Competition Model between the Invasive Sahara Mustard and Native Plants in the Sonoran Desert

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Abstract

Sahara Mustard (*Brassica tournefortii*) is an invasive weed that has become widespread throughout the southwestern United States. Its early germination, high fecundity, and dispersal effectiveness augment its ability to outcompete and possibly displace local flora. In this work, we model the dynamics of Sahara Mustard as it competes with winter annuals native to the Sonoran Desert, such as the widespread forb *Lepidium lasiocarpum*. A discrete-time competition model of plant-plant interactions is constructed to study factors that may affect competition between invasive and native species in favor of the native species. Through a system of non-linear difference equations we quantify each species' seed banks and flowering adult populations over several generations. We take into consideration the dependence of fecundity, survivability, and germination on total annual rainfall. A stochastic simulation is used to examine the effect of seasonal variability on existence of native species in competition with Sahara Mustard. We found that rainfall variability was advantageous to the native population, though the native forbs that compete with Sahara Mustard will likely be reduced in population or driven to extinction in absence of any control strategy.

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1 Introduction

Brassica tournefortii, commonly known as Sahara Mustard, African Mustard, or Asian Mustard, is an annual forb native to the deserts of North Africa and Southwestern Asia [12]. A forb is an annual or perennial flowering plant that lacks a woody stem and is not a grass. Annual forbs live for a single season and die away after flowering. Sahara Mustard was first spotted in the United States in California in 1927 and has since spread to Nevada, Arizona, New Mexico, and western Texas [20, 11], where it now competes with native plants, including winter annual forbs. Since Sahara Mustard germinates early in the winter season and reaches maturity before native annuals, it has been successful in displacing native species throughout the Mojave and Sonoran deserts [12, 3, 21]. Stands of dead Sahara Mustard are a serious fire hazard. To make matters worse, Sahara Mustard seeds can still germinate from the seed bank after a fire, while most Sonoran plants have no fire tolerance [12, 16, 15].

Though rodents and birds eat the delicious seeds of Sahara Mustard, grazers do not seem to find the rest of the Sahara Mustard plant palatable [11]. The Sahara Mustard might be having a detrimental effect on the Sonoran Pronghorn. In the United States, the Sonoran Pronghorn is limited in range to the Cabeza Prieta National Wildlife Refuge [17]. The invasive Sahara Mustard, common throughout the southwest, has appeared there as well, and could outcompete the main food source of Pronghorn fawns: native annual forbs.

Water is, somewhat obviously, a limiting factor for plant growth [9]. In the Sonoran Desert, where water is limited and winter rains vary in timing and amount [6], the fitness of a plant species can vary significantly from year to year. Thus, when examining the life cycle of desert annuals we consider the effect of rainfall on various parameters. The percentage of seeds that germinate in a season [18], the number of seedlings that survive to maturity [9], and the number of seeds that a mature plant will produce [1] can depend on how much water the plant receives in a season.

Some studies have been conducted on the impact of Sahara Mustard invasion on native Sonoran Desert plant communities. The studies show that over time the proportion of Sahara Mustard plants in an area increases while native plant populations decrease [4, 5]. Fortunately, Sahara Mustard is not yet omnipresent throughout the southwest, and so control of the plant in many areas is still possible [15]. The effectiveness of various control strategies on the mustard have also been studied. Two main methods of control, manual hand-pulling and herbicide, have been applied to pre-reproductive plants [2, 11]. Hand-pulling is only feasible for small invasions because of the man-power and time required [16]. Herbicide may often be the better option as it is more cost-effective and does not disturb the soil (which can make an area vulnerable to further invasion) [2]. Since Sahara Mustard germinates earlier than native plants [3], herbicide can be applied in a window of time before native annuals germinate [16], and this was shown to have minimal impact on native plants while still being effective at reducing invasive species populations [15].

We propose a model to determine the conditions necessary to contain Sahara Mustard and allow survival of native winter annuals by incorporating a stage structured ecological

framework. For the native plant parameters, we used information on *Lepidium lasiocarpum*, a widespread native of the Sonoran Desert. The exact identity of the competitors of Sahara Mustard will in reality vary substantially from region to region and depend on what microclimate the Sahara Mustard inhabits (Tom Philippi, personal correspondence, July 16, 2012).

In Section 2, we introduce the competition model for Sahara Mustard and *L. lasiocarpum*. We consider and analyze a simplified model with no seed bank in Section 3. The model with a seed bank is then considered in Section 4. The stability analysis of various equilibria such as extinction, coexistence, and competitive exclusion are also shown in Section 4. In Section 5 we discuss the analysis of both models. In Section 6, we introduce the values for parameters used in our model under varying weather conditions. We give the numerical results from deterministic simulations in Section 7 and the Stochastic simulations in Section 8.

2 Model for the Dynamics of Competing Plant Species

We introduce a system of non-linear discrete difference equations to model the competition between Sahara Mustard and a single species of native Sonoran Desert annual forb, *Lepidium lasiocarpum*. The generations are measured in years, with all the processes of germination, growth, competition, and new seed production occurring within one iteration of the system. Before we introduce the model explicitly, we will revisit the life history and ecology of Sahara Mustard and Sonoran Desert winter annuals.

Annual plants germinate, live, and die in a single season. Plants and seeds are assumed to be surveyed at the end of the winter season, during flowering and before new seeds are produced. Therefore, the plants counted are those that survive to flowering, and the seeds are those that have survived in the seed bank and not germinated. This means that although the number of seeds moving on to the next year is dependent on the plants of the previous generation, plant generations of both Sahara Mustard and native forbs are non-overlapping. Seeds for both species can become dormant and enter a seed bank that spans generations. Sahara Mustard is a winter annual; it germinates in winter and flowers and dies in late winter or spring. It grows quickly, taking only two to three months to age from seedling to flowering plant [16]. Seeds remain dormant during the summer when high temperatures prevent germination despite regular rainfall [3]. Native Sonoran winter annuals have a similar life cycle, but germinate later in the season (see Figure 1) [3].
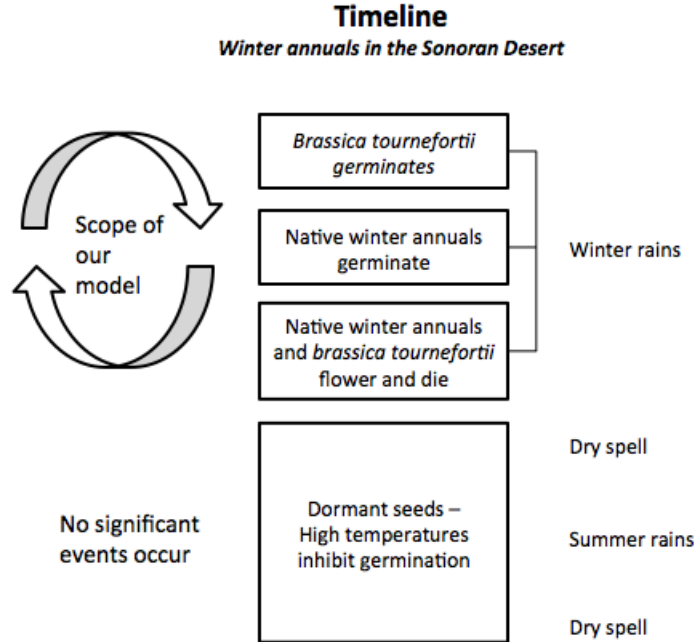
Timeline
Winter annuals in the Sonoran Desert

Scope of our model

No significant events occur

Brassica tournefortii germinates

Native winter annuals germinate

Native winter annuals and *brassica tournefortii* flower and die

Dormant seeds – High temperatures inhibit germination

Winter rains

Dry spell

Summer rains

Dry spell

Figure 1: Timing of pertinent events for (*B. tournefortii*) and *L. lasiocarpum*. The beginning of the winter season in the Sonoran Desert is customarily taken to be October. However, because the winter rainfall is highly erratic, the date of winter annual germination events varies from year to year. Sahara Mustard and native winter annuals have flowered and died by April, the end of the winter season.

Winter annuals in the Sonoran Desert are highly dependent on the sporadic winter rains. These plants' seeds have selected for innate dormancy strategies as a bet-hedging adaptation to the unpredictability of winter precipitation [18]. This implies that some percentage of viable seeds will not germinate even when given sufficient amounts of rain [18]. These dormant seeds are a safeguard against years where there is enough rain for germination, but not enough for plants to survive to maturity [22].

The presence of dormant seeds in addition to plants motivates a two-compartment stage-structured model for each plant species, with viable dormant seeds (S_i) and plants (P_i) for both Sahara Mustard (M) and the native forb (N), where $i \in \{M, N\}$. Figure 2 shows the model life cycle for both species in absence of intra- or interspecific competition.

Annual Life Cycle
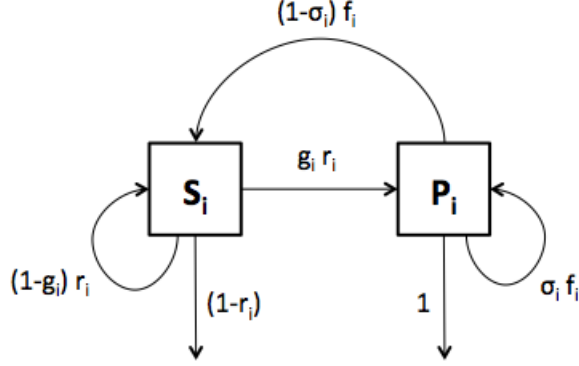*without competition or density dependence*

Figure 2: Life cycle of winter annuals, assuming no intra- or interspecies competition and 100% survivability of seedlings.

Each year, the winter annuals produce a certain number of viable seeds (given by f_i). Some fraction σ_i of these seeds germinate the next year, and so become plants within that year. The remainder of these seeds enter the seed bank. Seeds in the seed bank can either spoil and no longer be viable (with probability $1 - r_i$), germinate (with probability g_i), or remain viable in the seed bank (with probability r_i). As the plants being modeled are annuals, all the mature plants from the previous generation will die and contribute only indirectly to the next generation through seeds produced.

2.1 Competition Model

In arid regions like the Sonoran Desert, water is a limiting resource for plant growth. Consequently, there is competition for water among plants in desert ecosystems [9]. The model includes both intra- and interspecies competition that affect the survival of new seedlings.

The dynamics of our competition model are governed by the following system of non-linear difference equations:

$$S_N(t+1) = (1 - \sigma_N)f_N P_N(t) + (1 - g_N)r_N S_N(t), \tag{2.1.1}$$

$$P_N(t+1) = \frac{\mu_N \sigma_N f_N}{1 + \alpha_N G_N(t) + \beta G_M(t)} P_N(t) + \frac{\mu_N g_N r_N}{1 + \alpha_N G_N(t) + \beta G_M(t)} S_N(t), \tag{2.1.2}$$

$$S_M(t+1) = (1 - \sigma_M)f_M P_M(t) + (1 - g_M)r_M S_M(t), \tag{2.1.3}$$

$$P_M(t+1) = \frac{\mu_M \sigma_M f_M}{1 + \alpha_M G_M(t)} P_M(t) + \frac{\mu_M g_M r_M}{1 + \alpha_M G_M(t)} S_M(t). \tag{2.1.4}$$

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Let

$$G_i(t) = \sigma_i f_i P_i(t) + g_i r_i S_i(t), \tag{2.1.5}$$

be the new seedlings, or all the seeds that germinate just before time t+1 for the Sahara Mustard or native species. The terms

$$\frac{1}{1 + \alpha_M G_M} \tag{2.1.6}$$

$$\text{and} \quad \frac{1}{1 + \alpha_N G_N + \beta G_M} \tag{2.1.7}$$

represent the competition functions, which are thus dependent on the number of new seedlings.

Then Equations 2.1.2 and 2.1.4 can be rewritten as

$$P_N(t+1) = \frac{\mu_N G_N(t)}{1 + \alpha_N G_N(t) + \beta G_M(t)}, \tag{2.1.8}$$

$$P_M(t+1) = \frac{\mu_M G_M(t)}{1 + \alpha_M G_M(t)}. \tag{2.1.9}$$

Many models of multi-species plant competition have been used and successfully fit to data. For our competition functions we chose functions that would be relatively easy to analyze but still had been shown to be effective in modeling plant competition [13]. We assume the competition term for $P_M(t+1)$ does not depend on G_N because the Sahara Mustard germinates earlier and grows faster, and so it is already well-established by the time the native annual seedlings are attempting to grow. Table 1 summarizes the parameters used in our competition model.

