \gamma_{23})\sigma_6 S(k + 0.5))$ . Next, a proportion of seedlings from the previous dry season transition into the sapling class by the end of the wet season ( $\gamma_{12}\sigma_5 N(k + 0.5)$ ).

For the juvenile class in Eq. (7), a proportion of the juveniles from the previous dry season survive ( $\sigma_7$ ) and then a proportion of those transition out to the adult class ( $\gamma_{34}$ ). Thus, the remaining juveniles by the end of the wet season is represented by  $((1 - \gamma_{34})\sigma_7 J(k + 0.5))$ . Next, a proportion of the saplings from the previous dry season transition into the juvenile class by the end of the wet season ( $\gamma_{23}\sigma_6 S(k + 0.5)$ ). For Eq. (8), a proportion of the adults from the previous dry season survive ( $\sigma_8$ ) to the end of the wet season. Next, a proportion of the juveniles from the previous dry season transition into the adult class by the end of the wet season ( $\gamma_{34}\sigma_7 J(k + 0.5)$ ).

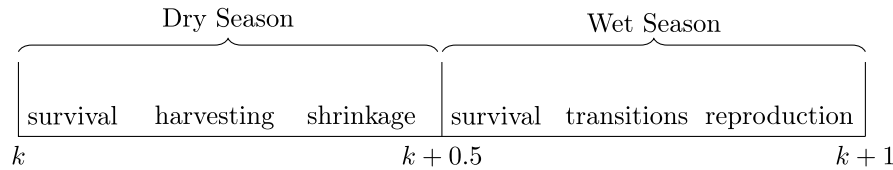


Fig. 1. A summary of the seasonal order of events for *K. senegalensis* in Benin where in year  $k$ , the dry season goes from  $k$  to  $k+0.5$  and the wet season goes from  $k+0.5$  to  $k+1$ .

Our model does not incorporate density dependence since we assume that harvesting has a strong top-down effect and already keeps the population below carrying capacity. In order to utilize data and rate information from [25,40] for African Mahogany populations, we compose our seasonal difference equation model into a matrix model with yearly time steps. To do so, we will compose matrices  $D$  and  $W$  for the dry and wet seasons based on the ecology of the system and subsequently multiply them together for the yearly model [41].

First, we represent our dry season difference Eqs. (1)–(4) with the dry season matrix,  $D$ , where

$$D = \begin{pmatrix} d_{11} & \rho_{21}(1 - \alpha_2 h_L(k))\sigma_2 & 0 & 0 \\ 0 & (1 - \rho_{21})(1 - \alpha_2 h_L(k))\sigma_2 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 \\ 0 & 0 & 0 & (1 - h_L(k))\sigma_4 \end{pmatrix}$$

with  $d_{11} = (1 - h_N(k) - \alpha_1 h_L(k) - h_J(k))\sigma_1$ . In vector notation, we multiply  $D$  with  $x_k = (N_k, S_k, J_k, A_k)^T$ , our vector of classes at the beginning of the dry season, to obtain the vector of classes at the end of the dry season,  $x_{k+0.5} = Dx_k$ .

Furthermore, the wet season difference Eqs. (5)–(8) may be represented by the wet season matrix,  $W$ , where

$$W = \begin{pmatrix} (1 - \gamma_{12})\sigma_5 & 0 & 0 & \phi_A(h_N(k), h_L(k)) \\ \gamma_{12}\sigma_5 & (1 - \gamma_{23})\sigma_6 & 0 & 0 \\ 0 & \gamma_{23}\sigma_6 & (1 - \gamma_{34})\sigma_7 & 0 \\ 0 & 0 & \gamma_{34}\sigma_7 & \sigma_8 \end{pmatrix}$$

In vector notation, we multiply the wet season matrix,  $W$ , with  $x_{k+0.5} = (N_{k+0.5}, S_{k+0.5}, J_{k+0.5}, A_{k+0.5})^T$ , our vector of classes at the beginning of the wet season, to obtain the vector of classes at the end of the wet season,  $x_{k+1} = Wx_{k+0.5} = WDX_k$ , in which we can set  $Y = WD$ . Therefore, by multiplying the dry season matrix,  $D$ , with the wet season matrix,  $W$ , in which the dry season occurs first and then the wet season, this results in our annual population matrix  $Y$  [41]. This is given by

$$Y = \begin{pmatrix} y_{11} & (1 - \gamma_{12})(1 - \alpha_2 h_L(k))\sigma_5 \rho_{21} & 0 & y_{14} \\ y_{21} & y_{22} & 0 & 0 \\ 0 & (1 - \rho_{21})(1 - \alpha_2 h_L(k))\sigma_6 \sigma_2 \gamma_{23} & (1 - \gamma_{34})\sigma_7 \sigma_3 & 0 \\ 0 & 0 & \gamma_{34}\sigma_7 \sigma_3 & (1 - h_L(k))\sigma_8 \sigma_4 \end{pmatrix} \tag{9}$$

where  $y_{11} = (1 - \gamma_{12})(1 - h_N(k) - \alpha_1 h_L(k) - h_J(k))\sigma_5 \sigma_1$ ,  $y_{21} = \gamma_{12}(1 - h_N(k) - \alpha_1 h_L(k) - h_J(k))\sigma_5 \sigma_1$ ,  $y_{22} = \gamma_{12}\sigma_5 \rho_{21}(1 - \alpha_2 h_L(2k + 1))\sigma_2 + (1 - \gamma_{23})\sigma_6(1 - \rho_{21})(1 - \alpha_2 h_L(2k + 1))\sigma_2$ , and  $y_{14} = \phi_A(h_N(k), h_L(k))(1 - h_L(k))\sigma_4$ . Next, we demonstrate the method used to extract information on rate values from previous work.

### 2.3. Matrix compression

The compression of a square matrix from one dimension to a smaller one is necessary in some cases and can be performed using one of two previously established algorithms, depending on whether the goal is to maintain long-term dynamics [42] or short-term dynamics [43].

In our work, we have the  $4 \times 4$  matrix (9), in which all adults are in one class, that we wish to gain rate information for. Much of this rate information is available in the  $5 \times 5$  matrix found in [25] which uses parallel notation to our population matrix but has adults separated into two groups. Rate information is more easily extracted if that matrix is

compressed to a  $4 \times 4$  matrix with the two adult groups combined like our matrix is structured, a previously discussed idea in Section 2.2. This better reflects the reality of harvesting practices performed on adult trees since both of the adult classes are reproductive and non-lethally and lethally harvested.

Therefore, in order to use rate data from previous work to inform our novel difference equation model and population matrix,  $Y$ , we first compress the  $5 \times 5$  population matrix from [25] to a  $4 \times 4$  matrix where the two adults groups are combined into one. The general process of matrix compression for matrix (10) from [25], modified to fit the context of our work, is outlined below. Applications of this process to specific tree populations will be described in Sections 3.1 and 3.2 in which rate values for our novel  $4 \times 4$  harvesting population matrices for these populations are able to be determined.

The matrix projection model in [25] is given by

$$U = \begin{pmatrix} \sigma_1(1 - \gamma_{12}) & \sigma_2 \rho_{21} & 0 & \sigma_4 \phi_4 & \sigma_5 \phi_5 \\ \sigma_1 \gamma_{12} & \sigma_2(1 - \gamma_{23} - \rho_{21}) & 0 & 0 & 0 \\ 0 & \sigma_2 \gamma_{23} & \sigma_3(1 - \gamma_{34}) & 0 & 0 \\ 0 & 0 & \sigma_3 \gamma_{34} & \sigma_4(1 - \gamma_{45}) & 0 \\ 0 & 0 & 0 & \sigma_4 \gamma_{45} & \sigma_5 \end{pmatrix} \tag{10}$$

Rates for shrinkage of the juvenile, small adult, and large adult classes have been set to zero, as we do not consider those dynamics in our work. We now collapse classes 4 and 5 in matrix (10) using two different algorithms depending on whether the goal is to maintain long-term dynamics or transient dynamics.

