SPATIALLY HETEROGENEOUS INVASION
OF TOXIC PLANT MEDIATED BY HERBIVORY

Zhilan Feng

Department of Mathematics
Nanjing University of Information Science and Technology
Nanjing 210044, China
and
Department of Mathematics, Purdue University
West Lafayette, IN 47907, USA

Wenzhang Huang*

Department of Mathematical Sciences
University of Alabama in Huntsville
Huntsville, AL 35899, USA

Donald L. DeAngelis

Department of Biology, University of Miami
Coral Gables, Florida 33124, USA

Abstract. Spatially homogeneous (ODE) and reaction-diffusion models for plant-herbivore interactions with toxin-determined functional response are analyzed. The models include two plant species that have different levels of toxicity. The plant species with a higher level of toxicity is assumed to be less preferred by the herbivore and to have a relatively lower intrinsic growth rate than the less toxic plant species. Two of the equilibrium points of the system representing significant ecological interests are E_1, in which only the less toxic plant is present, and E_2, in which the more toxic plant and herbivore coexist while the less toxic plant has gone to extinction. Under certain conditions it is shown that, for the spatially homogeneous system all solutions will converge to the equilibrium E_2, whereas for the reaction-diffusion model there exist traveling wave solutions connecting E_1 and E_2.

1. **Introduction.** Climate change is apparently already causing latitudinal and altitudinal shifts in ecosystems, as a result of changes in temperature and precipitation over the past few decades, as reviewed by Walther et al. [34]. The upward shift in temperatures in some places is creating conditions favorable to the invasion of vegetation that is adapted to warmer temperatures. Ecotones are places where the effects of climate changes are most likely to be evident [27], and one type of ecotone at which changes in vegetation have been observed both latitudinally and altitudinally is that between woody vegetation and tundra or Alpine sedges, grasses and mosses, where woody shrubs have advanced in places; see [26] for documentation in numerous sites. Woody vegetation, either in prostrate or erect form, may

have an advantage over graminoids and other non-woody plants as temperatures increase. An important question is whether the woody plant – tundra ecotone will advance at a pace set by climate change, or whether biological factors will also affect this rate. In addition to shifts in ecotones, shifts in community composition may occur within biomes, as species adapted to higher temperatures already present increase in abundance or new ones invade. For example, the boreal forest is being invaded by more temperate species, changing its composition [14], and alpine grassland plant communities may appear to be changing in composition [32]. However, there is evidence that climatic factors alone may not determine the changes that occur. In particular, herbivory by small and large mammals may slow the advance [14, 17, 28, 30, 32]. Post and Pedersen [30] noted that caribou and reindeer can constrain biomass of deciduous shrubs such as dwarf birch and willow, and perhaps slow their advance into tundra. Speed et al. [32] report on the effect of sheep in slowing the advance of alpine grassland communities, or even causing a downslope shift. Modeling has been used to describe possible interaction of temperature change and grazing rate on a tundra plant community is Siberia, showing a shift away from deciduous shrub towards graminoid and moss tundra in some cases, but towards less palatable evergreen species in others [35].

The apparent importance of herbivory in relation to vegetation changes accompanying climate change indicates that it is also important to obtain a better understanding of how the level of plant chemical defense affects herbivory, and thus, indirectly, the relationship between climate and the invasion of new plant species in a community. Our work is based on the knowledge from field studies and modeling that plant toxins can have a significant impact on the outcomes of plant-herbivore interactions (see, for example, [4, 9, 10, 12, 19]. In our previous studies, we have used mathematical models to test the hypothesis that toxin-determined selective herbivory by mammals has resulted in invasion of more toxic plants during plant succession in taiga forest [1, 2, 18, 19], the southern boreal forest [29], and temperate grasslands [5, 6].

To investigate the effect of plant toxins on plant-herbivore interactions we previously developed toxin-determined functional response models (acronym TDFRM), which have been used to study various ecological questions [3, 9, 10, 11, 12, 22, 24]. For example, in Feng et al [9] and Liu et al. [24] we focused on a 2-dimesional model that included only plant species and one herbivore population. We provided detailed discussions on both the mathematical properties of the model and the critical role that plant toxins may play in plant-hebivore interactions. The 2-dimensional model was extended in [10] by including two plant species with different levels of toxicity. When the model outcomes were compared with the willow-alder transition data from the Alaska Bonanza Creek Long-Term Ecological Research Project (BNZ LTER), it showed that the model with toxin-determined functional response (TDFR) provided a much better description of the observed plant composition than the model with the traditional Holling Type II functional response.

The 3-dimensional TDFRM was further extended in [11, 12] by including a carnivore that preyed on the herbivore. The results suggested that the toxin-determined functional response can have a significant impact on the tri-trophic interactions in the ecosystem. Specifically, our results demonstrated that the herbivore, by feeding selectively on low-toxicity deciduous woody vegetation such as willow, speeds succession towards high-toxicity evergreens, while the predators, by keeping moose

populations down, can help slow the succession. Simulations indicated that management reductions in predator densities could reduce the mean time to transition from deciduous to spruce vegetation by more than 15 years.

In all of the TDFR models mentioned above, the spatial component was ignored and the models were systems of ordinary differential equations (ODE). In this paper, we extend the ODE model in [11] to allow the movement of the herbivore by considering a reaction-diffusion model. The model includes one herbivore population (P) and two plant species with plant species 1 (N_1) being less toxic than plant species 2 (N_2). We assumed that N_2 is highly defended against herbivore browsing but has a lower intrinsic growth rate than N_1. Using this model we can explore possible spatial patterns of vegetation composition formed by spatio-temporal nonlinearities within the ecosystem, as well as the invasion of toxic plant in space. These types of spatial self-organization patterns in ecosystems have been observed on landscapes and can be described mathematically by traveling wave solutions (see [13, 15, 25, 31] and references therein). In this paper we will identify conditions under which the model has a traveling wave solution, which connects the equilibrium where only plant species 1 is present ($N_1 > 0$) to another equilibrium at which $N_1 = 0$ while the more toxic plant and the herbivore coexist.