Parameter	Range	Definition
σ_i	$0 \leq \sigma_i \leq 1$	probability of germination of fresh seeds
g_i	$0 \leq g_i \leq 1$	probability of germination out of the seed bank
r_i	$0 \leq r_i \leq 1$	probability of surviving dormancy in the seed bank
μ_i	$0 \leq \mu_i \leq 1$	probability of surviving from seedling to flowering plant
f_i	$f_i \geq 0$	number of seeds produced per plant
α_i	$0 < \alpha_i < 1$	quantifies the intensity of intraspecific competition
β	$0 < \beta < 1$	quantifies the intensity of Sahara Mustard's effect on native annuals

Table 1: Parameter definitions for the competition model.

Here, α_N and α_M are reduction constants that relate to the amount of intraspecific competition for the native forbs and Sahara Mustard, respectively. The parameter β is a

reduction constant that determines how strongly the Sahara Mustard competes with and disrupts the growth of the native annual. Since α_i and β are always positive fractions, the competition functions (Formulas 2.1.6 and 2.1.7) are always less than one, and, similar to μ_i, reduces the number of seedlings surviving to adulthood. For both P_N and P_M, α_i plays a role in setting the carrying capacity. This is because as $G_i \to \infty$, $P_i \to \frac{\mu_i}{\alpha_i}$, so the population cannot increase above this value. Increasing α_i increases intraspecific competition by reducing each species' carrying capacity depending on the population of that species. We always set $\alpha_i \ll \mu_i$ to avoid having fractional plants at equilibrium.

3   Seed bank-free Model

We begin with an analysis of the seed bank-free model (i.e. $r_i = 0$). The analysis of this simplified model will provide some important insights into the dynamics of System 2.1.1-2.1.4. The seed bank-free model tells us how the full system would behave if the only germinating seeds came from plants from the previous years. This means that seeds entering the seed bank are never viable. As such, we disregard those seeds.

Biologically, the seed bank-free model represents a location where both the Sahara Mustard and native annuals have not yet set up a seed bank. For those seeking to halt the invasion of Sahara Mustard, these types of locations are essential for conservation. In many parts of the Sonoran desert, including the Cabeza Prieta National Wildlife Refuge, ecologists and rangers work to create semi-wild feeding areas for the local fauna, including the endangered Sonoran Pronghorn [17]. Irrigation systems are created to bring water to previously dry desert locations. These newly wet areas are meant to provide a haven of native forbs for local fauna to consume, but they are also open to invasion by the Sahara Mustard.

Our seed bank-free model is obtained by letting $r_i = 0$ in System 2.1.1-2.1.4 and is given by:

$$S_N(t+1) = (1 - \sigma_N)f_N P_N(t), \tag{3.0.10}$$

$$P_N(t+1) = \frac{\mu_N \sigma_N f_N P_N(t)}{1 + \alpha_N \sigma_N f_N P_N(t) + \beta \sigma_M f_M P_M(t)}, \tag{3.0.11}$$

$$S_M(t+1) = (1 - \sigma_M)f_M P_M(t), \tag{3.0.12}$$

$$\text{and } P_M(t+1) = \frac{\mu_M \sigma_M f_M P_M(t)}{1 + \alpha_M \sigma_M f_M P_M(t)}. \tag{3.0.13}$$

Since Equations 3.0.11 and 3.0.13 are decoupled from Equations 3.0.10 and 3.0.12, respectively, the dynamics of the system are determined explicitly from Equations 3.0.11 and 3.0.13.

The equilibria of the equations are found by setting $f(P_i^*) = P_i^*$, where $f(P_N)$ and $f(P_M)$ are the right hand sides of Equations 3.0.11 and 3.0.13, respectively. From these equations we obtain the equilibria values P_N^* and P_M^* given by the solutions of the following

equations:

$$P_N^* = \frac{\mu_N \sigma_N f_N P_N^*}{1 + \alpha_N \sigma_N f_N P_N^* + \beta \sigma_M f_M P_M^*} \quad \text{and} \quad P_M^* = \frac{\mu_M \sigma_M f_M P_M^*}{1 + \alpha_M \sigma_M f_M P_M^*}.$$

Therefore, the two dimensional system obtained from Equations 3.0.11 and 3.0.13 has two equilibria. One of these is the extinction equilibrium $\mathbf{E_0} = (0,0)$. The other is the coexistence equilibrium $\mathbf{E_1}$.

$$\mathbf{E_1} = \left(\frac{\alpha_M(\mu_N \sigma_N f_N - 1) - \beta(\mu_M \sigma_M f_M - 1)}{\alpha_M \alpha_N \sigma_N f_N}, \frac{\mu_M \sigma_M f_M - 1}{\alpha_M \sigma_M f_M} \right).$$

In order for the coexistence equilibrium to exist, we need $\alpha_M(\mu_N \sigma_N f_N - 1) - \beta(\mu_M \sigma_M f_M - 1) > 0$ and $\mu_M \sigma_M f_M - 1 > 0$, that is,

$$\frac{\beta}{\alpha_M} \left(\frac{\mu_M \sigma_M f_M - 1}{\mu_N \sigma_N f_N - 1} \right) < 1, \tag{3.0.14}$$

and

$$\mu_M \sigma_M f_M > 1. \tag{3.0.15}$$

3.1 Stability of Equilibria for the Seed Bank-Free Model

To determine the stability of the equilibrium points, we linearize the system around the equilibria by taking the Jacobian matrix:

$$J(\mathbf{E}) = \begin{pmatrix} \frac{\partial P_N}{\partial P_N}\big|_{\mathbf{E}} & \frac{\partial P_M}{\partial P_N}\big|_{\mathbf{E}} \\ \frac{\partial P_N}{\partial P_M}\big|_{\mathbf{E}} & \frac{\partial P_M}{\partial P_M}\big|_{\mathbf{E}} \end{pmatrix},$$

where $\mathbf{E} = (P_N^*, P_M^*)$ is a equilibrium of the system provided by Equations 3.0.11 and 3.0.13. The equilibrium point is said to be asymptotically stable if $\rho(J(\mathbf{E})) < 1$, where $\rho(x)$ is the spectral radius operator of $J(\mathbf{E})$ (i.e. $\rho(J(\mathbf{E})) = |\max\{\lambda_1, \lambda_2\}|$, where λ_1 and λ_2 are the eigenvalues of $J(\mathbf{E})$).
The Jacobian matrix at the extinction equilibrium $\mathbf{E_0}$ is:

$$J(\mathbf{E_0}) = \begin{pmatrix} \mu_N \sigma_N f_N & 0 \\ 0 & \mu_M \sigma_M f_M \end{pmatrix}.$$

Hence the eigenvalues of $J(\mathbf{E_0})$ are $\lambda_1^0 = \mu_N \sigma_N f_N$ and $\lambda_2^0 = \mu_M \sigma_M f_M$. Therefore, in order for $\mathbf{E_0}$ to be asymptotically stable we must have $\rho(J(\mathbf{E_0})) = |\max\{\lambda_1^0, \lambda_2^0\}| < 1$. In other words, either

$$|\lambda_1^0| = \mu_N \sigma_N f_N < 1 \quad \text{or} \quad |\lambda_2^0| = \mu_M \sigma_M f_M < 1. \tag{3.1.1}$$

Thus, $\mathbf{E_0}$ is locally asymptotically stable, provided that $\rho(J(\mathbf{E_0})) < 1$. However, if either of these conditions in Inequality 3.1.1 hold, the coexistence equilibrium $\mathbf{E_1}$ will not exist (see Inequalities 3.0.14 and 3.0.15).

The Jacobian matrix at $\mathbf{E_1}$ is given by:

$$J(\mathbf{E_1}) = \begin{pmatrix} \Lambda & 0 \\ \Phi & \frac{1}{\mu_M \sigma_M f_M} \end{pmatrix},$$

where $\Lambda = \frac{\alpha_M + \beta(\mu_M \sigma_M f_M - 1)}{\alpha_M \mu_N \sigma_N f_N}$ and $\Phi = \frac{\beta \sigma_M f_M}{\alpha_N \sigma_N f_N}(\Lambda - 1)$. Hence the eigenvalues of $J(\mathbf{E_1})$ are:

$$\lambda_1^1 = \Lambda \quad \text{and} \quad \lambda_2^1 = \frac{1}{\mu_M \sigma_M f_M}.$$

Therefore, the coexistence equilibrium $\mathbf{E_1}$ is locally asymptotically stable provided that:

$$\rho(J(\mathbf{E_1})) = |\max\{\lambda_1^1, \lambda_2^1\}| < 1. \tag{3.1.2}$$

If $\lambda_1^1 < \lambda_2^1$ ($\rho(J(\mathbf{E_1})) = |\lambda_2^1|$) and

$$\mu_M \sigma_M f_M > 1, \tag{3.1.3}$$

(which is always true whenever $\mathbf{E_1}$ exists by Inequality 3.0.15), then $\mathbf{E_1}$ will be locally asymptotically stable.

On the other hand, if $\lambda_2^1 < \lambda_1^1$, $\rho(J(\mathbf{E_1})) = |\Lambda| = \Lambda$, since $\mu_M \sigma_M f_M > 1$ is required for $\mathbf{E_1}$ to exist. The condition for local asymptotical stability of $\mathbf{E_1}$ becomes:

$$\Lambda < 1 \Rightarrow \frac{\beta}{\alpha_M}\left(\frac{\mu_M \sigma_M f_M - 1}{\mu_N \sigma_N f_N - 1}\right) < 1. \tag{3.1.4}$$

Equation 3.1.4 is satisfied by the existence condition of $\mathbf{E_1}$, therefore $\mathbf{E_1}$ is locally asymptotically stable wherever it exists.

3.2 Conditions for global asymptotic stability of the extinction equilibrium

Here, we will show that $\mathbf{E_0}$, the extinction equilibrium for both plant species, is globally asymptotically stable. In order to prove this we designate a Lyapunov function V such that: $V : \mathbb{R}^n \to \mathbb{R}$, is a continuous scalar function that is locally positive-definite, i.e.

$$V(\mathbf{0}) = 0,$$

$$V(\mathbf{X}) > 0 \quad \forall \, \mathbf{X} \in U \, / \{\mathbf{0}\},$$

where U is a neighborhood around $\mathbf{X} = 0$

Theorem 1. (Case $r = 0$) Global stability of the extinction equilibrium.
Assume $\mu_N \sigma_N f_N < 1$ (or $f_N < \frac{1}{\mu_N \sigma_N}$) and $\mu_M \sigma_M f_M < 1$ (or $f_M < \frac{1}{\mu_M \sigma_M}$) then the extinction steady state, $\mathbf{E_0} = (0,0)$, is globally asymptotically stable. Furthermore, $\mathbf{E_0}$ is the only equilibrium point of the system.

Consider the Lyapunov function:

$$V(P_N, P_M) = P_N^2 + P_M^2 > 0. \tag{3.2.1}$$

If $\nabla V(\mathbf{X}) < 0 \quad \forall\, \mathbf{X} \in \mathbb{R}^n \,/\, \{0\}$, and $V(\mathbf{X}) \to \infty$ as $\|\mathbf{X}\| \to \infty$, then the equilibrium is globally asymptotically stable (g.a.s.). Where here $\nabla V(\mathbf{X})$ is defined as:

$$\nabla V(\mathbf{X}) = V(f(\mathbf{X})) - V(\mathbf{X}). \tag{3.2.2}$$

for $f(\mathbf{X}) = \mathbf{X}(t+1)$.

$f \begin{pmatrix} P_N \\ P_M \end{pmatrix} = \begin{pmatrix} P_N(t+1) \\ P_M(t+1) \end{pmatrix}$. Since $P_N(t+1)$ and $P_M(t+1)$ are always positive, we must show that $\nabla V \begin{pmatrix} P_N \\ P_M \end{pmatrix} < 0$.

$$
\begin{aligned}
\nabla V \begin{pmatrix} P_N \\ P_M \end{pmatrix} &= V \left(f \begin{pmatrix} P_N \\ P_M \end{pmatrix} \right) - V \begin{pmatrix} P_N \\ P_M \end{pmatrix} \\
&= V \begin{pmatrix} P_N(t+1) \\ P_M(t+1) \end{pmatrix} - V \begin{pmatrix} P_N \\ P_M \end{pmatrix} \\
&= \left(\frac{\mu_N \sigma_N f_N P_N}{1 + \alpha_N \sigma_N f_N P_N + \beta \sigma_M f_M P_M} \right)^2 + \left(\frac{\mu_M \sigma_M f_M P_M}{1 + \alpha_M \sigma_M f_M P_M} \right)^2 - P_N^2 - P_M^2 \\
&= \left[\left(\frac{\mu_N \sigma_N f_N}{1 + \alpha_N \sigma_N f_N P_N + \beta \sigma_M f_M P_M} \right)^2 - 1 \right] P_N^2 \\
&\quad + \left[\left(\frac{\mu_M \sigma_M f_M}{1 + \alpha_M \sigma_M f_M P_M} \right)^2 - 1 \right] P_M^2 \\
&\leq [(\mu_N \sigma_N f_N)^2 - 1] P_N^2 + [(\mu_M \sigma_M f_M)^2 - 1] P_M^2 \\
&< 0
\end{aligned}
$$

if and only if $\mu_N \sigma_N f_N < 1$ and $\mu_M \sigma_M f_M < 1$.