For preserving long-term dynamics, a compression algorithm in [42] regarding matrix models with both transitions and reproduction seeks to maintain the dominant eigenvalue  $\lambda$  from an original  $n \times n$  matrix model  $U$  for the collapsed  $(n - 1) \times (n - 1)$  matrix  $C_1$ . It also seeks to maintain the associated eigenvector  $\mathbf{u} = (u_1, u_2, \dots, u_i, u_{i+1}, \dots, u_n)^T$  in  $C_1$  as  $\mathbf{c}_1 = (u_1, u_2, \dots, u_i + u_{i+1}, \dots, u_n)^T$  when collapsing classes  $u_i$  and  $u_{i+1}$ . Applying this algorithm to collapse classes 4 and 5 while maintaining long-term behavior results in the collapsed matrix  $C_1$ , where

$$C_1 = \begin{pmatrix} \sigma_1(1 - \gamma_{12}) & \sigma_2 \rho_{21} & 0 & \sigma_4 \phi_4 \frac{u_4}{u_4 + u_5} + \sigma_5 \phi_5 \frac{u_5}{u_4 + u_5} \\ \sigma_1 \gamma_{12} & \sigma_2(1 - \gamma_{23} - \rho_{21}) & 0 & 0 \\ 0 & \sigma_2 \gamma_{23} & \sigma_3(1 - \gamma_{34}) & 0 \\ 0 & 0 & \sigma_3 \gamma_{34} & \sigma_4 \frac{u_4}{u_4 + u_5} + \sigma_5 \frac{u_5}{u_4 + u_5} \end{pmatrix} \tag{11}$$

In this algorithm, the long-term behavior is ensured in the compressed matrix by multiplying matrix (10) on the left and right by specific matrices, denoted  $P$  and  $Q$ , that satisfy  $Q\mathbf{c}_1 = \mathbf{u}$  and  $\mathbf{P}\mathbf{u} = \mathbf{c}_1$ , with  $Q$  utilizing proportions from the stable stage distribution as weights ( $\frac{u_4}{u_4 + u_5}$  and  $\frac{u_5}{u_4 + u_5}$ ). This results in

$$C_1 \mathbf{c}_1 = \mathbf{P}UQ\mathbf{c}_1 = \mathbf{P}U\mathbf{u} = P\lambda\mathbf{u} = \lambda\mathbf{P}\mathbf{u} = \lambda\mathbf{c}_1$$

and therefore our resulting matrix  $C_1$ , matrix (11), has the same eigenvalue as matrix  $U$ , matrix (10), and desired associated eigenvector. The specific application of this matrix compression process to an unharvested population (Nipuni) is given in Section 3.1.

However, for some populations, maintaining accurate short-term, or transient, dynamics is of interest. A compression algorithm by Spears [43] is for probability transition matrices (Markov chain models)

with entries representing the probability of transitioning from state to another in one step. The focus of this algorithm is on maintaining accurate transient behavior and minimizing the associated error.

To apply the algorithm presented in [43] on matrix (10) we only focus on the juvenile, small adult, and large adult classes since these are the only *transitions* involved with the compression of the last two classes. Thus, we instead consider the matrix

$$M = \begin{pmatrix} \sigma_3(1 - \gamma_{34}) & 0 & 0 \\ \sigma_3\gamma_{34} & \sigma_4(1 - \gamma_{45}) & 0 \\ 0 & \sigma_4\gamma_{45} & \sigma_5 \end{pmatrix}.$$

This algorithm utilizes weights  $(\frac{m_2}{m_2+m_3}, \frac{m_3}{m_2+m_3})$  representing proportions of each adult class out of the total adult population based on information from the matrix on the time spent in each of these classes. A weighted average is then taken of rows 2 and 3 and after simplification, columns 2 and 3 are combined, and then rows 2 and 3 are combined in order to produce a  $2 \times 2$  compressed matrix. The compressed matrix resulting from this algorithm is given by

$$M_c = \begin{pmatrix} \sigma_3(1 - \gamma_{34}) & 0 \\ \sigma_3\gamma_{34} & \sigma_4 \frac{m_2}{m_2+m_3} + \sigma_5 \frac{m_3}{m_2+m_3} \end{pmatrix}.$$

Spears' algorithm [43] only includes information on how to properly adapt transition probabilities, and not fertility rates, to obtain a compressed matrix. However, we observe that the result of the algorithm used for transition terms in [43] is comparable to the result of the algorithm in [42] with the only difference being the weights, which depended on what dynamics the algorithm was trying to maintain. Thus, we apply a similar intuition for the fertility rates in this case as the algorithm in [42], where the fertility will now be weighted based on how long trees spend in each of the adult classes. This results in

$$\sigma_4\phi_4 \frac{m_2}{m_2+m_3} + \sigma_5\phi_5 \frac{m_3}{m_2+m_3}.$$

Thus, we have the following compressed matrix with 4 classes from this algorithm focused on maintaining transient dynamics

$$C_2 = \begin{pmatrix} \sigma_1(1 - \gamma_{12}) & \sigma_2\rho_{21} & 0 & \sigma_4\phi_4 \frac{m_2}{m_2+m_3} + \sigma_5\phi_5 \frac{m_3}{m_2+m_3} \\ \sigma_1\gamma_{12} & \sigma_2(1 - \gamma_{23} - \rho_{21}) & 0 & 0 \\ 0 & \sigma_2\gamma_{23} & \sigma_3(1 - \gamma_{34}) & 0 \\ 0 & 0 & \sigma_3\gamma_{34} & \sigma_4 \frac{m_2}{m_2+m_3} + \sigma_5 \frac{m_3}{m_2+m_3} \end{pmatrix}. \tag{12}$$

The application of this matrix compression process to a harvested population, Soassaraoru, is provided in Section 3.2.

We have outlined compressing a  $5 \times 5$  population matrix to a  $4 \times 4$  population matrix dependent on the dynamics to be maintained. In the next few sections, we outline how this compression process will be performed on specific populations, including an unharvested and a harvested population, and how the compressed matrix in this section will be compared to our harvesting matrix model. This will all be put together to extract rate information.

### 3. Results

Using methodologies from Section 2.3, we now collapse the matrix population models with 5 classes found in [25] (with corresponding data in [40]) to 4 classes for two specific populations of the tree species, applying the appropriate algorithm depending on the desired behavior to be maintained. One population of *K. Senegalensis* we focus on in this work is an unharvested population, Nipuni, which is a gallery forest in a national park where it has never been logged or pruned, and therefore is considered unharvested or pristine, compressed in Section 3.1. Another population, Soassararou, is a harvested population found in the same region but not protected in a national park. Instead, it is a population in the wild that the Fulani people have been harvesting for several decades, and this population matrix is compressed in Section 3.2. Since

**Table 2**

Rates for the unharvested (Nipuni) population using data from [25] and referenced in Matrix (10).

| Rate in matrix (10) | Value from [40] | Rate in matrix (10) | Value from [40] |
|---------------------|-----------------|---------------------|-----------------|
| $\sigma_1$          | 0.4354          | $\gamma_{12}$       | 0.028           |
| $\sigma_2$          | 0.7269          | $\gamma_{23}$       | 0.2102          |
| $\rho_{21}$         | 0               | $\sigma_3$          | 1               |
| $\gamma_{34}$       | 0.0304          | $\sigma_4$          | 1               |
| $\phi_4$            | 0.0001          | $\gamma_{45}$       | 0.0417          |
| $\sigma_5$          | 0.9999          | $\phi_5$            | 0.1603          |

Nipuni is in the same ecological zone, we consider this population to be the unharvested baseline for the harvested population Soassararou. We consider the transient phase of the trees to be 5 years because that is when management decisions need to be re-evaluated due to human interference. Remaining rates for these populations are estimated in Sections 3.4 and 3.5 and eigenvalue analysis for varying harvest rates is given in Section 3.6. For clarity of reading and reminding the reader of the status of harvest, Nipuni will henceforth often be referred to as our unharvested population and Soassararou our harvested population.