The paper is organized as follows. In Section 2 we describe the ODE system of the TDFRM with one herbivore population and two plant species, and some dynamical properties of this system are discussed. Section 3 is devoted to the analysis of the reaction-diffusion model and the existence of traveling wave solutions. The results are discussed in Section 4 and the Appendix collects some of the proofs.

2. **The spatially homogeneous model.** The models we consider in this paper are based on the two-plant and one herbivore TDFRM considered in [10]. The main difference between the two plant species is the level of toxicity, which leads to different consumption rates by the herbivore. Before we present and analyze the reaction-diffusion model, we first investigate further the spatially homogeneous ODE system and the properties of its solutions that are useful for the analysis of the reaction-diffusion system.

Let $N_1(t)$ and $N_2(t)$ denote the biomass densities at time t of plant species 1 and 2, respectively, with plant species 2 being more toxic than plant species 1. Let $P(t)$ benote the biomass density of the herbivore at time t. For demonstration purposes, we consider the following ODE system, which is similar to the TDFRM in [10]:

$$
\begin{aligned}
\dot{N_i} &= B_i(N_1, N_2) - C_i(N_1, N_2)P, \qquad i = 1, 2, \\
\dot{P} &= [\beta_1 C_1(N_1, N_2) + \beta_2 C_2(N_1, N_2) - \mu] P,
\end{aligned}
\tag{1}
$$

where

$$
\begin{aligned}
B_1(N_1, N_2) &= r_1 N_1 \left(1 - \frac{N_1 + a_{12} N_2}{K_1} \right), \\
B_2(N_1, N_2) &= r_2 N_2 \left(1 - \frac{N_2 + a_{21} N_1}{K_2} \right), \\
C_1(N_1, N_2) &= \frac{\sigma_1 N_1}{F(N_1, N_2)}, \\
C_2(N_1, N_2) &= \frac{\sigma_2 N_2}{F(N_1, N_2)} \left[1 - \frac{\sigma_2 N_2}{4GF(N_1, N_2)} \right]
\end{aligned}
\tag{2}
$$

with

$$F(N_1, N_2) = 1 + h_1\sigma_1 N_1 + h_2\sigma_2 N_2. \tag{3}$$

The parameters r_i denote the intrinsic plant growth rate and K_i denote the carrying capacity of plant species i, $i = 1, 2$; a_{12} (a_{12}) denotes the competition coefficient representing the negative impact of species 2 (species 1) on species 1 (species 2). For plant species i, $i = 1, 2$, σ_i is the rate at which the herbivore encounters plant species i; β_i the conversion coefficient of plant biomass to herbivore biomass; h_i the handling time; and μ the removal rate of the herbivore, including both the natural mortality and human hunting. The parameter G measures the toxicity level of plant species 2 with a lower value corresponding to higher toxicity. The function $C_2(N_1, N_2)$ describes a toxin-determined functional response, with the second factor representing the reduction in herbivore consumption due to plant toxicity. It is assumed that

$$G > \frac{1}{4h_2}, \tag{4}$$

so that $C_2(N_1, N_2)$ is positive (see [10] for more detailed explanations about the TDFR).

As the plant species 2 is more toxic than plant species 1, the following conditions are biologically reasonable and assumed to hold in this study:

(I) $\sigma_1 > \sigma_2$, which represents the fact that the toxic plant species is less preferred by the herbivore;

(II) $r_1 > r_2$, which implies that the toxic plant species has a reduced intrinsic growth rate as a tradeoff of cost for its investment in in defense against herbivore browsing.

Remark. As will be pointed out in the Discussion, our results hold for the case $r_1 < r_2$ as well.

The system (1) has several possible equilibria. However, in this paper we focus on only the following two equilibria:

$$E_1 = (K_1, 0, 0) \quad \text{and} \quad E_2 = (0, N_2^*, P^*),$$

where $N_2^* > 0$ and $P^* > 0$. E_1 is the equilibrium at which only plant species 1 is present, whereas at E_2 the plant species 2 and the herbivore coexist with the plant specis 1 being absent. The reason we consider only these two equilibria is because the main biological question we are interested in is how herbivore browsing may influence the invasion of the toxic plant in space, and the approach we use to address this question is by exploring the existence of traveling wave solutions connecting from E_1 to E_2. To this end, we need additional assumptions. The first assumption concerns the relative fitness of the two plant species. Let

$$
\begin{aligned}
g_i(N_1, N_2) &= \frac{B_i(N_1, N_2)/N_i}{C_i(N_1, N_2)/N_i} \\[2mm]
&= \begin{cases} \dfrac{r_1\left[1 - (N_1 + a_{12}N_2)/K_1\right]}{\sigma_1/F(N_1, N_2)}, & i = 1, \\[5mm] \dfrac{r_2\left[1 - (N_2 + a_{21}N_1)/K_2\right]}{\dfrac{\sigma_2}{F(N_1, N_2)}\left[1 - \dfrac{\sigma_2 N_2}{4GF(N_1, N_2)}\right]}, & i = 2, \end{cases}
\end{aligned}
\tag{5}
$$

where B_i, C_i, $i = 1, 2$, and F are given in (2) and (3). Note that the numerator $B_i(N_1, N_2)/N_i$ is the per-capita growth rate of plant species i, and the denominator $C_i(N_1, N_2)/N_i$ is the per-capita consumption rate of plant i per herbivore. Thus, g_1 and g_2 represent the ratios of the growth to loss of plant species 1 and 2, respectively, which can be used as a measure for the overall competitive ability (or fitness) of the plant. The first assumption we need to impose is:

A1 $g_1(N_1, N_2) > g_2(N_1, N_2)$

where g_1 and g_2 are defined in (5). The assumption **A1** implies that plant species 2 is an overall superior competitor in the presence of the herbivore.