Since fecundity (f_i) is greater than one and often a large number, the last two inequalities will be satisfied if $\mu_i \sigma_i$ is sufficiently smaller than 1, or $\mu_i \sigma_i < \frac{1}{f_i}$. Table 2 summarizes the stability analysis for the seed bank-free model.

Equilibrium	Existence Criteria	Stability Conditions
Extinction	always exists	$\rho(\mathbf{E}) = \mu_i f_i \sigma_i < 1$
Coexistence	$\mu_M f_M \sigma_M > 1$ and $\frac{\beta(\mu_M \sigma_M f_M - 1)}{\alpha(\mu_N \sigma_N f_N - 1)} < 1$	$\mu_M f_M \sigma_M > 1$ and $\frac{\beta(\mu_M \sigma_M f_M - 1)}{\alpha(\mu_N \sigma_N f_N - 1)} < 1$

Table 2: Fixed point existence and stability, where $i \in \{N, M\}$.

4   Seed Bank Model

Our competition model including a seed bank is, as mentioned previously,

$$S_N(t+1) = (1 - \sigma_N)f_N P_N(t) + (1 - g_N)r_N S_N(t), \tag{4.0.3}$$

$$P_N(t+1) = \frac{\mu_N \sigma_N f_N}{1 + \alpha_N G_N(t) + \beta G_M(t)}P_N(t) + \frac{\mu_N g_N r_N}{1 + \alpha_N G_N(t) + \beta G_M(t)}S_N(t), \tag{4.0.4}$$

$$S_M(t+1) = (1 - \sigma_M)f_M P_M(t) + (1 - g_M)r_M S_M(t), \tag{4.0.5}$$

$$P_M(t+1) = \frac{\mu_M \sigma_M f_M}{1 + \alpha_M G_M(t)}P_M(t) + \frac{\mu_M g_M r_M}{1 + \alpha_M G_M(t)}S_M(t). \tag{4.0.6}$$

Where

$$G_i(t) = \sigma_i f_i P_i(t) + g_i r_i S_i(t). \tag{4.0.7}$$

As with the $r = 0$ case, we solve for the equilibria of the system by setting $f(\mathbf{E}^*) = \mathbf{E}^*$. The equilibrium values for the seeds can simply be written as a function of the corresponding plant equilibrium values, where:

$$S_i^* = \frac{(1 - \sigma_i)f_i P_i^*}{1 - r_i(1 - g_i)}.$$

If an annual produces no seeds ($f_i = 0$) or all of its seeds germinate ($\sigma_i = 1$) within the first year, there will be no seed bank ($S_i^* = 0$). Also, as $r \to 0$, $S_i^* \to (1 - \sigma_i)f_i P_i^*$, which is simply the number of seeds that do not germinate the first year, coinciding with the reduced model where $r = 0$. Clearly, if there are no plants then there is no seed bank at equilibrium.

There are four equilibria associated to System 4.0.3-4.0.6, corresponding to the extinction, native forb exclusion, Sahara Mustard exclusion, and co-existence equilibria, respectively, of the form $\mathbf{E} = (S_N^*, P_N^*, S_M^*, P_M^*)$. These are

$$\mathbf{E_0} = (0, 0, 0, 0), \tag{4.0.8}$$

$$\mathbf{E_1} = \left(0, 0, \frac{(1 - \sigma_M)f_M P_{M1}^*}{1 - r_M(1 - g_M)}, P_{M1}^*\right), \tag{4.0.9}$$

$$\mathbf{E_2} = \left(\frac{(1 - \sigma_N)f_N P_{N1}^*}{1 - r_N(1 - g_N)}, P_{N1}^*, 0, 0\right), \tag{4.0.10}$$

$$\mathbf{E_3} = \left(\frac{(1 - \sigma_N)f_N P_{N2}^*}{1 - r_N(1 - g_N)}, P_{N2}^*, \frac{(1 - \sigma_M)f_M P_{M1}^*}{1 - r_M(1 - g_M)}, P_{M1}^*\right). \tag{4.0.11}$$

The terms of the equilibria are given by:

$$P^*_{M1} = \frac{\mu_M f_M \Theta_M - 1}{\alpha_M f_M \Theta_M},$$

$$P^*_{N1} = \frac{\mu_N f_N \Theta_N - 1}{\alpha_N f_N \Theta_N},$$

$$P^*_{N2} = \frac{\alpha_M(\mu_N f_N \Theta_N - 1) - \beta(\mu_M f_M \Theta_M - 1)}{\alpha_M \alpha_N f_N \Theta_N},$$

$$\text{and } \Theta_i = \frac{\sigma_i + r_i(g_i - \sigma_i)}{1 - r_i(1 - g_i)}.$$

If $r_i = 0$, $\Theta_i = \sigma_i$, reducing the system to the seed bank-free model. For $i = M$, $\sigma_M = g_M$ (see discussion of parameters in Section 4 for justification) and so Θ_M simplifies to

$$\Theta_M = \frac{\sigma_M}{1 - r_M(1 - \sigma_M)}.$$

The equilibrium values for the Sahara Mustard are independent of the native annual plant equilibria, as expected, since the equations associated with Sahara Mustard (4.0.5, 4.0.6) are decoupled from those associated with the native annuals (4.0.3, 4.0.4).

The conditions for the existence of $\mathbf{E_1}$, the native annual exclusion equilibrium, and $\mathbf{E_2}$, the Sahara Mustard exclusion equilibrium, are:

$$\mu_M f_M \Theta_M > 1 \text{ and} \tag{4.0.12}$$

$$\mu_N f_N \Theta_N > 1, \tag{4.0.13}$$

respectively, while for $\mathbf{E_3}$ (the coexistence equilibrium) to exist, we need that:

$$\frac{\beta(\mu_M f_M \Theta_M - 1)}{\alpha_M(\mu_N f_N \Theta_N - 1)} < 1, \tag{4.0.14}$$

$$\mu_M f_M \Theta_M > 1, \text{ and } \mu_N f_N \Theta_N > 1. \tag{4.0.15}$$

To analyze the stability of the equilibria we linearize the system around each point by computing the Jacobian matrix and study the spectral radius in each case. For details see Appendix A. Table 3 summarizes the existence criteria needed for the equilibria and their respective stability conditions.

Fixed Point	Existence Criteria	Stability Conditions
Extinction	always exists	$\mathcal{R}_i < 1$
Native Annual Exclusion	$\mathcal{R}_M > 1$	$\mathcal{R}_M > 1$, $\frac{\beta(\mathcal{R}_M - 1)}{\alpha_M(\mathcal{R}_N - 1)} > 1$
Sahara Mustard Exclusion	$\mathcal{R}_N > 1$	$\mathcal{R}_N > 1$, $\mathcal{R}_M < 1$
Coexistence	$\mathcal{R}_i > 1$, $\frac{\beta(\mathcal{R}_M - 1)}{\alpha_M(\mathcal{R}_N - 1)} < 1$	$1 < \mathcal{R}_N < 2$, $\mathcal{R}_M > 1$

Table 3: Fixed point existence and stability, where $i \in N, M$.

5   Discussion of Analytical Results

Definition 1. *Persistence:* $\mathcal{R}_i = \mu_i f_i \Theta_i$.

$f_i \Theta_i$ *represents the ratio of seedlings to the population of plants of the previous generation. Thus $\mu_i f_i \Theta_i$ is the average ratio of surviving seedlings to the previous year's plant population absent competition. In order for a population to increase in a single generation, this ratio must be greater than one. If $\mathcal{R} > 1$, the population is said to be* <u>persistent</u>.

Absent considerations of competition, $\mathcal{R}_i = \mu_i f_i \Theta_i = 1$ would imply that the population remain constant in size. However, in this model, the competition between native annuals and Sahara Mustard, both intra- and interspecific, create more stringent conditions for stability which are dependent on the values of α_M and β.

The global asymptotic stability of the extinction equilibrium in the seed bank-free model gives a lower bound on the amount of control that must be applied to the Sahara Mustard. If the fecundity (the number of viable seeds produced by an average plant) of the Sahara Mustard (f_M) is kept less than the number of seeds which germinate and survive to flowering ($\frac{1}{\mu_M \sigma_M}$), then the population of Sahara Mustard will eventually die out, assuming that a seed bank is never allowed to develop. There are several ways to control the spread of Sahara Mustard, which vary in their effectiveness. Marushia analyzes the effectiveness of hand-pulling of seedlings and herbicide treatment [16]. Hand-pulling of seedlings can disturb the stratum of the seed bank and allow Sahara Mustard seeds to germinate but in the case that a seed bank does not yet exist this is no longer a problem. Hand-pulling effectively decreases the proportion of seedlings which survive to adulthood ($\mu_M^C < \mu_M$), with minimal effect on the native annual population [16]. Herbicide treatments of seedlings does not halt seed production but has been shown to decrease seed viability to 0% ($f_M^C = 0$) for at least one generation while having a small but not insignificant effect on native annuals [16]. The development of herbicide-resistant strains of Sahara Mustard is a definite concern, therefore herbicides should only be used judiciously.

Table 3 illustrates the conditions for stability of the four equilibria in the seed-bank model. Expanding from the simple case of the seed bank-free model grants us strikingly similar results. As noted earlier, $r_i = 0$ implies $\Theta_i = \sigma_i$. Although the full model has two more equilibria (the competitive exclusion cases) than the seed bank-free model, there are clear similarities between the equilibrium existence criteria and stability conditions of the seed bank-free model and the full model. Figure 5 plots persistence of the native population against persistence of Sahara Mustard. If both plant species are not persistent, the extinction equilibrium is stable. If one species is not persistent and the other is, there is exclusion of the non-persistent species. The more interesting case is if both species are persistent. The stability then depends further on α_M and β. If $\beta > \alpha_M$ (that is, interspecific competition is greater than the Sahara Mustard intraspecific competition), coexistence will occur for a smaller range of persistence values. If $\alpha_M > \beta$, the native annuals are more likely to coexist with the Sahara Mustard.

The trivial or extinction equilibrium always exists but is only stable when, for both species, there are on average fewer surviving seedlings than there were adults in the previous year. Or, both species are below the persistence threshold.

The extinction equilibrium is not a desired equilibrium for our system. While Sahara Mustard elimination is a definite goal, it should not come at the expense of losing the native annual species. This is especially important to remember when considering use of herbicides. While studies have shown that herbicides have a minimal effect on annual species when applied at an appropriate time, if this effect is large enough to put the native species below its persistence threshold then that population will also go extinct.

The conditions for existence and stability of the Sahara Mustard exclusion equilibrium are analyzed as follows: if the native annual population is above its persistence threshold and the Sahara Mustard population is below its persistence threshold, then the Sahara Mustard exclusion equilibrium will have both existence and stability. This equilibrium represents the ideal goal of conservationists in the Sonoran Desert: complete elimination of Sahara Mustard. A perfect control method would push only the Sahara Mustard population beneath its persistence equilibrium, leading to its eventual demise.