#### 3.1. Compression algorithm [42] applied to preserve long-term dynamics for unharvested (Nipuni) population

For a population that is unharvested and protected in a national park, it can be thought of as at equilibrium. Therefore, we aim to maintain the long-term behavior of our unharvested population. The original matrix population model given in [40], and which follows the form of matrix (10) in Section 2.3, is

$$N = \begin{pmatrix} 0.4232 & 0 & 0 & 0.0001 & 0.1603 \\ 0.0122 & 0.5741 & 0 & 0 & 0 \\ 0 & 0.1528 & 0.9696 & 0 & 0 \\ 0 & 0 & 0.0304 & 0.9583 & 0 \\ 0 & 0 & 0 & 0.0417 & 0.9999 \end{pmatrix}. \tag{13}$$

The values of the individual rates that go into these entries are found in Table 2. The dominant eigenvalue for this population matrix 3.1 is  $\lambda = 1.001$  and the normalized stable stage distribution is

$$\mathbf{n} = \begin{pmatrix} 0.2053 \\ 0.0059 \\ 0.0285 \\ 0.0203 \\ 0.74 \end{pmatrix}.$$

Following the algorithm in [42] to maintain long-term behavior, we obtain the following compressed matrix (calculations to obtain matrix entries in the Appendix) with only one adult group

$$N_c = \begin{pmatrix} 0.4232 & 0 & 0 & 0.156 \\ 0.0122 & 0.5741 & 0 & 0 \\ 0 & 0.1528 & 0.9696 & 0 \\ 0 & 0 & 0.0304 & 0.9999 \end{pmatrix}, \tag{14}$$

which has dominant eigenvalue  $\lambda_c = 1.001$  and normalized stable stage distribution

$$\mathbf{n}_c = \begin{pmatrix} 0.2053 \\ 0.0059 \\ 0.0285 \\ 0.7603 \end{pmatrix}.$$

The proportion of adults in the original stable stage distribution  $\mathbf{n}$  matches the total proportion of adults in  $\mathbf{n}_c$ , and the other entries in the stable stage distributions  $\mathbf{n}$  and  $\mathbf{n}_c$  match exactly, as desired.

**Table 3**

Rates for the harvested (Soassararou) population with rates originally from [25] and referenced in Matrix (10).

| Rate in matrix (10) | Value from [40] | Rate in matrix (10) | Value from [40] |
|---------------------|-----------------|---------------------|-----------------|
| $\sigma_1$          | 0.3969          | $\gamma_{12}$       | 0.0003          |
| $\sigma_2$          | 0.8616          | $\gamma_{23}$       | 0.1091          |
| $\rho_{21}$         | 0               | $\sigma_3$          | 0.9721          |
| $\gamma_{34}$       | 0.0215          | $\sigma_4$          | 0.9604          |
| $\phi_4$            | 0.0732          | $\gamma_{45}$       | 0.0872          |
| $\sigma_5$          | 0.9785          | $\phi_5$            | 0.1564          |

**3.2. Compression algorithm [43] applied to preserve short-term dynamics for harvested (Soassararou) population**

On the other hand, for our harvested population, we wish to maintain the short-term or transient behavior of the population in our model. The original matrix population model given in [40] with corresponding rates in Table 3 is

$$S = \begin{pmatrix} 0.3968 & 0 & 0 & 0.0703 & 0.153 \\ 0.0001 & 0.7676 & 0 & 0 & 0 \\ 0 & 0.094 & 0.9512 & 0 & 0 \\ 0 & 0 & 0.0209 & 0.8767 & 0.0108 \\ 0 & 0 & 0 & 0.0837 & 0.9677 \end{pmatrix}. \tag{15}$$

We run this model for 5 years, a reasonable timeframe before re-evaluating forest management decisions, with initial conditions represented by  $[0.42, 0.05, 0.19, 0.18, 0.16]^T$  [32]. This results in the normalized population vector

$$s = \begin{pmatrix} 0.1204 \\ 0.0243 \\ 0.2926 \\ 0.2094 \\ 0.3533 \end{pmatrix}.$$

Next, we compress matrix (15) into 4 classes with the goal of having it closely match this distribution of classes at the 5 year mark. Using Spears' algorithm [43] and focusing on the juvenile, small adult, and large adult classes, we get

$$M = \begin{pmatrix} 0.9512 & 0 & 0 \\ 0.0209 & 0.8767 & 0.0108 \\ 0 & 0.0837 & 0.9677 \end{pmatrix}.$$

Then, following the algorithm described in detail in Section 2.3, with  $m_2 = 0.9084$  and  $m_3 = 1.051$  and other details outlined in the Appendix, we obtain:

$$M_c = \begin{pmatrix} 0.9512 & 0 \\ 0.0209 & 0.9701 \end{pmatrix}.$$

Finally, after calculation of the fertility rate as described in Section 2.3 and shown in the Appendix, we have the following compressed matrix for the harvested population of interest,

$$S_c = \begin{pmatrix} 0.3968 & 0 & 0 & 0.1147 \\ 0.0001 & 0.7676 & 0 & 0 \\ 0 & 0.094 & 0.9512 & 0 \\ 0 & 0 & 0.0209 & 0.9701 \end{pmatrix}. \tag{16}$$

Our compressed matrix has adult survival and adult reproduction rates as shown in Table 12 corresponding to the lower right hand entry and upper right hand entry, respectively.

Taking this 4 class matrix model and running it for 5 years with initial conditions  $[0.42, 0.05, 0.19, 0.34]^T$  results in the following normalized population vector

$$s_c = \begin{pmatrix} 0.117 \\ 0.0244 \\ 0.2937 \\ 0.5649 \end{pmatrix}.$$

**Table 4**

Rates for our unharvested population (Nipuni) model combining rate information from Tables 2 and 11 with rate notation in the third column denoting those from the compressed matrix (14) of [40], following the general form of matrix (11).

| Rate in our unharvested population (Nipuni) matrix model (17) | Value of rate | Corresponding rate in compressed matrix (11)                                |
|---|---------------|---|
| $\sigma_5 \sigma_1 = \sigma_N$                                | 0.4354        | $\sigma_1$  |
| $\gamma_{12}$   | 0.028         | $\gamma_{12}$   |
| $\sigma_6 \sigma_2 = \sigma_S$                                | 0.7269        | $\sigma_2$  |
| $\gamma_{23}$   | 0.2102        | $\gamma_{23}$   |
| $\sigma_7 \sigma_3 = \sigma_J$                                | 1             | $\sigma_3$  |
| $\gamma_{34}$   | 0.0304        | $\gamma_{34}$   |
| $\sigma_8 \sigma_4 = \sigma_A$                                | 0.9999        | $\sigma_4 \frac{u_4}{u_4+u_5} + \sigma_5 \frac{u_5}{u_4+u_5}$               |
| $\phi_A \sigma_4$   | 0.156         | $\sigma_4 \phi_4 \frac{u_4}{u_4+u_5} + \sigma_5 \phi_5 \frac{u_5}{u_4+u_5}$ |

Comparing this to  $s$ , we see there is a 2.8% error in the seedling stage ( $\frac{0.1204-0.117}{0.1204} = 0.0282$ ), a 0.41% error in saplings ( $\frac{0.0244-0.0243}{0.0243} = 0.0041$ ), a 0.38% error in juveniles ( $\frac{0.2937-0.2926}{0.2926} = 0.0038$ ), and finally a 0.39% error in adults ( $\frac{0.5649-0.5627}{0.5627} = 0.0039$ ).

**3.3. Explicit harvesting models for each population**

We now apply our matrix model (9) to both the unharvested and harvested populations and relate rate information from previous work to this notation. For our unharvested population that is protected in a national park, all harvesting terms ( $h_J(k)$ ,  $h_N(k)$ , and  $h_L(k)$ ) in matrix (9) are set to zero. This population does not shrink from sapling to seedling size, so  $\rho_{21} = 0$ , as well. Yearly survival rates are equivalent to surviving both the dry season and wet season, which results in the multiplication of seasonal survival rates in our model. This results in the following matrix for our unharvested population, Nipuni, with rates recorded in Table 4:

$$N_h = \begin{pmatrix} (1 - \gamma_{12})\sigma_5 \sigma_1 & 0 & 0 & \phi_A \sigma_4 \\ \gamma_{12} \sigma_5 \sigma_1 & (1 - \gamma_{23})\sigma_6 \sigma_2 & 0 & 0 \\ 0 & \gamma_{23} \sigma_6 \sigma_2 & (1 - \gamma_{34})\sigma_7 \sigma_3 & 0 \\ 0 & 0 & \gamma_{34} \sigma_7 \sigma_3 & \sigma_8 \sigma_4 \end{pmatrix}. \tag{17}$$