2.1. **Asymptotical equations of system (1).** For the purpose of simplifying the notation and without loss of generality, we normalize the plant carrying capacities K_1 and K_2 in system (1) and let

$$K_1 = K_2 = 1.$$

The well posedness of the model (1) is proved in Lemma 2.1.

Lemma 2.1. *Let $(N_1(t), N_2(t), P(t))$ be a solution of (1).*

(1) If $N_i(0) \geq 0 \ (> 0)$, $i = 1, 2$, and $P(0) \geq 0 \ (> 0)$, then $N_i(t) \geq 0 \ (> 0)$, $i = 1, 2$, and $P(t) \geq 0 \ (> 0)$ for all $t \geq 0$.

(2) All nonnegative solutions of (1) are bounded.

Proof. Part (1) of the lemma follows easily from the facts that the planes $N_1 = 0$, $N_2 = 0$ and $P = 0$ are all invariant. For a solution $(N_1(t), N_2(t), P(t))$ we have $\dot{N}_i(t) < 0$ whenever $N_i(t) > 1$ for $i = 1, 2$. Hence, $\limsup N_i(t) \leq 1$. Finally let us show that $P(t)$ is bounded. For a fixed constant $\epsilon > 0$, there is a t_0 such that $N_i(t) < 1 + \epsilon$ for all $t \geq t_0$. Without loss of generality suppose $t_0 = 0$. Let $\mathcal{D} \subset \mathbb{R}^3$ be a region bounded below by the N_1-N_2 plane, on the sides by the planes $N_i = 0$, $N_i = 1 + \epsilon$, and on the top by the plane

$$P + \beta_1 N_1 + \beta_2 N_2 = \bar{P}, \tag{6}$$

where $\bar{P}$ is a positive number such that $(N_1(0), N_2(0), P(0)) \in \mathcal{D}$. We show that $P(t) \leq \bar{P}$ for all $t \geq 0$ if $\bar{P}$ is sufficiently large. To this end we show that $(N_1(t), N_2(t), P(t))$ will stay in $\mathcal{D}$ for all $t \geq 0$ if $\bar{P}$ is large enough. First, it is obvious that the solution cannot exit $\mathcal{D}$ from the bottom or sides of $\mathcal{D}$. Now let (N_1^0, N_2^0, P^0) be a point in the plane defined by (6). The out normal vector of the plane (6) is $(\beta_1, \beta_2, 1)^T$. Hence, the dot product of $(\beta_1, \beta_2, 1)^T$ and the vector field $(\dot{N}_1, \dot{N}_2, \dot{P})^T$ of (1) at the point (N_1^0, N_2^0, P^0) is

$$
\begin{aligned}
(\dot{N}_1, \dot{N}_2, \dot{P})\,(\beta_1, \beta_2, 1)^T \quad &= \beta_1 B_1(N_1^0, N_2^0) + \beta_1 B_2(N_1^0, N_2^0) - \mu P^0 \\
&= \beta_1 \left[B_1(N_1^0, N_2^0) + \mu N_1^0 \right] + \beta_1 \left[B_2(N_1^0, N_2^0) + \mu N_2^0 \right] \\
&\quad - \mu \bar{P}.
\end{aligned}
\tag{7}
$$

Since $0 \leq N_i^0 \leq 1 + \epsilon$, (7) implies that $(\dot{N}_1, \dot{N}_2, \dot{P})\,(\beta_1, \beta_2, 1)^T < 0$ for all large $\bar{P}$. This means the vector field $(\dot{N}_1, \dot{N}_2, \dot{P})^T$ at the plane given by (6) points towards the inside of the region $\mathcal{D}$. Hence, the solution cannot exit from this top plane. This completes the proof of Part (2). □

Lemma 2.2 provides the equivalent conditions to those in **A1** when $K_1 = K_2 = 1$.

Lemma 2.2. *The assumption* **A1** *is equivalent to*

1. $a_{12} > 1 > a_{21}$.
2. $\dfrac{r_2 \sigma_1}{r_1} > \sigma_2$.

Proof. First, noting that $F(N_1, N_2) > 0$ and $1 - \dfrac{\sigma_2 N_2}{4GF(N_1, N_2)} > 0$ by (4), the assumption **A1** implies that

$$\frac{r_2(1 - a_{21})}{F(1, 0)} = g_2(1, 0) > g_1(1, 0) = 0.$$

The above inequality implies that $a_{21} < 1$. Arguing in the same way by setting $N_1 = 0$ and $N_2 = 1$ shows that $a_{12} > 1$. This proves the inequality 1.