The native annual exclusion equilibrium requires only that the Sahara Mustard population be above its persistence threshold to exist. In order for this point to be stable, a second stability condition must also be satisfied. When the native annual population is below its persistence threshold, this condition is satisfied for all values of α_M and β.
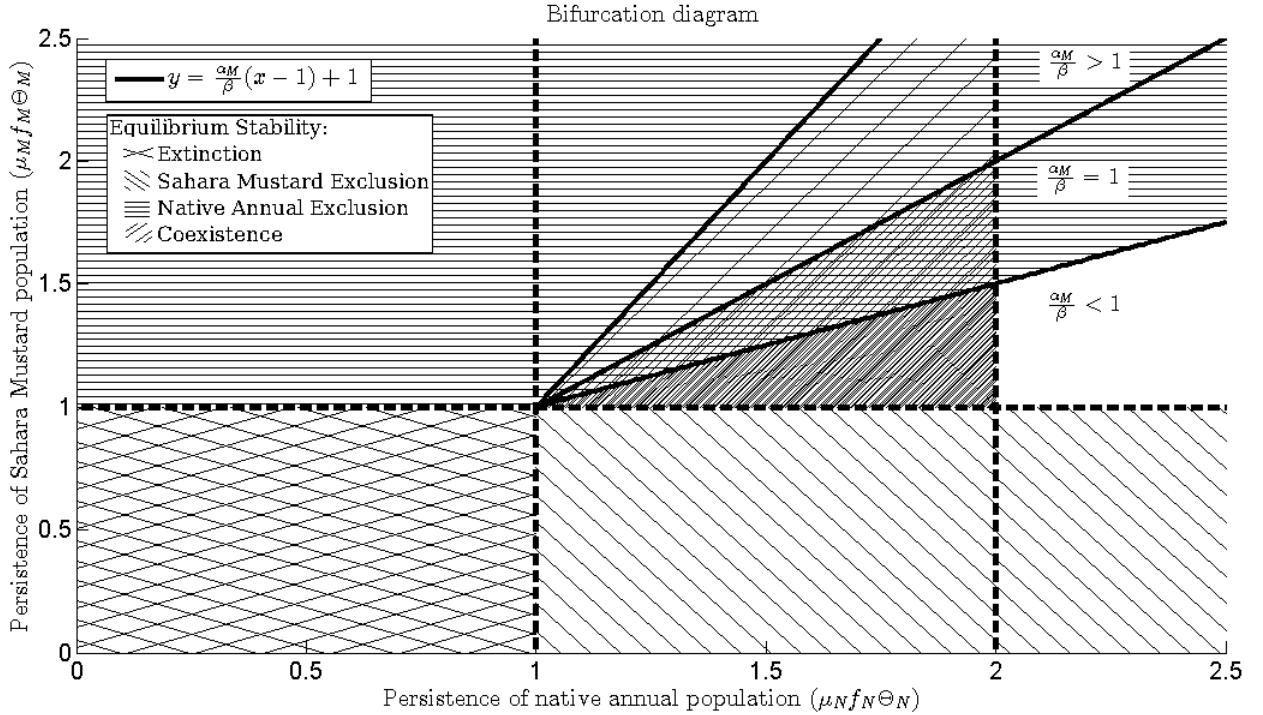
Figure 3: Bifurcation Diagram, in terms of Sahara Mustard and native annual persistence. The coexistence equilibrium is stable below the line of slope $\frac{\alpha_M}{\beta}$, and native annual exclusion is stable above this line. Three lines are plotted for different values of β for fixed values of α_M. In our deterministic simulations and stochastic realizations, $\frac{\alpha_M}{\beta} > 1$.

The existence criteria and stability conditions for coexistence are attainable for realistic parameter values. For β such that $\beta > \alpha_N, \alpha_M$ (i.e., inter-specific competition is stronger than intra-specific competition) the magnitude of the coexistence equilibrium for native annuals is very small relative to that of the Sahara Mustard. Biologically this could represent the ability of the native annual to find refuge in the presence of large populations of Sahara Mustard. Further field studies must be conducted to determine if this is a realistic scenario or simply an apocryphal product of the form of our model.

6 Parameters

Table 4 provides a list of parameter values for different environmental conditions. The probability of Sahara Mustard and native plant seeds surviving dormancy in the seed bank (r_N and r_M), as dormant seeds are assumed to be immune to weather conditions in our model.

Ranges (rainfall in inches)	$[3, \infty)$	$[1.5, 3)$	$[0.59, 1.5)$	$[0, 0.59)$	-
Parameter	Wet	Normal	Dry	Very Dry	Reference
σ_N	0.64	0.11	.04	0.0	[19] [18]
g_N	0.43	0.07	0.03	0.0	[18]
μ_N	0.5	0.1	0.05	-	[A]
f_N	1750	1000	200	-	[A]
σ_M	0.7	0.58	0.35	0.0	[7] [14]
g_M	0.7	0.58	0.35	0.0	[3]
μ_M	variable		0.0	-	-
f_M	6000	1000	0.0	-	[21]
r_N	0.37				[A]
r_M	0.55				[12]
α_N	0.001				[13]
α_M	0.001				[13]
β	0.01				[13]

Table 4: Parameter values for the stochastic model. [A]: (Tom Philippi, Personal Correspondence, July 16, 2012)

The orders of magnitude of the competition parameters were taken from a paper by Law and Watkinson[13], which studied competition between two winter annual grasses. Other parameter calculations and justifications are as follows.

6.1 Rainfall

We chose to classify years based on the biology of either Sahara Mustard or plants similar to *L. lasiocarpum*. For very dry years, we assumed no germination for either species ($g_i, \sigma_i = 0$). There is generally a critical value of rainfall below which there is no, or negligible, germination for even the best-adapted desert plants. The lowest germination rates for *L. lasiocarpum* were seen when 15mm of rainfall was simulated (about 0.59 inches) [10], which led us to choose 0.59 inches of rain as that critical value.

Although years such as this are rare, they do occur in the Sonoran Desert. For example, in the year 1995 not a single drop of rain fell in Ajo, AZ [6]. It is assumed that there would be no winter annuals germinating in such a year. For very dry years, then, μ_i and f_i are irrelevant, as no plants survive to set seeds. Sahara Mustard is capable of widespread germination when 1.5 or more inches of rainfall are present, so this was chosen as the lower bound for our normal years. The upper bound for a normal year was chosen based on the average rainfall in Ajo over several years [6], as we knew that sudden invasions of Sahara Mustard were seen after years with increased rainfall [8].

6.2 Native Plants

- σ_N: The values for normal and dry years were averages of numbers taken from a study by Philippi [19] where limited water was given to *L. lasiocarpum* seeds in order to track their germination. The value for a wet year was found in a second study, also by Philippi [18], where seeds were given enough water to ensure that water stress did not limit germination.

- g_N: In a lab study, germination of *L. lasiocarpum* was tracked over two years. The first set of seeds, given good germinating conditions two years in a row, had .47 probability of germination in the second year. The second set of seeds, given first bad and then good conditions, had .4 probability of germination in the second year [18]. Since it was outside the scope of our model to incorporate seed memory, we took an average to get 0.43 as the probability of second-year germination for a wet year. We then assumed that second-year germination rates were linearly dependent on first-year germination rates, or that $g_N = k\sigma_N$. Using .43 for g_N and .64 for σ_N in a wet year, we found that $k = .67$. The remaining values of g_N were calculated using the equation $g_N = .67\sigma_N$.

- μ_N: *L. lasiocarpum* can have 50% survivability under low-density greenhouse conditions and 0-10% survivability in the wild (Tom Philippi, personal correspondence, July 16, 2012). Because μ_i was assumed to be independent of density conditions, we chose 0.5 for survivability under wet conditions. Then we chose 0.1 as average survivability under normal weather conditions and 0.05 as survivability under less favorable conditions.

- f_N: *L. lasiocarpum* produces 0-2000 seeds in Arizona, and 0-200 in California (Tom Philippi, personal correspondence, July 16, 2012). We picked values that fell within these ranges.

- r_N: There are not many viable *L. lasiocarpum* seeds left in the seedbank after three years (Tom Philippi, personal correspondence, July 16 2012). We calculated r_N such that, ignoring germination and new seeds, only 5% of the seed bank would be viable after three years.

6.3 Sahara Mustard

- σ_M: In a study over 90 days, 58% of Sahara Mustard germinated within 14 days under good conditions, and up to 70% germinated if given an additional 90 days [7]. We chose 0.58 as the probability of germination in a regular year and 0.7 as the probability in a wet year, as a wet year would more likely allow for favorable conditions later in the season. In a separate study where watering conditions were varied, germination rates hit a minimum of about 0.35 [14], which we used as the first-year germination rate in dry years.

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- g_M: Three years of dormancy did not affect the germination of Sahara Mustard [3]. As such, we assumed that the probability of a seed germinating out of the seed bank was the same as the probability of first-year germination (i.e. $g_M = \sigma_M$).

- μ_M: We varied this parameter in order to model different control strategy efficacies.

- f_M: The number of seeds a plant produces varies linearly with its biomass [21]. We chose mid-range values from two plant sizes.

- r_M: Because we knew that seeds could last several years[12], we calculated r_M such that 5% of the bank's initial seeds would be viable after 5 years.

Beyond the theoretical analysis in Sections 3, 4, and 5, we ran simulations to observe long-term behavior of System 4.0.3-4.0.6. The parameter values explained in this section are further used in Sections 7 and 8, for our deterministic and stochastic simulations. Although there are possible conditions for the existence and stability of all equilibria (see Section 5), the presence of these equilibria in our simulations is dependent on the numerical parameter values for our system.

Year Type	Persistence		$\frac{\beta(\mathcal{R}_M-1)}{\alpha_M(\mathcal{R}_N-1)} < 1$	Equilibria	
	Native	Sahara Mustard		Existence	Stability
Wet	623	2263	36.3	$\mathbf{E_0}, \mathbf{E_1}, \mathbf{E_2}$	$\mathbf{E_1}$
Normal	14.5	339	250	$\mathbf{E_0}, \mathbf{E_1}, \mathbf{E_2}$	$\mathbf{E_1}$
Dry	0.5	0	23	$\mathbf{E_0}$	$\mathbf{E_0}$
Critically Dry	0	0	10	$\mathbf{E_0}$	$\mathbf{E_0}$

Table 5: Fixed point existence and stability for four year types.

Table 5 indicates which of the equilibria discussed in our analysis of the seed-bank model exist and are stable for our parameter values. We obtained these results by using the values from Table 4 in the definition of persistence (given in Section 5) and the formula for $\frac{\beta(\mathcal{R}_M-1)}{\alpha_M(\mathcal{R}_N-1)} < 1$, another constant seen in stability and existence conditions for equilibria.

7 Seed Bank Model Simulations

While the analysis provides equilibrium values and stability conditions, a numeric simulation illuminates the overall behavior of the system over a span of several years, allowing for a more comprehensive understanding. Matlab code was constructed to calculate and plot values over a reasonable time interval.

Parameter were assigned based on year types (shown in Table 4. An array of $N + 1$ indices was constructed for each population in the system. Here, N represents the number of years the simulation would iterate over (in our simulations, $N = 20$). A for-loop was responsible for the iteration and ranged between 1 and N with increments of 1. The unit

in this construction is one year. Another function was constructed to access the population sizes from the previous year as well as the proper parameters based on the year type, and return the deterministic population sizes for the current year as an array. This array was used to assign the proper values of populations for the current year's index in the four population arrays. As necessitated by the for-loop, this process was continued until the Nth year. See appendix for the Matlab code.