In the harvested population, adults are non-lethally harvested but not lethally harvested, nor are juveniles harvested. As a starting point, we will assume constant harvesting of this population and therefore, harvesting will occur at the same rate each dry season. From matrix (9), we do not know the unharvested rates  $\sigma_5 \sigma_1 = \sigma_N$  (seedling survival rate) and  $\gamma_{12}$  (rate of transition from seedling to sapling) for the population because harvesting is implicitly impacting the corresponding rates in matrix (15) we are drawing rate information from [25,40]. Applying our model to the harvested population results in the rates given in Table 5 (with the exception of the reproduction function which is derived in Section 3.4 and the values of the unknown parameters which are estimated in Section 3.5) and the following matrix:

$$S_h = \begin{pmatrix} (1 - \gamma_{12})(1 - h_N)\sigma_5 \sigma_1 & 0 & 0 & \phi_A(h_N)\sigma_4 \\ \gamma_{12}(1 - h_N)\sigma_5 \sigma_1 & (1 - \gamma_{23})\sigma_6 \sigma_2 & 0 & 0 \\ 0 & \gamma_{23} \sigma_6 \sigma_2 & (1 - \gamma_{34})\sigma_7 \sigma_3 & 0 \\ 0 & 0 & \gamma_{34} \sigma_7 \sigma_3 & \sigma_8 \sigma_4 \end{pmatrix}. \tag{18}$$

**3.4. Estimation of harvested population (Soassararou) adult reproduction function dependent on non-lethal harvesting**

In order to determine the effective non-lethal harvesting rate that occurs for adult individuals in our harvested population, we must first determine a form for the reproduction function for the population that depends on the non-lethal harvesting of adults,  $\phi_A(h_N)$ . We do so by

**Table 5**

Rates for our harvested population (Soassararou) model combining rate information from Tables 3 and 12 with rate notation in the third column denoting those from the compressed matrix (16) of [40] following the general form of matrix (12).

| Rate in our harvested population (Soassararou) matrix model (18) | Value of rate | Corresponding rate in compressed matrix (12)                                |
|--|---------------|---|
| $\sigma_5 \sigma_1 = \sigma_N$                                   | –             | $\sigma_1$  |
| $\gamma_{12}$  | –             | $\gamma_{12}$   |
| $\sigma_6 \sigma_2 = \sigma_S$                                   | 0.8616        | $\sigma_2$  |
| $\gamma_{23}$  | 0.1091        | $\gamma_{23}$   |
| $\sigma_7 \sigma_3 = \sigma_J$                                   | 0.9721        | $\sigma_3$  |
| $\gamma_{34}$  | 0.0215        | $\gamma_{34}$   |
| $\sigma_8 \sigma_4 = \sigma_A$                                   | 0.9701        | $\sigma_4 \frac{m_2}{m_2+m_3} + \sigma_5 \frac{m_1}{m_2+m_3}$               |
| $\phi_A(h_N)$  | –             | $\sigma_4 \phi_4 \frac{m_2}{m_2+m_3} + \sigma_5 \phi_5 \frac{m_1}{m_2+m_3}$ |
| $\sigma_4$   | –             | –   |
| $h_N$  | –             | –   |

analyzing the individual tree data for the population [44]. Since harvesting (pruning) and seed dispersal from fruits happen simultaneously throughout the dry season, we make the assumption that the number of fruits produced and reported in the data are those leftover at the end of the dry season. They therefore have the ability to disperse seeds, which have the potential of germinating/establishing to become seedlings.

*Generalized linear model between percent pruned and fruit production*

Next, we investigate the relationship between the percent loss of foliage of adults (i.e. the percent harvested/pruned per adult individual) and the number of fruits produced (that disperse seeds for seedlings). To find the function that represents the effect of harvest on reproduction, we fit a generalized linear model [45]. We use the negative binomial distribution with mean  $\mu$  for our response variable (which is the number of fruits produced per adult individual per year) since the variance is much bigger than the mean and is therefore overdispersed.

The systematic part, or linear combination of our predictor variables, is defined as

$$v = a + b(DBH) + c(h_N)$$

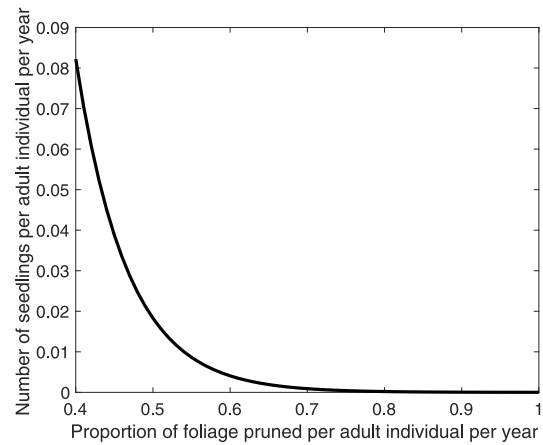
where  $DBH$  and  $h_N$  are the predictor variables and  $v$  is related to the mean of the response variable such that  $\log(\mu) = v$ . In other words, the mean of the number of fruits produced per adult individual per year is given by:

$$\mu = e^{a+b(DBH)+c(h_N)},$$

which ensures non-negativity for the mean of our response variable. We then estimate  $a, b,$  and  $c$  using maximum likelihood estimation as implemented by the `bbmle` package and `mle2` function with the software package R 2022.07.1.

*Utilizing data from similar populations*

After considering various sets of data to most accurately build this relationship of the number of fruits produced based on  $DBH$  and harvest levels, our results come from data of three different harvested populations (Soassararou, Nigoussourou, and Gbeba) from 2004–2007 (a total of 146 trees with an average  $DBH$  of 46.2089) since these populations are in similar ecological zones and all experience non-lethal harvesting of adults. As we do not have  $DBH$  explicitly in our model, we set  $DBH = DBH_{avg}$  using the average for the sample of trees in the data. In this manner, we get information on the mean fruit/seedling production per adult individual depending on its harvest level. Due to sparse harvesting level data between 0 and 0.4 during the years 2004–2007, we strictly used data with harvest levels of 0.4 or greater to establish a reproduction function based on non-lethal



**Fig. 2.** The reproduction function,  $\phi_A(h_N)$ , for the harvested population (Soassararou) representing the average number of seedlings produced from an adult individual as a function of average proportion of foliage pruned per adult individual. When all of the foliage is removed at a harvesting level of 1, the seedling production is very close to 0 as would be expected.

harvest. For any trees that had positive fruit leftover at the end of the season, we used an upper bound for the level of harvest to be 99.5% [44]. Moreover, we only used data from trees that had all of the following information: diameter breast height ( $DBH$ ), pruning intensity ( $h_N$ ), and fruit production.

In 2004, there were 3076 fruits produced overall for these three populations with 279 seedlings that germinated. Thus, we make the assumption that each fruit produces  $\frac{279}{3076}$  seedlings on average (i.e. we view each fruit as identical with the same number of seeds and the same potential for dispersing seeds/becoming seedlings). Therefore, to get the average number of *seedlings* per adult individual in 2004, we multiply the function  $\mu$  (the mean number of fruits produced per adult individual per year) by  $\frac{\text{number of seedlings}}{\text{number of fruits produced}} = \frac{279 \text{ seedlings in 2004}}{3076 \text{ fruits produced in 2004}}$  to get our reproduction function,  $\phi_A$ ,

$$\phi_A = \frac{279}{3076} \mu.$$

We implicitly make the assumption that the percent reduction in fruit production from increased harvest is equivalent to percent reduction in seedlings by using the same exponential function (i.e. 80% reduction in fruit from harvesting will be an 80% reduction in seedlings). To ensure that seedling production is near 0 when  $h_N = 1$ , i.e. the non-lethal harvesting rate is 100%, we constrain our seedling function to ensure this behavior.

We consider the constraint value to be 0.00001, so that

$$\phi_A(1) = \frac{279}{3076} e^{a+b(DBH_{avg})+c(1)} = 0.00001.$$

Solving for  $a$  from this equation results in  $a = -9.1128 - b(DBH_{avg}) - c$ . Substituting into our desired function, we obtain

$$\phi_A(h_N) = \frac{279}{3076} e^{-9.1128+b(DBH-DBH_{avg})+c(h_N-1)}.$$

Returning to the following fruit reproduction function to solve for  $b$  and  $c$  using maximum likelihood estimation,

$$\mu(h_N) = e^{-9.1128+b(DBH-DBH_{avg})+c(h_N-1)},$$

we obtain  $b = 0.1216$ ,  $c = -15.0242$ , and can then solve for  $a = 0.2924$ .