Next by setting $N_1 = N_2 = 0$ and using **A1** we obtain the following inequality

$$\frac{r_2}{\sigma_2} = g_2(0, 0) > g_1(0, 0) = \frac{r_1}{\sigma_1},$$

which is equivalent to the inequality 2. Conversely, one is able to verify that the inequalities 1 and 2 imply the assumption **A1**. □

Theorem 2.3. *Let $(N_1(t), N_2(t), P(t))$ be a nonnegative solution of (1). If $N_2(0) > 0$, then $N_1(t) \to 0$ as $t \to \infty$.*

Proof. Let $(N_1(t), N_2(t), P(t))$ be a nonnegative solution of (1) with $N_2(0) > 0$. If $N_1(0) = 0$, then the theorem is trivial because $N_1(t) = 0$ for all $t \geq 0$. Suppose $N_1(0) > 0$. Then $N_i(t) > 0$ for $t \geq 0$ and $i = 1, 2$. We claim that $N_1(t) \to 0$ as $t \to \infty$. If this is not the case, then there is a sequence $t_n \to \infty$ and a positive number N_0 such that $\ln N_1(t_n) \geq N_0$ for all n. By Lemma 2.1 $\dot{N}_1(t)$ for $t \geq 0$ is uniformly bounded. Hence $|\dot{N}_1(t)| \leq M_1$ for all $t \geq 0$. Let $\rho = \dfrac{N_0}{2M_1}$. Then for each n and $s \in [t_n - \rho, t_n + \rho]$, by the Mean-value theorem we have

$$|N_1(t_n) - N_1(s)| \leq M_1 |t_n - s| \leq M_1 \rho = \frac{N_0}{2}.$$

The above inequality yields that

$$N_1(s) \geq N_1(t_n) - \frac{N_0}{2} \geq \frac{N_0}{2}, \qquad s \in [t_n - \rho, t_n + \rho]. \tag{8}$$

Since $t_n \to \infty$ as $n \to \infty$, without loss of generality we can suppose that $t_1 > \rho$ and $t_{n+1} - t_n \geq 2\rho$ for all n. From (8) it therefore follows that

$$\int_0^{t_n} N_1(s)ds \geq \sum_{k=1}^{n-1} \int_{t_k - \rho}^{t_k + \rho} N_1(s)ds \geq \sum_{k=1}^{n-1} \rho N_0 = (n-1)\rho N_0 \to \infty \tag{9}$$

as $n \to \infty$. Next we let

$$f(s) \quad = F(N_1(s), N_2(s)),$$

$$b_i(s) \quad = \frac{B_i(N_1(s), N_2(s))}{N_i(s)}, \quad c_i(s) = \frac{C_i(N_1(s), N_2(s))}{N_i(s)}, \quad i = 1, 2.$$

Then, with the use of (1), we arrive at

$$
\begin{aligned}
N_0 - \ln N_1(0) \quad &\leq \ln N_1(t_n) - \ln N_1(0) \\
&= \int_0^{t_n} \left[\frac{d}{ds} \ln N_1(s) \right] ds \\
&= \int_0^{t_n} [b_1(s) - c_1(s)P(s)] \, ds.
\end{aligned}
\tag{10}
$$

From (10) and the first equation of (1) we deduce that

$$
\begin{aligned}
\ln N_2(t_n) \quad &= \ln N_2(0) + \int_0^{t_n} \left[\frac{d}{ds} \ln N_2(s) \right] ds \\
&= \ln N_2(0) + \int_0^{t_n} [b_2(s) - c_2(s)P(s)] \, ds. \\
&= \ln N_2(0) + \int_0^{t_n} \left[b_2(s) - \frac{r_2}{r_1} b_1(s) + \left(\frac{r_2}{r_1} c_1(s) - c_2(s) \right) P(s) \right] ds \\
&\quad + \frac{r_2}{r_1} \int_0^{t_n} [b_1(s) - c_1(s)P(s)] \, ds. \\
&\geq \int_0^{t_n} \left[b_2(s) - \frac{r_2}{r_1} b_1(s) + \left(\frac{r_2}{r_1} c_1(s) - c_2(s) \right) P(s) \right] ds + M_0
\end{aligned}
\tag{11}
$$

with

$$
M_0 = \frac{r_2}{r_1} \left[N_0 - \ln N_1(0) \right] + \ln N_2(0).
$$

By the definitions of $b_i(s)$, $c_i(s)$, $f(s)$ and Lemma 2.2 one is able to verify that

$$
\begin{aligned}
&b_2(s) - \frac{r_2}{r_1} b_1(s) + \left(\frac{r_2}{r_1} c_1(s) - c_2(s) \right) P(s) \\
&= r_2 \Big[(a_{12} - 1)N_1(s) + (1 - a_{21})N_2(s) \Big] + \left[\left(\frac{r_2 \sigma_1}{r_1} - \sigma_2 \right) \frac{1}{f(s)} + \frac{\sigma_2^2}{f^2(s)} \right] P(s) \\
&> r_2(a_{12} - 1)N_1(s).
\end{aligned}
\tag{12}
$$

From (9), (11) and (12) we therefore conclude that $\ln N_2(t_n) \to \infty$ as $n \to \infty$, a contradiction to Lemma 2.1. $\qquad\square$

Theorem 2.3 shows that the population $N_1(t)$ will converge to 0 as $t \to \infty$. Hence, one can expect that eventually a solution of (1) is asymptotic to a solution of the following reduced system of (1):

$$
\begin{aligned}
\dot{N} &= C(N) \left[g(N) - P \right], \\
\dot{P} &= \left[\beta_2 C(N) - \mu \right] P
\end{aligned}
\tag{13}
$$

where

$$
C(N) = C_2(0, N), \quad g(N) = \frac{B_2(0, N)}{C_2(0, N)}.
\tag{14}
$$

2.2. **Asymptotic behaviors of system (1).** From the result for asymptotically autonomous systems [33], we can study the asymptotic behaviors of the system (1) by analyzing the properties of (13). The system (13) has been previously analyzed in [3] and [24] and shown to have complex dynamics including Hopf and homoclinic bifurcations as well as bistable attractors. However, for the purpose of studying the spatial extension of the model (1) and the existence of traveling wave solutions, we focus on the parameter regions in which specific properties of the system hold. This requires two more assumptions:

A2 There is a unique $N_2^* \in (0, 1)$ such that $\beta_2 C(N_2^*) - \mu = 0$. This excludes the parameter region in which multiple interior equilibria of (13) exist.