As mentioned previously, several of the system parameters are affected by the amount of winter rainfall. Because of this, four different deterministic situations were examined; one corresponding to each of our four winter rainfall classifications (critically dry, dry, normal, and wet). Each simulation assumed that weather conditions would be consistent over the time interval. Figures 4, 5, 6, and 7 show the deterministic simulations of Sahara Mustard and native annual plant and seed populations. We choose the initial conditions $(S_N(0), P_N(0), S_M(0), P_M(0)) = (1000, 100, 1000, 100)$, intraspecific competition parameters of $\alpha_N = \alpha_M = .001$, and an interspecific competition parameter of $\beta = .01$ (see Section 6).
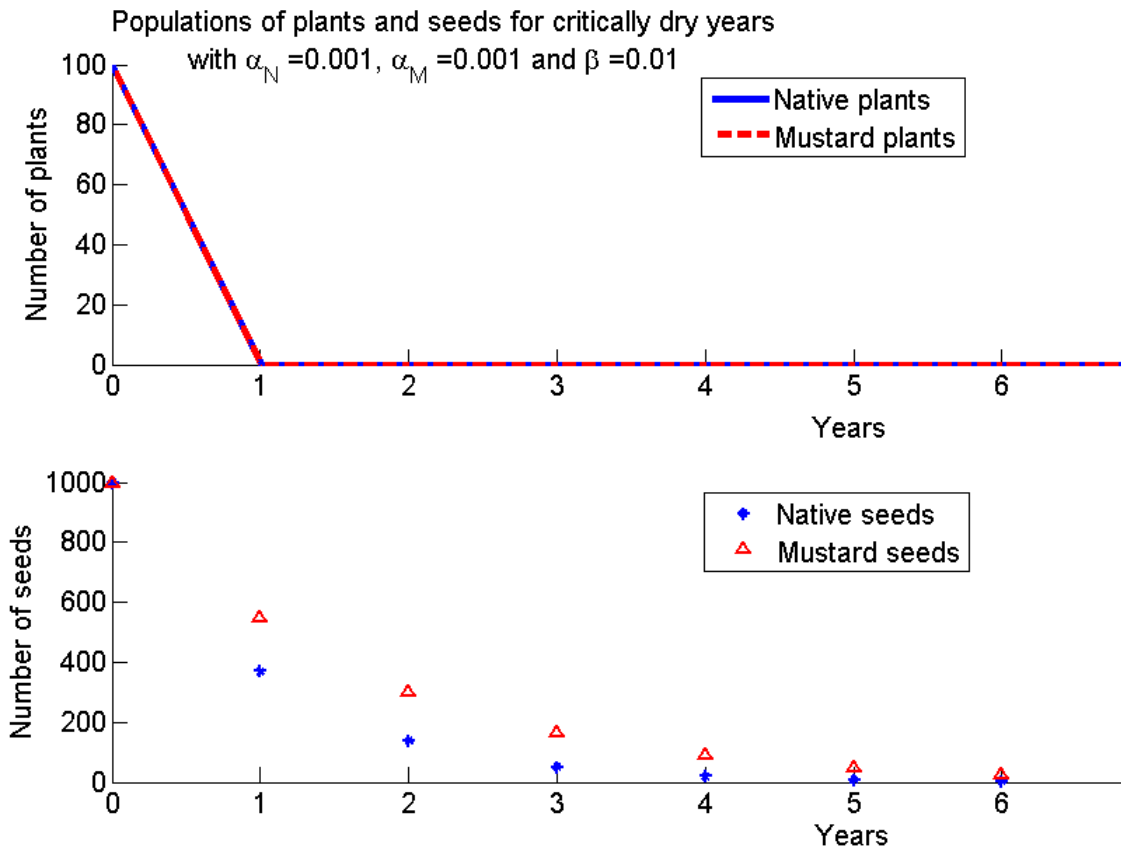
Figure 4: Deterministic simulation assuming constant critically dry weather conditions over several years.
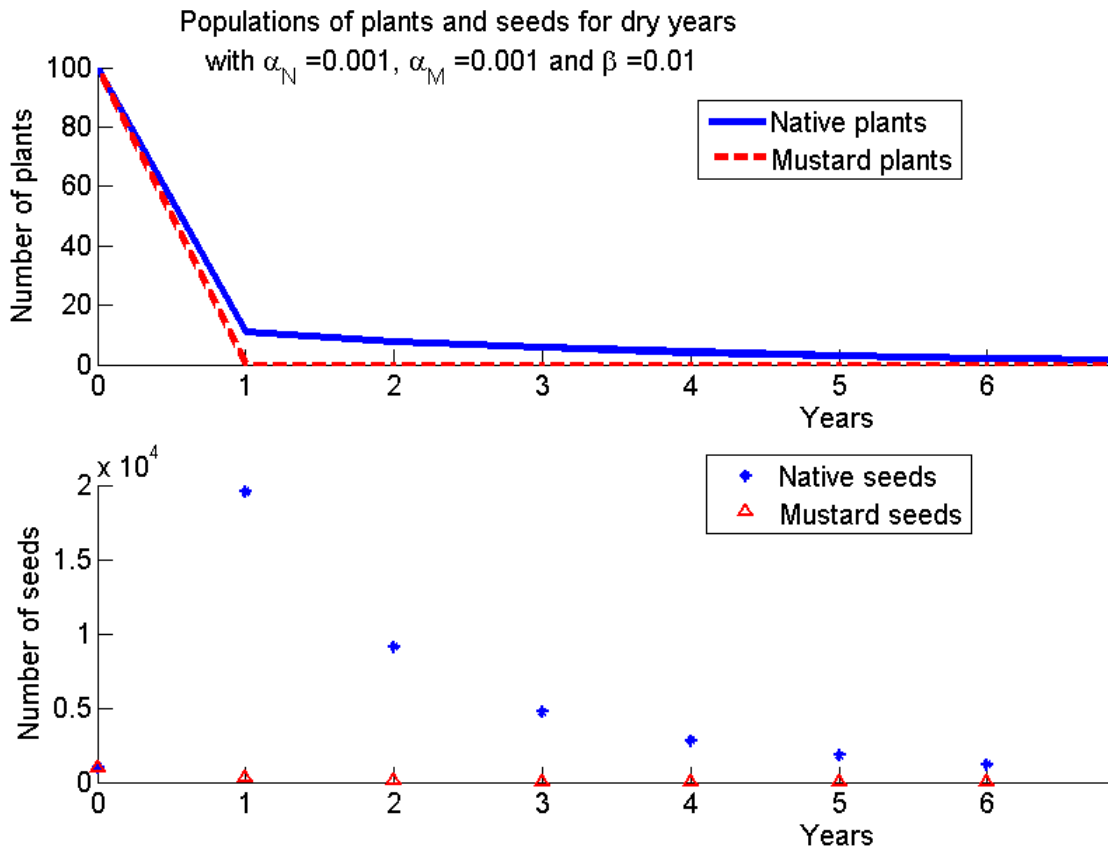
Figure 5: Deterministic simulation assuming constant dry weather conditions over several years.

Figures 4 and 5 show that although the natives fare better than the Sahara Mustard in the dry scenario, both species go extinct for the dry and critically dry years. This suggests that the occasional dry year may allow the native annuals to prosper while the Sahara Mustard dies away. Repeated several times in a row, however, these dry years cause the seed bank to die out without being replenished.
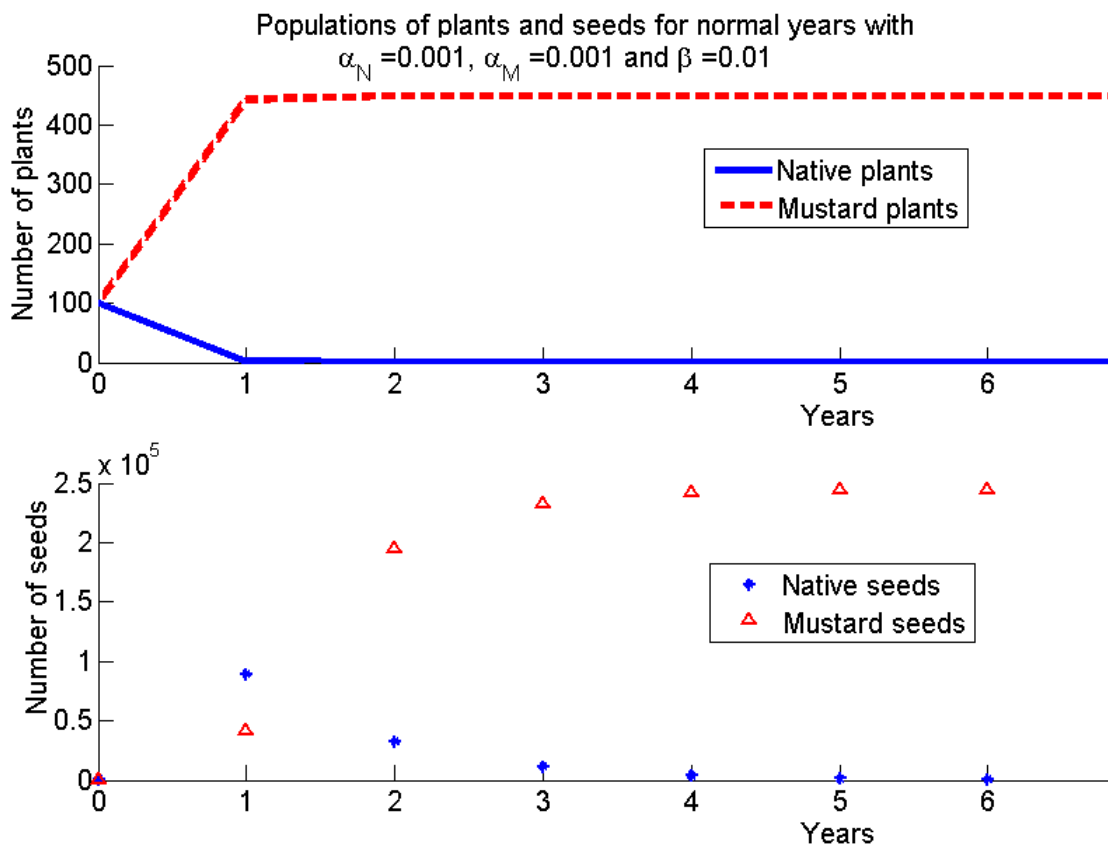
Figure 6: Deterministic simulation assuming constant normal weather conditions over several years.
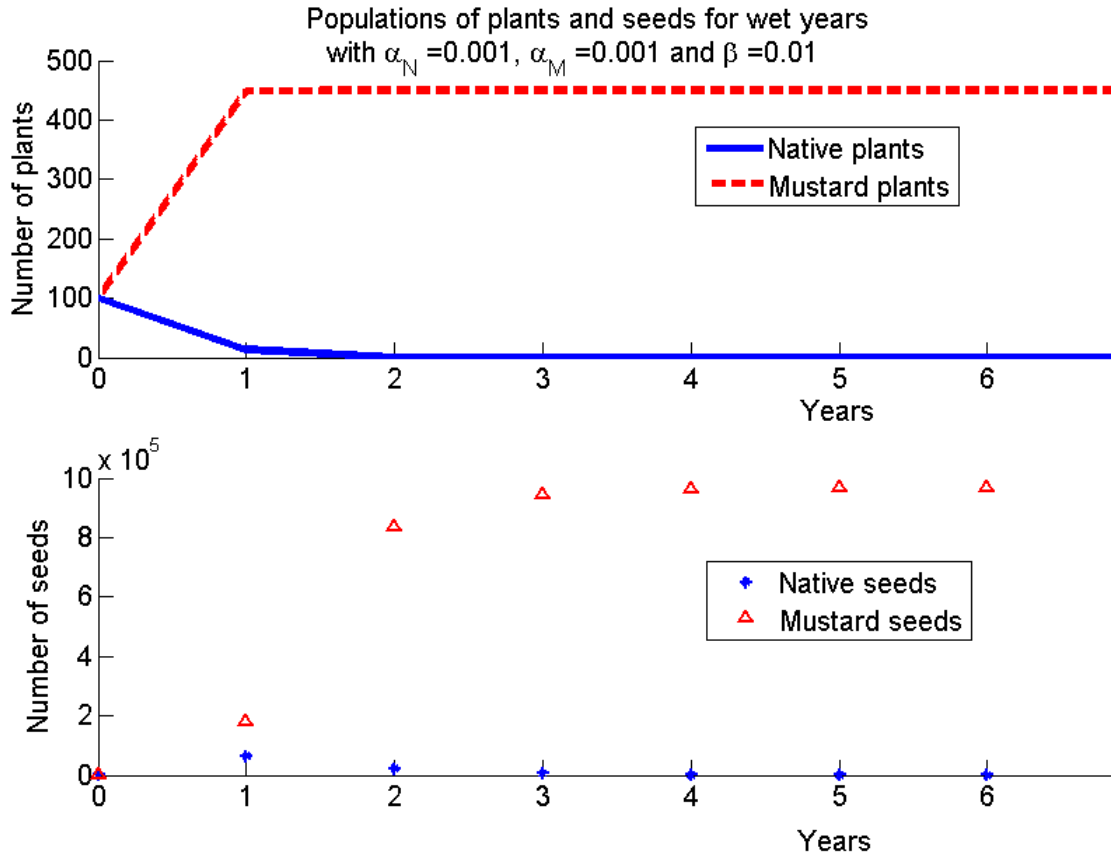
Figure 7: Deterministic simulations assuming constant wet conditions over several years.

For the normal and wet simulations in Figures 6 and 7, the Sahara Mustard plants and seeds reach a non-extinction equilibrium, while the native plants become extinct. In the wet scenario, the natives' improved parameter values allow them an extra year before they reach extinction, but they are ultimately overrun by the mustard. Unfortunately, this suggests that the native annuals cannot sustain a population over several average years when competing with the Sahara Mustard.