Therefore, the reproduction function for the harvested population (Soassararou) is given by

$$\phi_A(h_N) = \frac{279}{3076} e^{0.2924+0.1216(46.2089)-15.0242h_N} \tag{19}$$

from the constraint case of  $h_N(1) = 0.00001$ . The resulting seedling graph is shown in Fig. 2.

**Table 6**

Soassararou 2005–2007 observed data from [44] used for parameter estimation.

| Class    | Data         | Notation          |
|----------|--------------|-------------------|
| Seedling | [12, 10, 8]  | Data <sub>1</sub> |
| Juvenile | [19, 19, 18] | Data <sub>2</sub> |
| Adult    | [53, 53, 54] | Data <sub>3</sub> |

### 3.5. Estimation of harvesting rates with constant harvesting intensity on specific populations

For our harvested (Soassararou) population, a few rates need to be determined, including that of an effective harvesting rate for the population. From population level calculations in the field, Gaoue observed an average pruning rate of 84% for adult individuals [44]. For individuals that were debarked, the average debarking intensity was 28.35%. However, we cannot use these observed percentages directly in our model and instead need to calculate  $h_N$ , which is the effect harvesting has on certain vital rates, where we have assumed a linear effect on the survival rate of seedlings and a nonlinear effect on the reproduction rate. In addition, this harvested population has unknown rates that need to be estimated:  $\sigma_N$ , the survival rate of seedlings;  $\gamma_{12}$ , the rate of transition from the seedling to sapling class; and  $\sigma_4$ , the survival rate of adults in the dry season.

To estimate these rates, we compare the observed data from this harvested population (Soassararou) to simulations of our harvesting model applied to the same harvested population to determine what level of harvest gives the best fit and the optimal values of our unknown rates. In addition, we take the unharvested, pristine Nipuni population, apply simulated harvesting to it, and aim to match the output with observed data from the Soassararou naturally harvested population as best as possible. This allows us to determine what harvesting level the Nipuni population would need to experience to best match observed data from a harvested population in a similar ecological zone.

The model we will be using to simulate harvesting on both of these populations, which is the matrix model for the harvested population discussed in Section 3.3, is given by

$$S_h = \begin{pmatrix} (1 - \gamma_{12})(1 - h_N)\sigma_5\sigma_1 & 0 & 0 & \phi_A(h_N)\sigma_4 \\ \gamma_{12}(1 - h_N)\sigma_5\sigma_1 & (1 - \gamma_{23})\sigma_6\sigma_2 & 0 & 0 \\ 0 & \gamma_{23}\sigma_6\sigma_2 & (1 - \gamma_{34})\sigma_7\sigma_3 & 0 \\ 0 & 0 & \gamma_{34}\sigma_7\sigma_3 & \sigma_8\sigma_4 \end{pmatrix}. \tag{20}$$

Our model is formulated to start in the dry season and since the data we have available is for December (a few months into the dry season), we use those data for our initial conditions for 2004. The number of observed trees in December 2004 was 18 seedlings, 18 juveniles, and 54 adults; there is no information on the number of saplings so we estimate that number. The initial conditions are therefore IC = [18,  $S_0$ , 18, 54].

We use the 2004 observed harvested population (Soassararou) data points as initial conditions for both the unharvested population (Nipuni) and harvested population (Soassararou) harvesting models so we can observe the behaviors of the populations from the same starting point. Once the initial value of the sapling class,  $S_0$ , is estimated from the Soassararou fitting process, we will use that value for the fitting process with Nipuni. The remaining data points we have for the number of Soassararou seedlings, juveniles, and adults from 2005–2007 are shown in Table 6.

In order to estimate the unknown parameters, we aim to minimize the difference between the harvested population (Soassararou) observed data and the simulated output for each class from both the harvested population and unharvested population harvesting models, with simulated harvest applied to the latter population, given by matrix (20) and using the ordinary least squares method. We do this by

**Table 7**

Rates for harvested population (Soassararou) harvesting model with bold rates determined from parameter estimation process.

| Rate in estimation            | Value of rate | Rate in estimation            | Value of rate |
|-------------------------------|---------------|-------------------------------|---------------|
| $\sigma_5\sigma_1 = \sigma_N$ | <b>0.6</b>    | $\sigma_8\sigma_4 = \sigma_A$ | 0.9701        |
| $\gamma_{12}$                 | <b>0.01</b>   | $\phi_A(h_N)$                 | 0.1015        |
| $\sigma_6\sigma_2 = \sigma_S$ | 0.8616        | $\sigma_4$                    | <b>0.9701</b> |
| $\gamma_{23}$                 | 0.1091        | $h_N$                         | <b>0.3860</b> |
| $\sigma_7\sigma_3 = \sigma_J$ | 0.9721        | $S_0$                         | <b>14</b>     |
| $\gamma_{34}$                 | 0.0215        |                               |               |

summing over the differences at each time step and for each class, letting Diff<sub>1</sub> be the vector that represents the differences between Soassararou observed seedling data and simulated values for the respective population for seedlings from 2005–2007, Diff<sub>2</sub> the differences between juvenile data from 2005–2007, and Diff<sub>3</sub> the differences in the adult class data from 2005–2007. Then, our objective function takes the form of

$$\text{objective function} = \sum_{i=1}^3 \frac{\sqrt{\sum_{k=1}^3 \text{Diff}_i(k)^2}}{\sqrt{\sum_{k=1}^3 \text{Data}_i(k)^2}},$$

where the relative norm is taken due to differences in the sizes of the classes with  $k$  denoting the years and  $i$  denoting the classes.

We assume a constant harvest each dry season for the purposes of getting baseline harvesting values for each population and use the MultiStart algorithm and fmincon local solver from the Global Optimization Toolbox in MATLAB R2022B to minimize our objective function. For the harvested population (Soassararou) harvesting model, we estimate 5 parameters ( $\sigma_N$ ,  $\gamma_{12}$ ,  $\sigma_4$ ,  $h_N$ , and  $S_0$ ) with 9 data points. For the Nipuni harvesting model, we estimate 1 parameter ( $h_N$ ) with 9 data points.

In each case, we use 200 starting points - a sufficient number to obtain the same global minimum and parameter values upon multiple runs. With bounds given in Table 13 in the Appendix, the objective function value for fitting to the harvested population (Soassararou) harvesting matrix simulations was 0.1094 and the resulting rates for the harvested population are bolded in Table 7. The resulting value for  $S_0$  was 14.4546, which we round down to 14 since this is a number of trees. We also note that  $h_N = 0.3860$  is a reasonable value to evaluate  $\phi_A(h_N)$  at, as it is only a slight extension beyond the data ( $h_N = 0.4$  to  $h_N = 1$ ) the function was built upon in Section 3.4. Both  $\sigma_N$  and  $\gamma_{12}$  achieve their respective upper and lower bounds, and upon considering different bounds for these parameters, they achieve any bound that is provided. However, all of the resulting parameter estimates are very similar with the objective function changing only slightly.

From the finalized parameters given in Table 7, the Soassararou, harvested population matrix is given by

$$S_h(\text{Soas}) = \begin{pmatrix} 0.3647 & 0 & 0 & 0.0984 \\ 0.0037 & 0.7676 & 0 & 0 \\ 0 & 0.0940 & 0.9512 & 0 \\ 0 & 0 & 0.0209 & 0.9701 \end{pmatrix}.$$

We remark that this matrix, with harvesting explicitly included and estimated, is different than the compressed matrix (16) found in Section 3.2 since that matrix was compressed from the  $5 \times 5$  matrix from Gaoue [40], an average of matrices over four years (2004–2007) that did not have explicit harvest. Our rates were estimated using yearly observed data instead, leading to a few terms that differ between the matrices. In Fig. 3, the fits of the harvested population (Soassararou) harvesting model simulations to the seedling, juvenile, and adult Soassararou observed data points are shown.