A3 $g'(N_2^*) < 0$. This excludes the parameter region in which a limit cycle exists.

Under the assumption **A2**, the system (13) has a unique positive equilibrium (N_2^*, P^*) with $P^* = g(N_2^*)$. Regarding the stability of (N_2^*, P^*) we have the following proposition, which has been proved in [3].

Proposition 1. (N_2^*, P^*) *is a global attractor of all positive solutions of (13) if and only* **A2** *and* **A3** *hold.*

In what follows we shall show that, under the assumptions **A1**– **A3**, all positive solutions of (1) converge to the equilibrium $E_2 = (0, N_2^*, P^*)$. For this purpose, let us first establish

Lemma 2.4. *No positive solution of (1) will converge to the origin as $t \to \infty$. Moreover, if* **A2** *holds then no positive solution will converge to the equilibrium $(1, 0, 0)$ as $t \to \infty$.*

Proof. A straightforward computation yields that the linearization of (1) at the origin has two positive eigenvalues r_1 and r_2 and one negative eigenvalue $-\mu$. Hence, the stable manifold of the origin is one-dimensional. It is apparent that the stable manifold of the origin is the line $N_1 = N_2 = 0$. It follows that no positive solution can converge to the origin since it is not in the stable manifold of the origin. In addition, if **A2** is satisfied, then it can be verified that the stable manifold of $(1, 0, 0)$ must lie in the $N_1 - N_2$ plane. Consequently, no positive solution of (1) will converge to $(1, 0, 0)$ as $t \to \infty$. □

Using Lemma 2.4 and other results established in the previous section, we can proof the following result.

Theorem 2.5. *Under the assumptions* **A1**–**A3**, *all positive solutions of (1) converge to the equilibrium $E_2 = (0, N_2^*, P^*)$.*

Proof. Let $\phi(t) = (N_1(t), N_2(t), P(t))$ be a positive solution of (1). Then $\phi(t)$ is bounded for $t \geq 0$ by Lemma 2.1. Hence, its ω limit set, denoted by ω, exists and ω is in the $N_2 - P$ plane by Theorem 2.3. Proposition 1 implies that the limiting equation (13) of (1) does not have a periodic solution or a cyclical chain of equilibria. It therefore follows from Corollary 4.3 (due to Thieme in [33]) that either ω is the origin, or $\omega = (1, 0, 0)$, or $\omega = (0, N_2^*, P^*)$. However, Lemma 2.4 implies that the only possibility is $\omega = (0, N_2^*, P^*)$. Thus, $\phi(t) \to (0, N_2^*, P^*)$ as $t \to \infty$. □

3. **The reaction-diffusion model.** In this section, we consider a spatial extension of the model (1) by taking into consideration of the herbivore movement. Assume that the movement is random, which can be modeled as a diffusion process. Assume also that the movement (or seed dispersal) of the plant can be neglected on the short

time scale considered here. Then, the model (1) can be extended to the following reaction-diffusion system

$$
\begin{aligned}
\frac{\partial N_i}{\partial t} &= B_i(N_1, N_2) - C_i(N_1, N_2)P, \qquad i = 1, 2, \\
\frac{\partial P}{\partial t} &= d\Delta P + \left[\beta_1 C_1(N_1, N_2) + \beta_2 C_2(N_1, N_2) - m\right] P,
\end{aligned}
\tag{15}
$$

where $N_i(t, x)$ and $P(t, x)$ are population densities of plants and herbivore, respectively, at time t and location $x \in \mathbb{R}^n$ (with $n = 2$ for realistic situation); $\Delta = \sum_{i=1}^{n} \partial^2/\partial x_i^2$ is the Laplace operator; d denotes the diffusivity of herbivore; B_i and C_i are defined in (2).

3.1. **An ODE system for traveling wave solutions.** Our main interest is to study possible invasion of plant N_2 into an environment in which plant N_1 has established in the absence of plant N_2 and herbivore P. This steady-state can be described by the equilibrium of (15), $E_1 = (1, 0, 0)$, which obviously always exists. A successful invasion by plant N_2 in the presence of the herbivore and extinction of plant N_1 can be represented by a stable equilibrium of (15) of the form $E_2 = (0, N_2^*, P^*)$, which is guaranteed to exist under the assumption **A2**. Our main objective here is to investigate whether there will be a zone of transition from the equilibrium E_1 to the equilibrium E_2. Mathematically, this transition can be described by a particular type of solutions, i.e., the traveling wave solutions of the form

$$
\begin{aligned}
N_i(t, x) &= U_i(k \cdot x + ct), \quad i = 1, 2, \\
P(t, x) &= V(k \cdot x + ct)
\end{aligned}
\tag{16}
$$

under the boundary condition

$$
\begin{aligned}
(U_1(-\infty), U_2(-\infty), V(-\infty)) &= E_1 = (1, 0, 0), \\
(U_1(\infty), U_2(\infty), V(\infty)) &= E_2 = (0, N_2^*, P^*).
\end{aligned}
\tag{17}
$$

The constant c is the wave speed and $k \in \mathbb{R}^n$ is a unit vector denoting the direction of wave propagation. The importance of the existence of traveling waves in an ecosystem can be found, for example, in [25] and [31]. (15) has a traveling wave solution of form (16) connecting E_1 and E_2 if and only if the functions $U_1(\xi)$, $U_2(\xi)$, and $V(\xi)$, with $\xi = x \cdot k + ct$, form a solution of the system

$$
\begin{aligned}
\dot{U}_i &= B_i(U_1, U_2) - C_i(U_1, U_2)V, \qquad i = 1, 2, \\
c\dot{V} &= d\ddot{V} + \left[\beta_1 C_1(U_1, U_2) + \beta_2 C_2(U_1, U_2) - \mu\right] V.
\end{aligned}
\tag{18}
$$