In addition to plotting the basic behavior of the deterministic model, we mapped the effect that critical parameters have on it. In order to do so, we created plots that show the Sahara Mustard and native plant's final population size as a function of different parameters in our model. Although some parameters proved to be irrelevant to the native plant's long-term population dynamics, we saw that the interspecific competition parameter β and parameters that limit the survival of Sahara Mustard plants (α_M and μ_M) had a significant effect on the native plants' ability to avoid extinction.
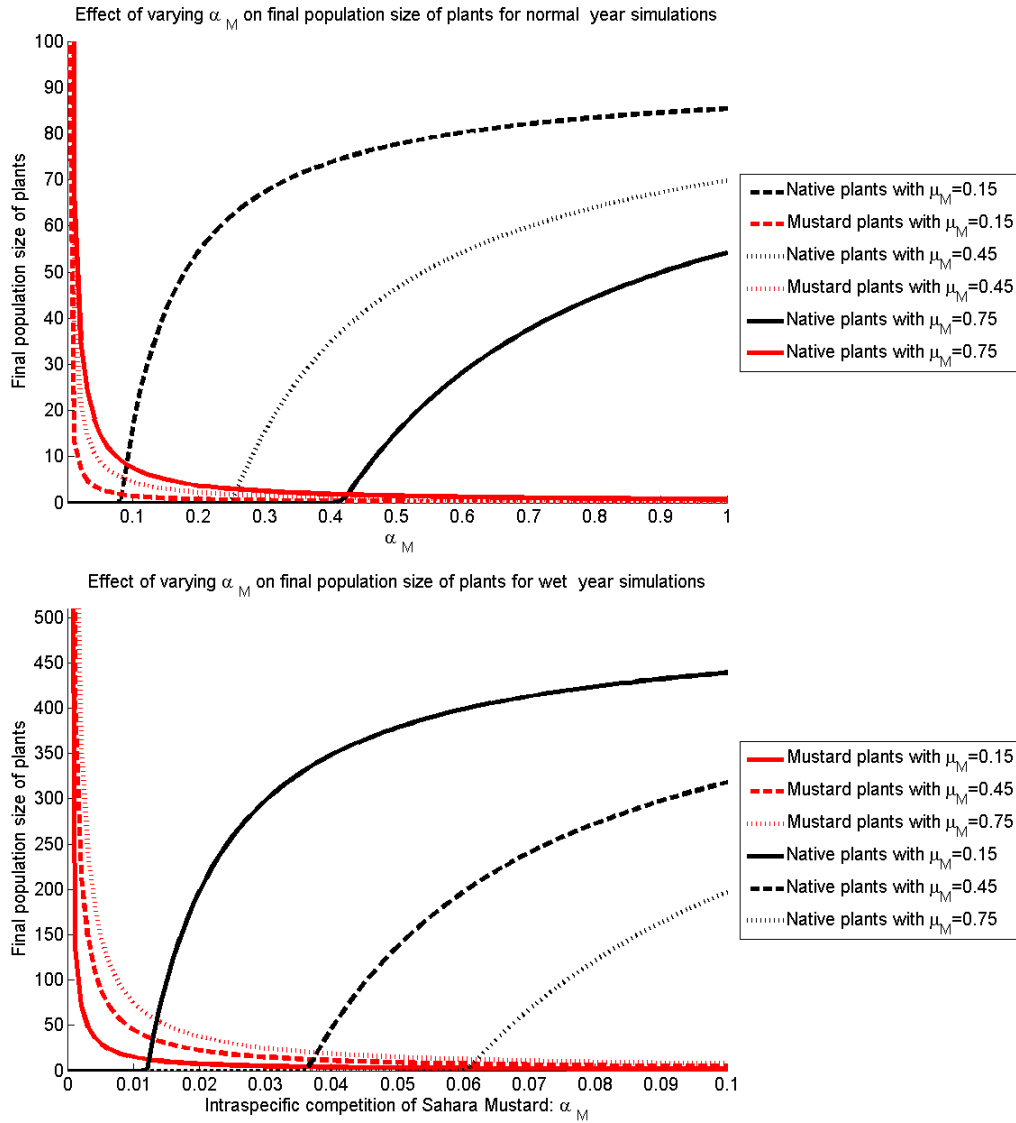
Figure 8: The effect of varying μ_M and α_M on the native plants' final population size.

Figure 8 indicates that higher levels of intraspecific competition for Sahara Mustard (α_M) or low levels of Sahara Mustard survivability (μ_M) allow the native annuals to reach higher final population sizes. In both cases, this means that more Sahara Mustard seedlings die before reaching adulthood and there are less plants for the native annuals to compete with when germination begins. Since μ_M would be affected by methods such as hand-pulling or herbicide, native annuals can persist if sufficient controls are in place to contain the Sahara Mustard population. However, if Sahara Mustard survivability

is not sufficiently low, then only large values of α_M allow the native annuals to avoid extinction, supporting the assumption that native plants are not well-equipped to compete with Sahara Mustard's prolific, fast-growing populations.
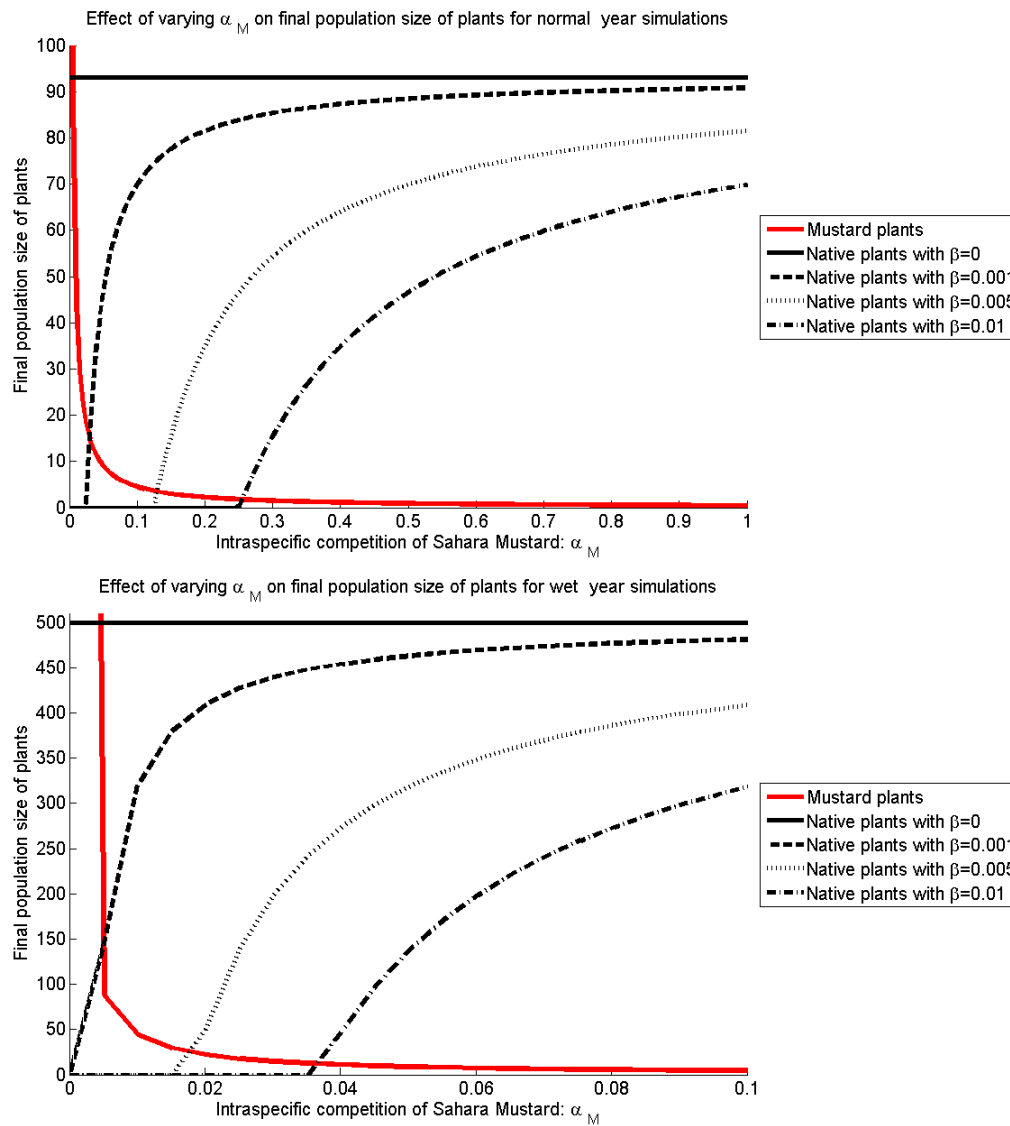
Figure 9: The effect of varying β and α_M on the native plants' final population size.

Figure 9 plots the final population size of each species against values of α_M, showing trajectories for various values of β. Note the effect that Sahara Mustard interspecific competition (β) has on final population size of both native annuals and Sahara Mustard when wet years are simulated. In our other deterministic simulations, values of $\alpha_M = 0.001$

and $\beta = 0.01$ were used. For these values the native annual population will eventually go extinct for wet year simulations. But for smaller values of β (e.g. $\beta < 0.001$) we see that the native annuals will persist, even in the presence of Sahara Mustard. Alternatively, if α_M were increased beyond 0.02, the native annuals would also persist but in the presence of less Sahara Mustard. This displays the importance of the relative strength of intraspecific competition of Sahara Mustard to the interspecific competition on the final population size of both species.

8 Stochastic Simulations

To explore the potential role of environmental variability in the competition between Sahara Mustard and native annuals, we also ran stochastic simulations that added annual climate variation to the deterministic model. Each generation, random sampling using data on the total amount of winter rain in Ajo, Arizona over the past twenty years was performed. The rainfall data was acquired through the National Oceanic and Atmospheric Administration (NOAA) website [6]. The randomly sampled data point determined the type of year (very dry, dry, normal, or wet), and the type of year determined which parameters would be used (see Table 4). Here we define winter rain as that occurring from October of the previous year to April of the following year. Our focus is on winter rain since summer rain does not affect native winter annual or Sahara Mustard populations of plants and seedlings.

Figure 10 plots inches of winter rainfall from 2012 back to 1926. The most recent year is left-most on the graph, with preceding years falling to the right. The ten-year mean for each year is the average for winter rainfall over the previous ten years. This figure shows the variability in winter rainfall over the years and is also our justification in only sampling data from the past twenty years. The ten-year average before 1990 is noticeably higher than it was from 1990 to 2012. While we will not speculate on the cause of this change, incorporating older data in our stochastic simulation may be unrealistic. Since the current climate is drier than that of the past, it would be ludicrous to allow for a plethora of wet years. Our stochastic model assumes that the climate over the next one or two decades can be predicted by previous conditions, and that the mean winter rainfall will not return to pre-1990 values.
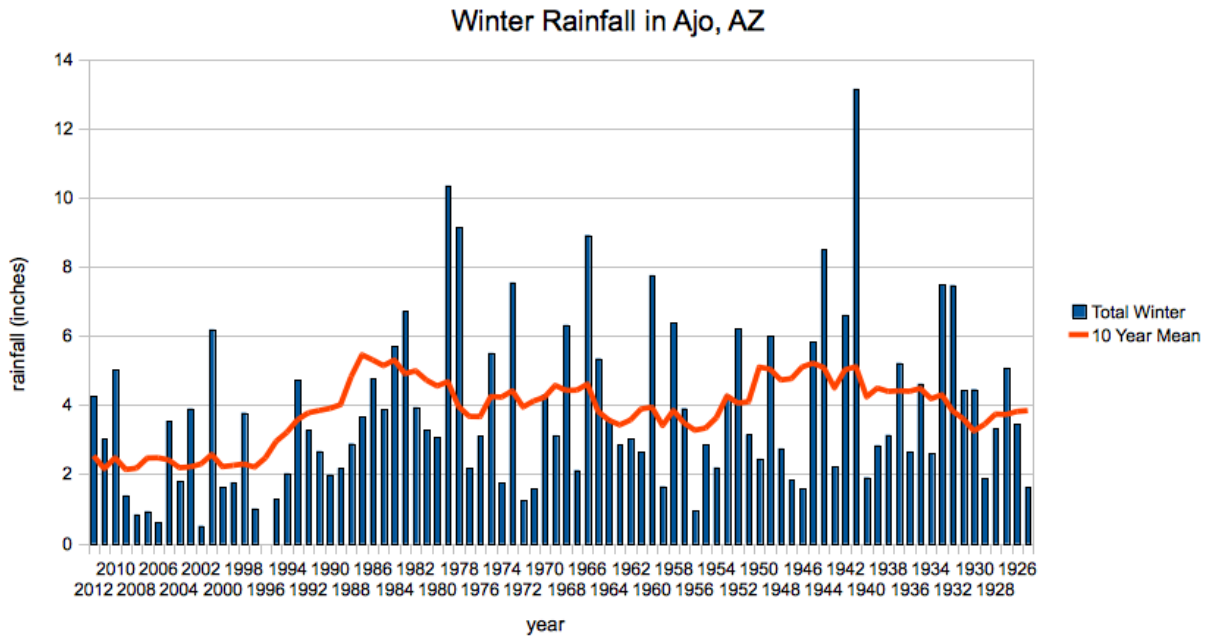
Figure 10: Total winter rain (November to April) in Ajo, AZ [6]. The ten-year mean show the average of the preceding ten years.