Using the estimated initial condition of approximately 14 saplings in 2004 from the harvested population (Soassararou), the only rate remaining to be estimated for the naturally unharvested population (Nipuni) harvesting model is  $h_N$ , a simulated harvest rate. With bounds



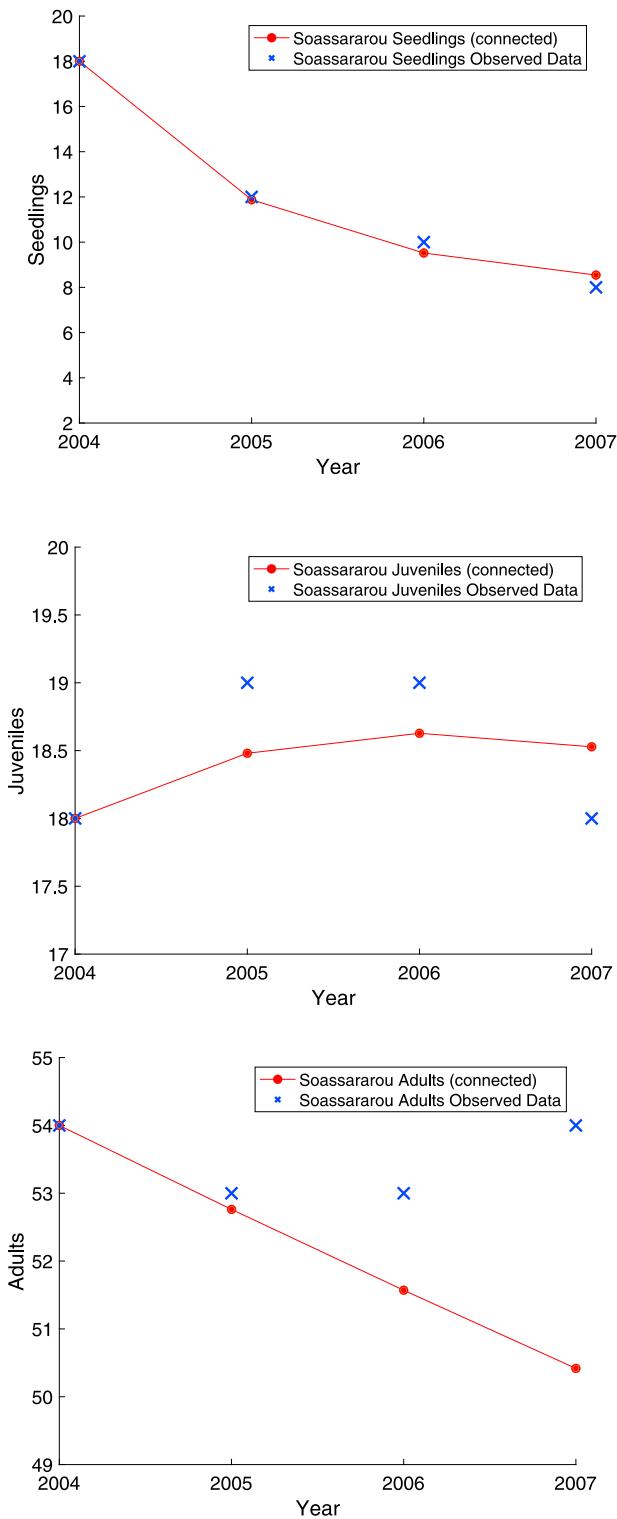


Fig. 3. Comparison of harvested population (Soassararou) harvesting model simulations to Soassararou observed data during fitting process for Soassararou rates.

on this rate given in Table 13 in the Appendix, the objective function value for fitting to the Nipuni harvesting matrix simulations was 0.2010 and a compilation of the rates for the naturally unharvested Nipuni population with simulated harvest is given in Table 8.

Table 8

Rates for unharvested population (Nipuni) harvesting model with the bold rate determined from parameter estimation process.

| Rate in estimation             | Value of rate | Rate in estimation             | Value of rate |
|--------------------------------|---------------|--------------------------------|---------------|
| $\sigma_5 \sigma_1 = \sigma_N$ | 0.4354        | $\gamma_{34}$                  | 0.0304        |
| $\gamma_{12}$                  | 0.028         | $\sigma_8 \sigma_4 = \sigma_A$ | 0.9999        |
| $\sigma_6 \sigma_2 = \sigma_S$ | 0.7269        | $\phi_A(h_N)$                  | 0.1195        |
| $\gamma_{23}$                  | 0.2102        | $\sigma_4$                     | 0.9999        |
| $\sigma_7 \sigma_3 = \sigma_J$ | 1             | $h_N$                          | <b>0.3751</b> |

Using parameters from Table 8, the Nipuni matrix with simulated harvest is given by

$$S_h(\text{Nipuni}) = \begin{pmatrix} 0.2645 & 0 & 0 & 0.1195 \\ 0.0076 & 0.5741 & 0 & 0 \\ 0 & 0.1528 & 0.9696 & 0 \\ 0 & 0 & 0.0304 & 0.9999 \end{pmatrix}$$

Similar to the harvested population, this matrix with explicit harvest is different than the compressed matrix (14) found in Section 3.2, due to the compressed matrix coming from a matrix that was an average over 4 years [40]. Although we do use many of those rates, we use yearly observed data from the harvested Soassararou population to determine an effective harvesting rate,  $h_N$ , which results in a few different terms between these matrices. In Fig. 4, the fits of the Nipuni harvesting model simulations to the seedling, juvenile, and adult Soassararou observed data points are shown.

### 3.6. Eigenvalue analysis

The dominant eigenvalue,  $\lambda_1$ , of a population matrix gives the long-term growth rate of a population and the damping ratio,  $\frac{\lambda_1}{|\lambda_2|}$ , suggests how quickly the population converges to the stable stage distribution. The critical threshold for stability occurs when the norm of the dominant eigenvalue is 1 [31,41]. We use the estimated effective harvesting rates for our harvested population (Soassararou) and unharvested population (Nipuni),  $h_N = 0.3860$  and  $h_N = 0.3751$ , respectively, in order to compare population dynamics for these two populations in the long-term. We compute the dominant eigenvalue and the damping ratio for our harvested population to determine how a population that is regularly perturbed responds to even more perturbation. We also compute these values for the naturally unharvested population to provide insight on how a pristine, unharvested population responds to perturbation.

From the results in Table 9, we see the long-term growth rate calculated for the unharvested population is larger than that of the harvested population for the above-mentioned respective harvesting rates. However, since we are fitting a deterministic model to noisy data, these results are essentially the same given that uncertainty. Since they are both close to 1, we can consider these populations as relatively stable. Moreover, the damping ratio for the unharvested population is quite similar to that of the harvested population, both being close to 1. This means the respective values of  $\lambda_1$  and  $\lambda_2$  are close in value for each population and thus the two eigenvalues have a similar effect on their respective populations.

Since our reproduction function is built based on harvest levels 0.4 or above, we can understand the effect of harvesting in our model for values in or around this range but we do not consider the case where harvest is set to 0 for baseline eigenvalues as that is too large of an extrapolation in the harvest level for the function. We explore the effect of harvest on eigenvalues by seeing how sensitive they are when harvest levels are altered. We consider various cases of harvest levels as shown in Table 9, reporting the values of the corresponding dominant eigenvalues and damping ratios. We observe for both the harvested (Soassararou) and unharvested (Nipuni) populations that varying the harvest levels does not make a significant difference in the eigenvalues