If we further introduce the variable

$$
W = cV - d\dot{V},
$$

then the system (18) and boundary condition (17) are transformed to the equivalent system

$$
\begin{aligned}
\dot{U}_i &= B_i(U_1, U_2) - C_i(U_1, U_2)V, \qquad i = 1, 2, \\
\dot{V} &= \frac{1}{d}[cV - W], \\
\dot{W} &= \left[\beta_1 C_1(U_1, U_2) + \beta_2 C_2(U_1, U_2) - \mu\right] V
\end{aligned}
\tag{19}
$$

with the boundary condition

$$
\begin{aligned}
(U_1(-\infty), U_2(-\infty), V(-\infty), W(-\infty)) &= E_1^* = (1, 0, 0, 0), \\
(U_1(\infty), U_2(\infty), V(\infty), W(\infty)) &= E_2^* = (0, N_2^*, P^*, cP^*).
\end{aligned}
\tag{20}
$$

3.2. **Existence of traveling wave solutions.** We will use a similar technique developed in [16] to show the existence of solutions of to (19) satisfying the boundary condition (20). Let

$$
M = \max \left\{ \beta_1 C_1(N_1, N_2) + \beta_2 C_2(N_1, N_2) : 0 \leq N_i \leq 1, \, i = 1, 2 \right\}.
\tag{21}
$$

In what follows we shall show that, under the conditions **A1**, **A2**, and a modification of **A3**, (19) and (20) have a nonnegative solution for $c > 2\sqrt{d(M - \mu)}$. It will take several steps to achieve this.

For $c > 2\sqrt{d(M - \mu)}$, we begin by constructing a set $\Omega \subset \mathbb{R}^4$ as follows. Let

$$
\Omega = \left\{
\begin{array}{l}
(U_1, U_2, V, W) : \quad 0 \leq U_i \leq 1, \, i = 1, 2, \, 0 \leq \gamma_1 V \leq W \leq \gamma_2 V, \\[4pt]
\qquad\qquad\qquad \beta_1 U_1 + \beta_2 U_2 + W \leq H
\end{array}
\right\}
\tag{22}
$$

where γ_1, γ_2 and H are constants with

$$
\begin{aligned}
\gamma_1 &= \frac{c}{2}, \qquad \gamma_2 = \frac{c + \sqrt{c^2 + 4d\mu}}{2}, \\[6pt]
H &> \frac{\gamma_2 M}{\mu} + \beta_1 + \beta_2.
\end{aligned}
\tag{23}
$$

The boundary of Ω consists of the faces $S_1 - S_8$ with

$$
\begin{aligned}
S_1 &= \{W = \gamma_1 V > 0, \, 0 < U_i < 1, \, i = 1, 2\}, \\
S_2 &= \{W = \gamma_2 V > 0, \, 0 < U_i < 1, \, i = 1, 2\}, \\
S_3 &= \{\beta_1 U_1 + \beta_2 U_2 + W = H, \, \gamma_1 V \leq W \leq \gamma_2 V, \, 0 < U_i \leq 1, \, i = 1, 2\}, \\
S_4 &= \{U_1 = 0, \, \gamma_1 V \leq W \leq \gamma_2 V, \, 0 < U_2 < 1, \, i = 1, 2\}, \\
S_5 &= \{U_2 = 0, \, \gamma_1 V \leq W \leq \gamma_2 V, \, 0 < U_1 < 1, \, i = 1, 2\}, \\
S_6 &= \{U_1 = 1, \, \gamma_1 V \leq W \leq \gamma_2 V, \, 0 < U_2 < 1, \, i = 1, 2\}, \\
S_7 &= \{U_2 = 1, \, \gamma_1 V \leq W \leq \gamma_2 V, \, 0 < U_1 < 1, \, i = 1, 2\}, \\
S_8 &= \{V = W = 0, \, 0 \leq U_i \leq 1\}.
\end{aligned}
\tag{24}
$$

Lemma 3.1. *A solution of (19) through a point in Ω can only exit from a point in $S_1 \cup S_2$ (see Figure 3.1).*

Proof. First, a solution cannot exit Ω from a point in $S_4 \cup S_5 \cup S_8$, which is invariant. Also a solution cannot exit Ω from a point in S_6 or S_7 because $\dot{U}_1 < 0$ at S_6 and $\dot{U}_2 < 0$ at S_7. Let us consider the direction of the vector field of (19) on S_3. For a point $(U_1, U_2, V, W) \in S_3$ we have

$$
\begin{aligned}
V &\geq \frac{W}{\gamma_2}, \\
W &= H - \beta_1 U_1 - \beta_2 U_2 \geq H - \beta_1 - \beta_2 > \frac{M \gamma_2}{\mu}, \\
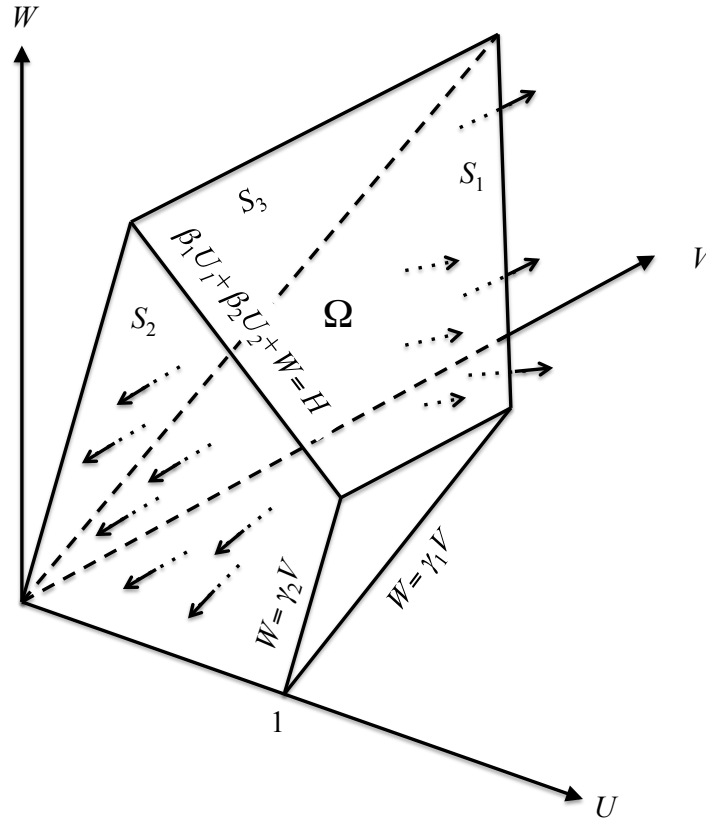M &\geq \beta_1 B_1(U_1, U_2) + \beta_2 B_2(U_1, U_2).
\end{aligned}
\tag{25}
$$