Figures 11 through 14 show plots of stochastic and deterministic simulations for the four populations of our model. Each graph depicts three stochastic realizations plotted against the four deterministic solutions. These stochastic realizations are different trials with the same seasonal parameters. To differentiate between the stochastic and deterministic simulations, the deterministic solutions were plotted with symbols at each data point.
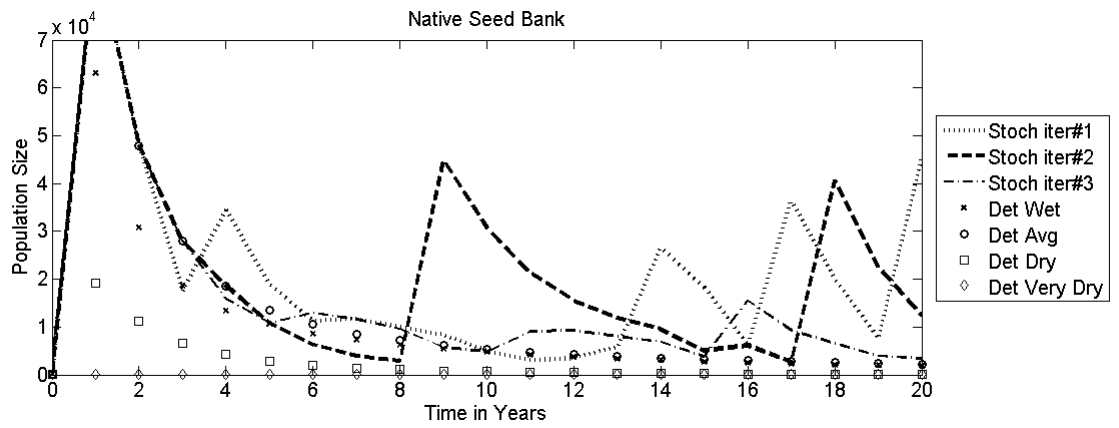
Figure 11: Three stochastic realizations and four deterministic solutions for native annual seeds.
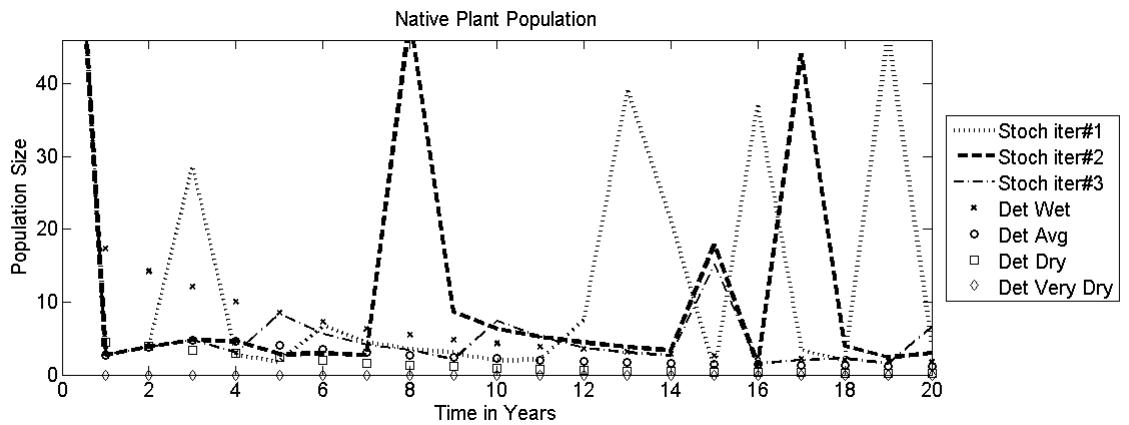
Figure 12: Three stochastic realizations and four deterministic solutions for native annual plants.

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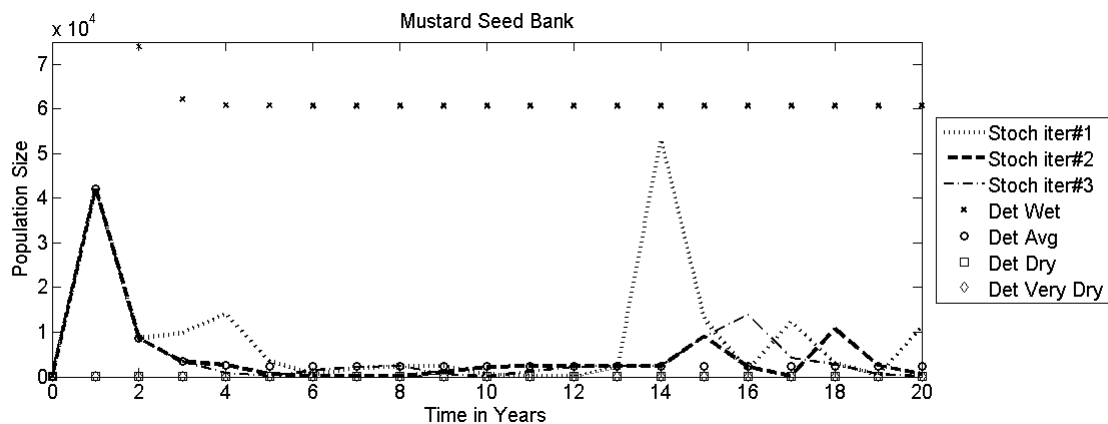
Figure 13: Three stochastic realizations and four deterministic solutions for Sahara Mustard seeds.
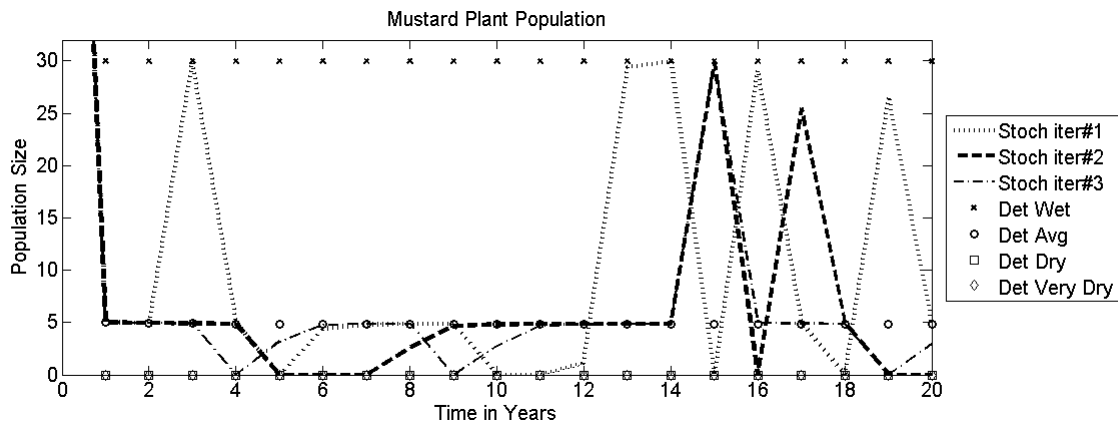
Figure 14: Three stochastic realizations and four deterministic solutions for Sahara Mustard plants.

From the stochastic realizations in Figure 11 it can be observed that after twenty years, the native seed bank is usually not empty. Only a series of critically dry years will completely eliminate the seed bank. Persistence of the seed bank even under variable conditions was anticipated, as the seed bank is a desert annual's defense against unfavorable seasons. We see that in most simulations, the random event of a dry or critically dry year is not enough to drive the native plant's seeds to extinction, as seeds are maintained within the bank under all conditions.

From Figure 12, it can be seen that in general, the native plants are at a critical population size after these twenty years. Also, from year to year, there are some large oscillations which coincide with the occurrence of wet years. A single wet year will increase

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native germination, but also drastically increases mustard fecundity, so that wet years favor the Sahara Mustard. The increased seedlings that result from this create overwhelming competition in the next year, and the mustard continues to thrive. Although all cases of the deterministic models resulted in extinction, in the stochastic simulations we see some native plants surviving the twenty years, indicating that environmental stochasticity favors the natives' survival.

Note the scale of the population size in Figure 13. The maximum value is two million (not shown). Thus, although it appears that the mustard seed bank is almost empty after the twenty years, it still has several thousand seeds. As in the case of native annual seeds, the seed bank allows for the seeds to avoid extinction under bad conditions. However, we also see a large spike in the second stochastic realization, indicating an extremely successful year for the mustard plants. Fortunately, we also see the seeds decrease and level out shortly after this sudden spike, due to intraspecific competition preventing the Sahara Mustard from further increasing its seed bank in the following years.

In Figure 14, the population of Sahara Mustard is bounded between zero and thirty plants, and oscillates between these values. In spite of Sahara Mustard tending to dominate, its plant population does not immediately outgrow the native plants' as the deterministic models suggest. Dry and critically dry years likely curb the population growth we expect from normal and wet years. However, the Sahara Mustard's massive seed bank provides the insurance necessary to survive long into the indefinite future, regardless of weather conditions.

8.1   Final Size Distributions

In order to provide a better understanding of the populations' stochasticity, histograms of the final population sizes were produced. We ran 10,000 realizations of the stochastic simulation and used the final size of the plant and seed populations after 20 years. The dashed line represents the deterministic end state for a wet year in the deterministic model. Table 6 provides a summary of the final population sizes under both the deterministic and stochastic simulations.

	S_N	P_N	S_M	P_M
Deterministic Wet	0	0	$6.5 \cdot 10^4$	30
Deterministic Normal	0	0	$0.25 \cdot 10^4$	5
Deterministic Dry/Critically Dry	0	0	0	0
Stochastic Mean	$4,340$	4.24	$5,690$	7.41
Stochastic Variance	$6,870$	8.27	$10,000$	9.75

Table 6: Comparison of final population sizes in deterministic and stochastic simulations.

The stochastic simulations allow for non-zero final population sizes for the natives, despite there being no such possibility in the deterministic models. This suggests that

climactic variation favors the natives. However, the Sahara Mustard still outcompetes the native annual.
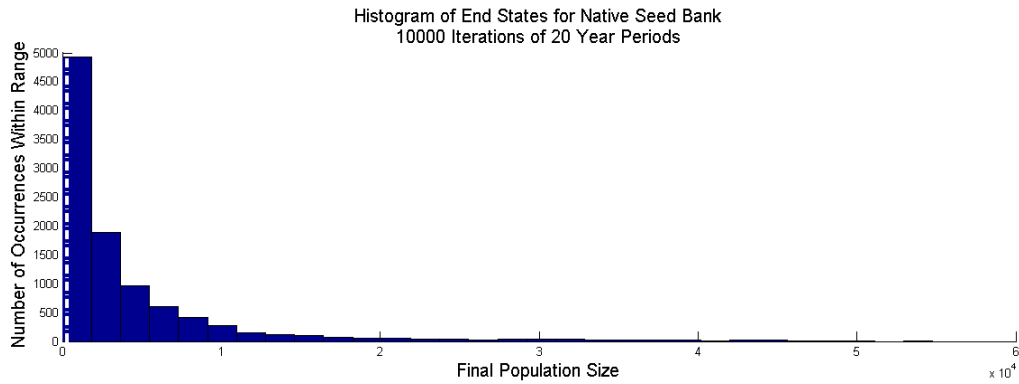

Figure 15: Sample Mean of 4393.4, Sample Standard Deviation of 6874.2

Figure 15 suggests that the seed bank for native plants will almost always end up between zero and 1000 seeds at the end of twenty years. From our understanding of the stochastic simulations, we can conclude that the seed bank might not reach zero in many cases. This histogram suggests that most of the final seed bank sizes are small relative to the Sahara Mustard, preventing extinction but not allowing for population explosions.
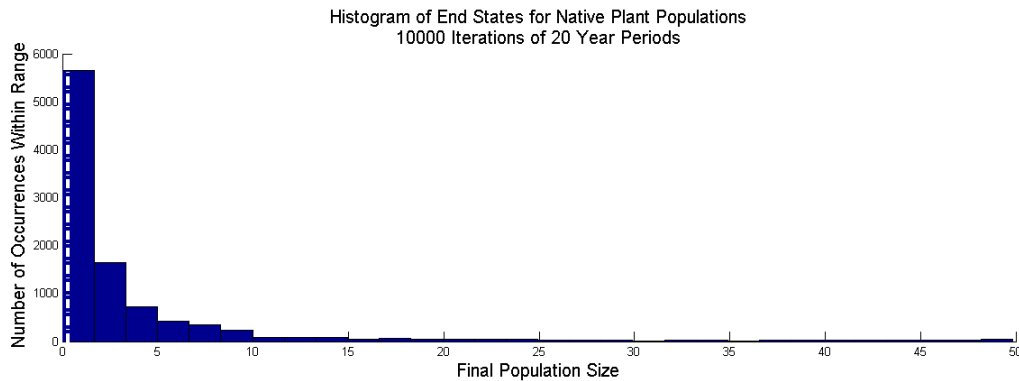
Figure 16: Sample Mean Value of 4.2356, Sample Standard Deviation of 8.2654

Figure 16 shows that the majority of the native annual plant's final population sizes are close to zero. This long term behavior for native plants does not look optimistic, but as long as the seed bank remains populated (similar to what Figure 15 provided) there will always be a few native plants present.
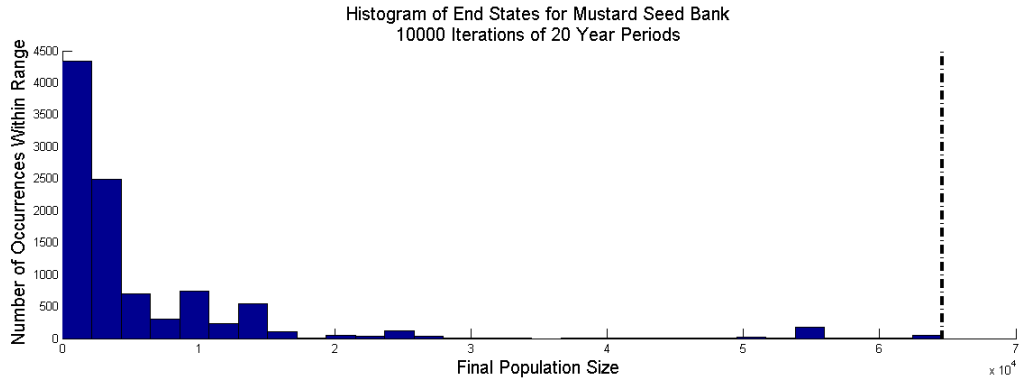
Figure 17: Sample Mean Value of 5691, Sample Standard Deviation of 10027