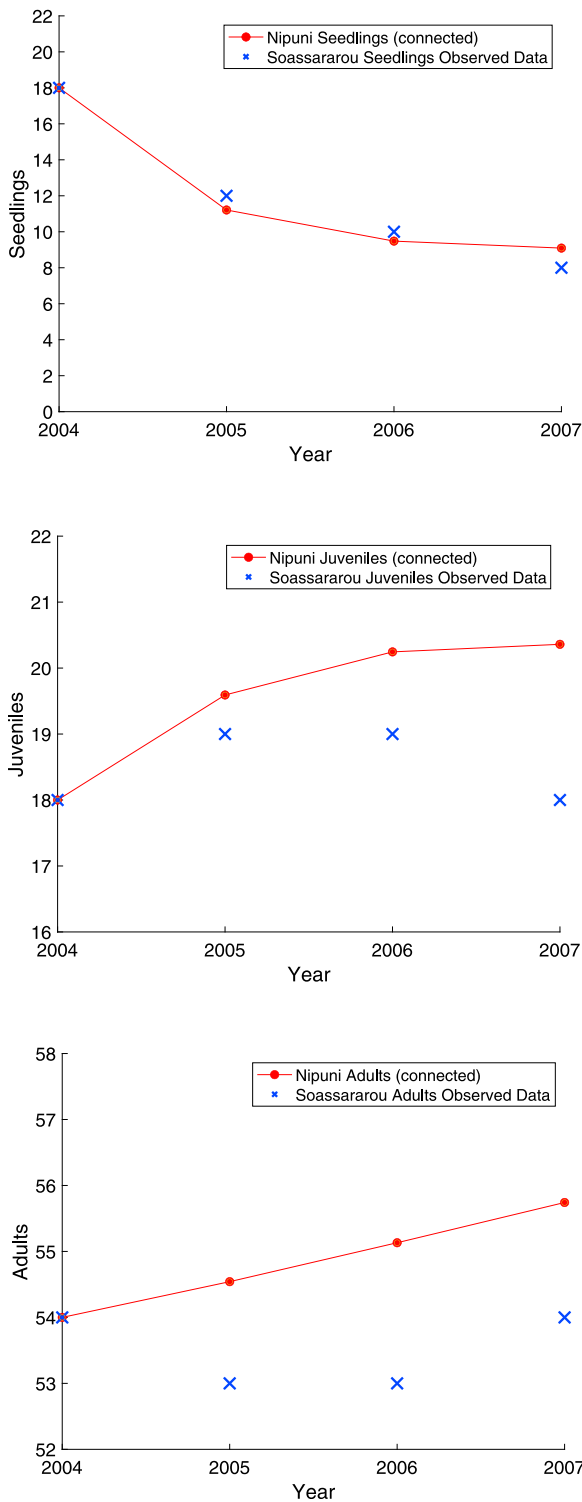


Fig. 4. Comparison of unharvested population (Nipuni) harvesting model simulations to Soassararou observed data during fitting process for Nipuni harvesting rate.

with the exception of the full defoliation case, in which the dominant eigenvalue, and therefore damping ratio, drastically drops. Moreover, for both populations, the lower the harvesting level, the higher the dominant eigenvalue is, as we would expect.

Table 9

Values of the dominant eigenvalue,  $\lambda_1$ , and the damping ratio,  $\frac{\lambda_1}{|\lambda_2|}$  for the Soassararou and Nipuni populations for varying harvest levels.

| Harvesting rate ( $h_N$ ) | $\lambda_1$ (Soas) | $\frac{\lambda_1}{ \lambda_2 }$ (Soas) | $\lambda_1$ (Nipuni) | $\frac{\lambda_1}{ \lambda_2 }$ (Nipuni) |
|---------------------------|--------------------|--|----------------------|--|
| 0.3751                    | –                  | –                                      | 1.0003               | 1.0322                                   |
| 0.3860                    | 0.9704             | 1.0205                                 | –                    | –  |
| 0.4                       | 0.9703             | 1.0204                                 | 1.0002               | 1.0319                                   |
| 0.5                       | 0.9701             | 1.0199                                 | 1.0000               | 1.0315                                   |
| 0.6                       | 0.9701             | 1.0199                                 | 0.9999               | 1.0312                                   |
| 0.7                       | 0.9701             | 1.0199                                 | 0.9999               | 1.0312                                   |
| 0.8                       | 0.9701             | 1.0199                                 | 0.9999               | 1.0312                                   |
| 0.9                       | 0.9701             | 1.0199                                 | 0.9999               | 1.0312                                   |
| 1                         | 0.7676             | 0.8070                                 | 0.5741               | 0.5921                                   |

#### 4. Discussion and conclusions

When considering the *K. senegalensis* population, small and large adult trees are not easily distinguished in the field as they are both reproductive and experience both lethal and non-lethal harvesting. Therefore, our model combined these adult trees into the same size class. Doing so required matrices from previous work [40] to be compressed in order to inform corresponding rates in our model. Compression of these matrices used algorithms [42,43] that relied on weighting survival and fertility rates with proportions of small or large adults out of all adults in the stable stage distribution if long-term dynamics were of importance, or using information on how long individuals remain in a certain class if short-term dynamics were under consideration. We implemented a novel application of these algorithms, in which the naturally unharvested Nipuni population was compressed to maintain long-term dynamics, and the harvested Soassararou population was compressed with a focus on transient dynamics.

Prior to estimating the level of harvest for the harvested population (Soassararou) and estimating the simulated level of harvest that the unharvested population (Nipuni) would require to match the Soassararou observed data, we first determined the relationship between the reproduction and pruning intensity of the Soassararou adult individuals. The resulting reproduction function was used for both populations as Nipuni is viewed as an unharvested baseline for Soassararou. Using ordinary least squares and comparing model simulations to Soassararou observed data, we were able to estimate the level of effect harvesting has on the Soassararou population as a parameter in our model,  $h_N = 0.3860$  (corresponding to 84% actual observed harvest for adult individuals), and subsequently estimate how much harvest the Nipuni population would need to experience to match this data Soassararou data,  $h_N = 0.3751$ . The fact that these values are similar speaks to the quality of our parameter fitting process: since Nipuni is considered an unharvested baseline for Soassararou, we would therefore expect these values to be similar.

Our study suggests that the populations are relatively stable since the dominant eigenvalues were close to 1. Therefore, we conclude that nothing drastic would happen to either population in the presence of harvesting. Further analysis of the effect of harvesting on eigenvalues demonstrated that altering harvest levels between 0.3751 and 1 had very little effect except for the extreme case of  $h_N = 1$ , in which the populations would be fully defoliated.

This work allows us to gain information about harvesting of populations beyond what is observed in nature since harvested populations may be experiencing other confounding factors that can lead to an over-estimation of harvesting effects on population dynamics. Thus, applying simulated harvested to an unharvested population that is comparable to a naturally harvested population allows us to compare dynamics and one can limit the influence of confounding factors directly when comparing (the same) population performance with and without harvest. This information may be useful in making policy decisions about when and how much to harvest since a better idea of the harvesting effects are known.

In future work, our novel harvesting model can be applied to other tropical tree populations including others in the *K. senegalensis* species. For example, the Nigoussorou population can be analyzed similarly to that of the Soassararou population, as it is also harvested. In addition, the effect on population dynamics from simultaneously varying all three types of harvest, lethal and non-lethal harvesting of adults and non-lethal harvesting of juveniles, can be explored.

This work represents only a piece of the overall effort to better understand the ecological processes that occur from harvesting with implications for management strategies in the short- and/or long-term. We recognize that our model has some limitations. One such limitation is not including fire and drought explicitly, which has effects on shrinkage of the trees—particularly from the sapling to seedling stage. Our model is also deterministic, whereas fire and drought are stochastic processes, and we work with noisy data. Other environmental factors such as floods, rainfall, temperature, and insects on the trees could also be incorporated in future work to capture a more realistic environment.

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Appendix**

*Benin calendar*

Detailed monthly events of the *K. senegalensis* species are outlined in Table 10.

*Compression calculations*

To compress the matrix for our unharvested population (Nipuni), we rely on information from the normalized stable stage distribution vector  $n$  in Section 3.1. From this eigenvector, we see that in the long-term, out of all of the adults, the proportion of small adults is:  $p_s = \frac{0.0203}{0.0203+0.74} = 0.0267$ , and the proportion of large adult is:  $p_l = \frac{0.74}{0.0203+0.74} = 0.9733$ . Then, we calculate

$$\sigma_A = \sigma_4(p_s) + \sigma_5(p_l) = 1(0.0267) + 0.9999(0.9733) = 0.9999$$

and

$$\begin{aligned} \phi_A \sigma_4(p_s) + \phi_5 \sigma_5(p_l) &= (0.0001)(1)(0.0267) + (0.1603)(0.9999)(0.9733) \\ &= 0.156, \end{aligned}$$

the adult survival and reproduction rates, respectively. These are recorded in Table 11.