FIGURE 1. The region Ω. In the figure the axis $\mathbf{U}$ stands for U_1-U_2 planne. A solution can only exits the region Ω from either a point in the face S_1 or a point in the face S_2.

Notice that the out normal vector of the face S_3 is $(\beta_1, \beta_2, 0, 1)^T$. Let $Z = (\dot{U}_1, \dot{U}_2, \dot{V}, \dot{W})^T$ be the vector filed of (19) at the point $(U_1, U_2, V, W) \in S_3$. Then, with the use of (19) and (25) we arrive at

$$
\begin{aligned}
Z \cdot (\beta_1, \beta_2, 0, 1)^T \quad &= \beta_1 B_1(U_1, U_2) + \beta_2 B_2(U_1, U_2) - \mu V \\
&\leq M - \frac{\mu}{\gamma_2} W \\
&\leq M - \frac{\mu}{\gamma_2}(H - \beta_1 - \beta_2) \\
&< 0.
\end{aligned}
\tag{26}
$$

The above inequality implies that the vector field at a point in S_3 points toward the inside of the region Ω.

Next, we consider the vector field on the face S_1. The out normal vector of the face S_1 is $(0, 0, \gamma_1, -1)^T$. Then, by (19), the definitions of γ_1 and the number M,

and the equality $W = \gamma_1 V$ for points in S_1, we obtain

$$
\begin{aligned}
Z \cdot (0, 0, \gamma_1, -1)^T \quad &= \frac{\gamma_1}{d} \big[cV - W \big] - \big[\beta_1 C_1(U_1, U_2) + \beta_2 C_2(U_1, U_2) - \mu \big] V \\
&\geq \Big(\frac{\gamma_1}{d} \big[c - \gamma_1 \big] - [M - \mu] \Big) V \\
&= \frac{1}{4d} \big[c^2 - 4d(M - \mu) \big] V \\
&> 0.
\end{aligned}
\tag{27}
$$

The inequality (27) implies that the vector field at a point in S_1 points toward the outside of the region Ω. Similarly, we can verify that the vector field at a point in S_2 points toward the outside of the region Ω.   □

Lemma 3.2. *Suppose the conditions* **A1** *and* **A2** *are satisfied. Let*

$$
\Psi(t) = (U_1(t), U_2(t), V(t), W(t))
$$

be a solution of (19). If

$$
\Psi(t) \in \text{Int}\,\Omega, \quad t \geq 0,
$$

where Int Ω denotes the interior of Ω, then

(a) $U_1(t) \to 0$ *as* $t \to \infty$.
(b) *As* $t \to \infty$, $\Psi(t)$ *does not converge to the origin* $E_0 = (0, 0, 0, 0)$ *or the equilibrium point* $E_0^* = (0, 1, 0, 0)$ *of (19).*

Proof. First, $\Psi(t) \in \text{Int}\,\Omega$ implies that $V(t) > 0$ and $0 < U_i(t) < 1$ for $i = 1, 2$. Thus, with the same argument that was used in the proof of Theorem 2.3 we deduce that $U_1(t) \to 0$ as $t \to \infty$. Next, we show that, as $t \to \infty$, $\Psi(t)$ does not converge to the origin as $t \to \infty$. By the definitions of $B_2(U_1, U_2)$ and $C_2(U_1, U_2)$ it is easy to see that there are positive constants ϵ and δ such that

$$
\frac{1}{U_2} \Big[B_2(U_1, U_2) - C_2(U_1, U_2)V \Big] \geq \delta
\tag{28}
$$

for $0 \leq V \leq \epsilon$, $0 < U_i \leq \epsilon$, $i = 1, 2$. Suppose $\Psi(t) \to E_0$ as $t \to \infty$. Then there is a t_0 such that $0 \leq V(t) \leq \epsilon$, $0 < U_i(t) \leq \epsilon$, $i = 1, 2$, for all $t \geq t_0$. On the other hand, (28) and the second equation of (19) imply that for $t \geq t_0$,

$$
\dot{U}_2(t) \geq U_2(t)\delta, \quad t \geq t_0.
$$

The last inequality implies that there must be a time $t_1 > t_0$ such that $U_2(t_1) > \epsilon$, which leads to a contradiction. Finally, we have $\beta_1 C_1(0, 1) + \beta_2 C_2(0, 1) - \mu > 0$ by **A2**. Hence, there is a small neighborhood $\mathcal{C}$ of $(0, 1) \in \mathbb{R}^2$ such that $\beta_1 C_1(U_1, U_2) + \beta_2 C_2(U_1, U_2) - \mu > 0$ for $(U_1, U_2) \in \mathcal{C}$. This inequality and the equation for W in (19) immediately yield that $\Psi(t)$ cannot remain in a sufficiently small neighborhood of E_0^*.   □