Figure 17 shows that the mustard seed bank is likely to have a population larger than the native seed bank. In this case we have a more varied distribution, compared to the distribution from the natives' seed bank. While the majority of the time the final population is around a few hundred, it is more likely to be around 5500 than it is to be anywhere in the range of 3000 to 5000. This inconsistent distribution can be explained by the prosperity of Sahara Mustard in wet years, when it is especially fecund. In stochastic simulations with several wet years, Sahara Mustard is likely to develop enormous seed banks, compared to stochastic and deterministic simulations for other year types.
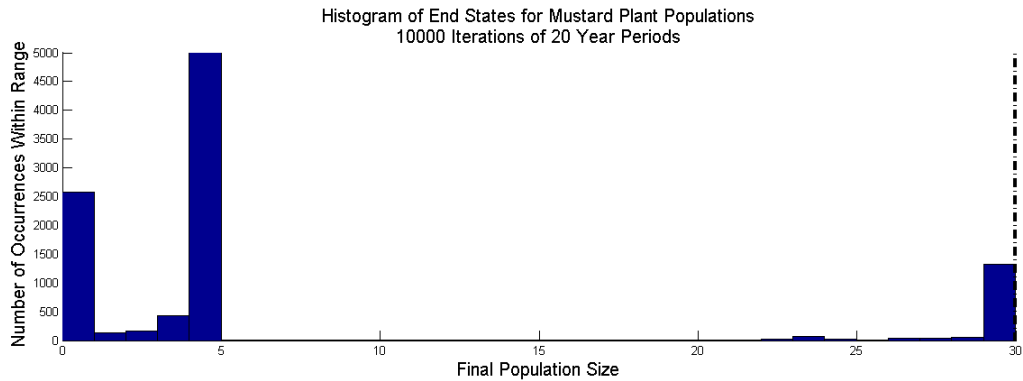

Figure 18: Sample Mean Value of 7.4062, Sample Standard Deviation of 9.7547

No population explosion is predicted for the Sahara Mustard plant population in the deterministic models, but the histogram demonstrates that increased frequencies of wet years, even if only by a small amount, can result in its population converging to thirty. We can see that the majority of the final population sizes of the Sahara Mustard plant population are around five, rather than close to zero as we saw with the native annual plant population. Again, we see that the Sahara Mustard is likely to outperform the native

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annuals, even in the presence of stochastic weather conditions.

9   Conclusion

Since parameters such as fecundity vary widely according to plant biomass and region, more studies on whether Sahara Mustard will outcompete or coexist with native annuals in a particular region are needed. However, fecundity will likely be a critical factor in determining the likelihood of survival of a native plant in competition with the invasive. There was a lack of data on competition parameters α_i and β. These values are very important in determining how the system will evolve and quantifying α_i and β for a particular location can give insight into the future evolution of the system. In normal years, values of β larger than 0.03 result in extinction of the native annuals, supporting the assumption that native plants are not well-equipped to compete with Sahara Mustard's prolific, fast-growing populations.

In our stochastic model, climate variability appeared to act favorably upon the native annuals. Although all cases of the deterministic models resulted in extinction, in the stochastic simulations some native plants survive the twenty years. The entire population can grow greater than predicted by the wet year deterministic model. The Sahara Mustard population, however, appears to remain bounded above by the wet year predictions. This indicates that climate variability in an environment can influence the dynamics of the system in complex ways. In our model, this variability has the most significant impact on the native annuals, while the final Sahara Mustard populations adhere more closely to the deterministic model. End-states for Sahara Mustard populations in the stochastic simulation remain bounded above by wet year predictions.

Since spatial dynamics can be an important part of plant competition in arid regions, it would be worthwhile to add a spatial component to this model, incorporating density and even dynamics of seed dispersal. Also, a different model could be created exploring the dynamics of competition within a season and not just from year to year. This model could potentially investigate the effect of features such as the timing and amount of winter rains. Further studies should also be conducted on how fecundity and survival of Sahara Mustard and native forbs vary with environmental conditions. Although it was beyond the scope of this project, optimal control strategies for the containment of Sahara Mustard are also important for future study. Experiments to quantify the competition between Sahara Mustard and various native plant species would be useful as well.

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Appendix A: Eigenvalues of Jacobian Matrices

Consider a generic equilibrium $\left(\frac{(1-\sigma_N)f_N P_N^*}{1-r_N(1-g_N)}, P_N^*, \frac{(1-\sigma_M)f_M P_M^*}{1-r_M(1-g_M)}, P_M^* \right)$ and let
$Z = (1 + \alpha_N \Theta_N f_N P_N^* + \beta \Theta_M f_M P_M^*)^2$. Then the Jacobian at this generic equilibrium is:

$$
\begin{pmatrix}
(1-g_M)r_M & 0 & (1-\sigma_M)f_M & 0 \\
0 & (1-g_N)r_N & 0 & (1-\sigma_N)f_N \\
\frac{\mu_M g_M r_M}{(1+\alpha_M \Theta_M f_M P_M^*)^2} & 0 & \frac{\sigma_M f_M \mu_M}{(1+\alpha_M \Theta_M f_M P_M^*)^2} & 0 \\
\frac{-\beta \Theta_N f_N P_N^* \mu_N g_M r_M}{Z} & \frac{(1+\beta \Theta_M f_M P_M^*)\mu_N g_N r_N}{Z} & \frac{-\beta \Theta_N f_N P_N^* \mu_N \sigma_M f_M}{Z} & \frac{(1+\beta \Theta_M f_M P_M^*)\mu_N \sigma_N f_N}{Z}
\end{pmatrix}
$$

with corresponding eigenvalues:

$$
\begin{aligned}
\lambda_{1,2} &= \frac{1}{2}\left[C_1 \pm \sqrt{C_1^2 - 4C_2} \right], \\
\lambda_3 &= 0, \\
\text{and } \lambda_4 &= (1-g_M)r_M + \frac{\sigma_M f_M \mu_M}{(1 + \alpha_M \Theta_M f_M P_M^*)^2}.
\end{aligned}
$$

Where C_1 and C_2 are defined as:

$$
\begin{aligned}
C_1 &= \frac{(1 + \beta \Theta_M f_M P_M^*)\mu_N f_N \sigma_N}{(1 + \alpha_N \Theta_N f_N P_N^* + \beta \Theta_M f_M P_M^*)^2} + (1 - g_N)r_N, \\
\text{and } C_2 &= \frac{(1 + \beta \Theta_M f_M P_M^*)\mu_N f_N r_N (\sigma_N - g_N)}{(1 + \alpha_N \Theta_N f_N P_N^* + \beta \Theta_M f_M P_M^*)^2}.
\end{aligned}
$$

The only way we can have complex eigenvalues is if $4C_2 > C_1^2$. However, a sufficient condition for this never to occur is:

$$
\frac{2g_N}{\sigma_N(1 + g_N)} < 1,
$$

which holds for all of our parameters. We can ignore the possibility of complex or negative eigenvalues and also conclude that $\lambda_2 < 1$ is satisfied whenever $\lambda_1 < 1$ because $\lambda_2 < \lambda_1 < 1$ for all parameters.

Extinction Equilibrium Stability

The conditions for asymptotic stability are:

$$
\mu_i f_i \Theta_i < 1.
$$

These conditions are contrary to those given by 4.0.12 and 4.0.13 for existence of $\mathbf{E_1}$, $\mathbf{E_2}$, and $\mathbf{E_3}$, the native exclusion, mustard exclusion, and coexistence equilibria, respectively. Thus, the trivial equilibrium point is unstable whenever $\mathbf{E_1}$, $\mathbf{E_2}$, or $\mathbf{E_3}$ exist.

The eigenvalues at $\mathbf{E_0}$ are:

$$\lambda_{1,2} = \frac{1}{2}\left(A_0 \pm \sqrt{A_0^2 - 4B_0}\right),$$
$$\lambda_3 = 0,$$
$$\text{and } \lambda_4 = (1-g_M)r_M + \frac{\sigma_M \mu_M f_M}{\Theta_M^2}.$$

where

$$A_0 = (1-g_N)r_N + \sigma_N \mu_N f_N,$$
$$\text{and } B_0 = r_N(\sigma_N - g_N)\mu_N f_N.$$

Native Exclusion Equilibrium Stability

$\mathbf{E_1}$ is the native exclusion equilibrium, where $P_N^* = S_N^* = 0$. The eigenvalues are:

$$\lambda_{1,2} = \frac{1}{2}\left(A_1 \pm \sqrt{A_1^2 - 4B_1}\right),$$
$$\lambda_3 = 0,$$
$$\text{and } \lambda_4 = (1-g_M)r_M + \frac{\sigma_M \mu_M f_M}{\Theta_M^2}.$$

where

$$A_1 = (1-g_N)r_N + \frac{\alpha_M \sigma_N \mu_N f_N}{\alpha_M + \beta(\mu_M f_M \Theta_M - 1)},$$
$$\text{and } B_1 = r_N(\sigma_N - g_N)\frac{\alpha_M \mu_N f_N}{\alpha_M + \beta(\mu_M f_M \Theta_M - 1)}.$$

This yields the conditions:

$$\lambda_1 < 1,$$
$$\text{and } (1-g_M)r_M + \frac{\sigma_M \mu_M f_M}{\Theta_M^2} < 1.$$

The conditions for asymptotic stability are:

$$\frac{\beta(\mu_M f_M \Theta_M - 1)}{\alpha_M(\mu_N f_N \Theta_N - 1)} > 1 \text{ and}$$
$$\mu_M f_M \Theta_M > 1.$$

Therefore, the native exclusion equilibrium is locally asymptotically stable only whenever E_{M1}^* exists but E_{N1}^* does not.

Sahara Mustard Exclusion Equilibrium Stability

$\mathbf{E_2}$ is the no-mustard equilibrium, where $P_M = S_M = 0$. The corresponding eigenvalues are:

$$
\begin{aligned}
\lambda_{1,2} &= \frac{1}{2}\left(A_2 \pm \sqrt{A_2^2 - 4B_2}\right), \\
\lambda_3 &= 0, \\
\text{and } \lambda_4 &= (1 - g_M)r_M + \sigma_M \mu_M f_M.
\end{aligned}
$$

where

$$
\begin{aligned}
A_2 &= (1 - g_N)r_N + \frac{\sigma_N}{\mu_N f_N \Theta_N^2}, \\
\text{and } B_2 &= \frac{r_N(\sigma_N - g_N)}{\mu_N f_N \Theta_N^2}.
\end{aligned}
$$

Then the conditions for asymptotic stability are:

$$
\begin{aligned}
\mu_N f_N \Theta_N &> 1 \text{ and} \\
\mu_M f_M \Theta_M &< 1.
\end{aligned}
$$

Then, the Sahara Mustard exclusion equilibrium exists whenever the native exclusion and coexistence equilibria do not exist.

Coexistence Equilibrium Stability

For the coexistence equilibrium, the eigenvalues are:

$$
\begin{aligned}
\lambda_{1,2} &= \frac{1}{2}\left(A_3 \pm \sqrt{A_3^2 - 4B_3}\right), \\
\lambda_3 &= 0, \\
\text{and } \lambda_4 &= (1 - g_M)r_M + \frac{\sigma_M \mu_M f_M}{\Theta_M^2}.
\end{aligned}
$$

where

$$
\begin{aligned}
A_3 &= (1 - g_N)r_N + \frac{(\alpha_M + \beta \mu_M f_M \Theta_M)\sigma_N f_N \mu_N}{\alpha_M \mu_N f_N \Theta_N + 2\beta \mu_M f_M \Theta_M}, \\
\text{and } B_3 &= \frac{(\alpha_M + \beta \mu_M f_M \Theta_M)(\sigma_N - g_N)f_N r_N \mu_N}{\alpha_M \mu_N f_N \Theta_N + 2\beta \mu_M f_M \Theta_M}.
\end{aligned}
$$

The conditions for asymptotic stability are:

$$
\begin{aligned}
1 &< \mu_N f_N \Theta_N < 2, \\
\text{and } \mu_M f_M \Theta_M &> 1.
\end{aligned}
$$

Therefore, when the coexistence equilibrium is stable, it is the only stable equilibrium