In order to compress matrix (15) for the harvested population in our work (Soassararou) as shown in Section 3.2, first we will transpose matrix  $M$  found in that section to match the algorithm and notation in [43]:

$$M_u = \begin{pmatrix} 0.9512 & 0.0209 & 0 \\ 0 & 0.8767 & 0.0837 \\ 0 & 0.0108 & 0.9677 \end{pmatrix}.$$

**Table 10**

Events that occur each month for *K. senegalensis* in Benin.

| Month     | Season        | Events  |
|-----------|---------------|---|
| October   | dry           | “early fire” to burn vegetation, lethal harvest, grass growth, flowering on trees begins                      |
| November  | dry           | lethal harvest, flowering continues on trees and fruit production begins at end of November                   |
| December  | very dry      | fruit production, non-lethal harvest, lethal harvest  |
| January   | very dry      | fruit production, non-lethal harvest, fruits open and drop/disperse seeds, lethal harvest                     |
| February  | dry           | fruit production, non-lethal harvest, fruits open and drop/disperse seeds, lethal harvest, “late fire” begins |
| March     | dry           | non-lethal harvest, lethal harvest, “late fire” occurs  |
| April     | dry/start wet | germination of grass, “late fire” that kills trees, lethal harvest, no non-lethal harvest                     |
| May       | wet           | grass growth  |
| June      | wet           | seedlings emerge, grass growth  |
| July      | wet           | seedlings emerge, grass growth  |
| August    | wet           | flooding, some seedlings die because submerged, grass growth  |
| September | wet/start dry | grass growth  |

**Table 11**

Unharvested population (Nipuni) compressed values with  $p_s$  representing the proportion of small adults out of all adults in the stable-stage distribution and  $p_l$  representing the proportion of the large adults out of all adults in the stable stage distribution.

| Calculation for compression                                     | Value of rate |
|---|---------------|
| $p_s$   | 0.0267        |
| $p_l$   | 0.9733        |
| $\sigma_A = \sigma_4(p_s) + \sigma_5(p_l)$                      | 0.9999        |
| $\phi_A \sigma_4 = \phi_4 \sigma_4(p_s) + \phi_5 \sigma_5(p_l)$ | 0.156         |

Then, following the algorithm described in detail in Section 2.3, we obtain

$$M_{u_c} = \begin{pmatrix} 0.9512 & 0.0209 \\ 0 & 0.9701 \end{pmatrix},$$

and then transposing back,

$$M_c = \begin{pmatrix} 0.9512 & 0 \\ 0.0209 & 0.9701 \end{pmatrix}$$

since  $m_2 = 0.0209 + 0.8767 + 0.0108 = 0.9084$ ,  $m_3 = 0 + 0.0837 + 0.9677 = 1.051$ , and

$$\begin{aligned} \sigma_A &= \sigma_4 \frac{m_2}{m_2 + m_3} + \sigma_5 \frac{m_3}{m_2 + m_3} \\ &= (0.9604) \left( \frac{0.9084}{0.9084 + 1.051} \right) + (0.9785) \left( \frac{1.051}{0.9084 + 1.051} \right) \\ &= 0.9701 \end{aligned}$$

which corresponds to the lower right entry in the matrix.

The fertility rate is calculated via

$$\begin{aligned} \phi_A \sigma_4 &= \sigma_4 \phi_4 \frac{m_2}{m_2 + m_3} + \sigma_5 \phi_5 \frac{m_3}{m_2 + m_3}, \\ &= (0.9604)(0.0732) \left( \frac{0.9084}{0.9084 + 1.051} \right) \\ &\quad + (0.9785)(0.1564) \left( \frac{1.051}{0.9084 + 1.051} \right) \\ &= 0.1147. \end{aligned}$$

**Table 12**

Harvested population (Soassararou) compressed values where  $m_2$  represents the sum of probabilities of staying in the small adult class and  $m_3$  represents the sum of probabilities of staying in the large adult class.

| Calculation for compression   | Value of rate |
|---|---------------|
| $\frac{m_2}{m_2+m_3}$   | 0.4636        |
| $\frac{m_3}{m_2+m_3}$   | 0.5364        |
| $\sigma_A = \sigma_4 \frac{m_2}{m_2+m_3} + \sigma_5 \frac{m_3}{m_2+m_3}$                      | 0.9701        |
| $\phi_A \sigma_4 = \phi_4 \sigma_4 \frac{m_2}{m_2+m_3} + \phi_5 \sigma_5 \frac{m_3}{m_2+m_3}$ | 0.1147        |

**Table 13**

Bounds for harvested population (Soassararou) harvest model rates and unharvested population (Nipuni)  $h_N$  rate in parameter estimation process.

| Rate estimated                 | Bounds      | Explanation  |
|--------------------------------|-------------|--|
| $\sigma_5 \sigma_1 = \sigma_N$ | [0.4,0.6]   | Based on rates from Nipuni and Barabon.                                    |
| $\gamma_{12}$                  | [0.01,0.04] | Based on rates from Nipuni and Barabon.                                    |
| $\sigma_4$                     | [0.9701,1]  | Constraints of $\sigma_8 \leq 1$ and $\sigma_A = 0.9701$ .                 |
| $S_0$                          | [1,50]      | Based on size of other classes in 2004.                                    |
| $h_N$ (Soas)                   | [0.001,1]   | Wide range, effect $\leq 1$ so entry (1,1) of matrix (18) is non-negative. |
| $h_N$ (Nipuni)                 | [0.001,1]   | Wide range, effect $\leq 1$ so entry (1,1) of matrix (18) is non-negative. |

The values of the rates for Soassararou for the compressed matrix,  $S_{c^*}$ , are recorded in Table 12.

We can check the accuracy of the compression according to [43] by comparing  $M_{u_c}^5$  (i.e. compressing the original matrix and then performing matrix exponentiation for 5 time steps) and  $(M_u)^5_c$  (i.e. performing matrix exponentiation of the original matrix for 5 times steps and then compressing the resulting matrix). Here,

$$M_{u_c}^5 = \begin{pmatrix} 0.7787 & 0.0890 \\ 0 & 0.8592 \end{pmatrix}$$

and

$$M_u^5_c = \begin{pmatrix} 0.7787 & 0.0733 & 0.0142 \\ 0 & 0.5247 & 0.3048 \\ 0 & 0.0393 & 0.8561 \end{pmatrix}.$$

Compressing this matrix using Spears' algorithm results in

$$(M_u)^5_c = \begin{pmatrix} 0.7787 & 0.0875 \\ 0 & 0.8722 \end{pmatrix}.$$

The upper right hand entry of the matrix has a 1.7% error ( $\frac{0.0890-0.0875}{0.0875} = 0.0171$ ) and the lower right hand entry of the matrix has a 1.5% error ( $\frac{0.8722-0.8592}{0.8722} = 0.0149$ ).

**Parameter estimation**

We assume the form of the reproduction function is the same for our unharvested population (Nipuni) as our harvested population (Soassararou) from equation (19) since these populations are in a similar ecological zone and a similar function relying on harvest cannot be built for Nipuni (as it is not a harvested population). We need to know the value of  $\sigma_4$  for both populations since it is multiplied by the reproduction function in entry (1,4) of matrix (18). Since  $\sigma_A = \sigma_8 \sigma_4 = 0.9701$  for the Soassararou population and each rate in this term is between 0 and 1, we know that each rate cannot be below 0.9701 (or the other would have to be above 1). Therefore, we set a lower bound of 0.9701 for  $\sigma_4$  for estimation as shown in Table 13 in Appendix. For the Nipuni population,  $\sigma_8 \sigma_4 = 0.9999$  and therefore we make the simplifying assumption that  $\sigma_4 = 0.9999$  and  $\sigma_8 = 1$ , and therefore do not need to estimate  $\sigma_4$  for this population.

To have an idea of realistic bounds for  $\sigma_N$  and  $\gamma_{12}$  for the Soassararou fitting process, we use information from unharvested populations in a similar ecological zone. The Nipuni and Barabon populations (both unharvested populations in a similar ecological zone) have values of  $\sigma_N = 0.4354$  and  $0.5795$ , respectively, and therefore we set the bounds of  $\sigma_N$  to be 0.4 and 0.6. Moreover, these populations have rates of  $\gamma_{12} = 0.028$  and  $0.0309$ , respectively, and therefore, we set the range of  $\gamma_{12}$  to be 0.01 to 0.04. The bounds used for the estimation process are listed in Table 13.

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