Lemma 3.2 implies that for a solution $\Psi(t)$ of (19), if it stays inside of Ω for $t \geq 0$, then its ω-limit set exists and it is a bounded, connected invariant set of the

reduced system of (19) for which $U_1 \equiv 0$:

$$
\begin{aligned}
\dot{U} &= C(U)\left[g(U) - V\right], \qquad i = 1, 2, \\
\dot{V} &= \frac{1}{d}[cV - W], \\
\dot{W} &= \left[\beta_2 C(U) - \mu\right] V
\end{aligned}
\tag{29}
$$

where, as in (14),

$$
C(U) = C_1(U, 0), \quad g(U) = \frac{B_1(U, 0)}{C_1(U, 0)}.
$$

Let us assume that, in addition to the condition **A2**, $g(U)$ satisfies the condition

A3' $g(U) > g(N_2^*)$ for $0 \leq U < N_2^*$ and $g(U) < g(N_2^*)$ for $N_2^* < U \leq 1$.

Proposition 2. *Under the assumptions **A2** and **A3'**, all positive solutions of (29) converge to the equilibrium $\bar{E}^* = (N_2^*, P^*, cP^*)$, where $P^* = g(N_2^*)$.*

Proof. Define a function $L : \mathrm{Int}\,\mathbb{R}_+^3 \to \mathbb{R}$, which is associated with (29), by

$$
\begin{aligned}
L(U, V, W) &= \int_{N_2^*}^{U} \frac{1}{C(s)}\left[C(s) - C(N_2^*)\right] ds \\
&\quad + \frac{1}{\beta_2}\left[W - g(N_2^*)\frac{W}{V} - cg(N_2^*)\ln V\right].
\end{aligned}
\tag{30}
$$

Then L is well defined. Upon a straightforward computation and with the use of the system (29) we obtain the derivative of L along (29) as

$$
\dot{L}(U, V, W) = \left[C(U) - C(N_2^*)\right]\left[g(U) - g(N_2^*)\right] - \frac{g(N_2^*)}{d\beta_2 V^2}\left[cV - W\right]^2.
\tag{31}
$$

The equation (31) and assumption **A3'** imply that $\dot{L}$ is negative and that the set

$$
\Sigma = \left\{(U, V, W) : \dot{L}(U, V, W) = 0\right\} = \{U = N_2^*,\ W = cV\}.
\tag{32}
$$

It is obvious that, by (32), the set $\Sigma \setminus \bar{E}^*$ does not contain any globally defined solution of (29) (i.e., a solution (29) defined for all $t \in \mathbb{R}$). Thus, by Lasalle's Invariance principle, we conclude that all positive and bounded solutions of (29) converge to $\bar{E}^*$ as $t \to \infty$. $\qquad\square$

Before we prove the existence of traveling wave solutions of (15) we need the following lemma. The proof of this lemma is quite involved so we shall give a complete proof in the Appendix.

Lemma 3.3. *For each $c > 2\sqrt{d(M - \mu)}$, let E_1^{*U} be the unstable manifold of the equilibrium E_1^*. Then there is a point $p_* \in \mathrm{Int}\,\Omega \cap E_1^{*U}$ such that the solution $\Psi_*(t)$ of (19) through the point p_* stays in $\mathrm{Int}\,\Omega$ for all $t \geq 0$.*

Now we are ready to establish the following theorem for the existence of traveling wave solutions.

Theorem 3.4. *Under the conditions **A1**, **A2**, and **A3'**, for each $c > 2\sqrt{d(M - \mu)}$, the system (19) has a nonnegative heteroclinic orbit satisfying the condition (20). Hence, the reaction-diffusion system (15) has a traveling wave solution connecting the equilibrium points E_1^* and E_2^*.*

Proof. Let $\Psi_*(t)$ be a solution of (19) defined in Lemma 3.3. Then $\Psi_*(t) \to E_1^*$ as $t \to -\infty$ because $\Psi_*(t)$ is in the unstable manifold of E_1^*. Moreover, $\Psi_*(t) \in \text{Int}\,\Omega$ for all $t \geq 0$. Hence, $\Psi_*(t)$ is positive and bounded, and its component $U_1(t) \to 0$ as $t \to \infty$ by Lemma 3.2. It follows that its ω-limit set, ω, exists and

$$\omega \subset \{U_2 = 0,\ 1 \leq U_1 \leq 1,\ 0 \leq \gamma_1 V \leq W \leq \gamma_2 V\}.$$

Proposition 2 and a result from Corollary 4.3 in [33] imply that ω must be an equilibrium point. By Lemma 3.2, $\omega \neq \{(0,0,0,0)\}$ and $\omega \neq \{(0,1,0,0)\}$. Hence, with the use of Proposition 2, we deduce that $\omega = (0, N_2^*, P^*, cP^*) = E_2^*$. Consequently, $\Psi_*(t) \to E_2^*$ as $t \to \infty$. $\qquad\square$

From Theorem 3.4 we know that the reaction-diffusion system (15) has traveling wave solutions connecting from $E_1 = (1,0,0)$ to $E_2 = (0, N_2^*, P^*)$. This provides a description of dynamic landscape patterns with which changes in the vegetation composition may occur. In particular, the results provide information about the conditions under which the invasion of toxic plant species through the space is possible.

4. **Discussion.** The main finding of this study is the existence of traveling wave solutions that represent landscape patterns with ecological significance. Specifically, the reaction-diffusion system (15) can give rise to traveling wave solutions connecting the equilibrium $E_1 = (1,0,0)$, where only the less toxic plant species 1 is present, to the equilibrium $E_2 = (0, N_2^*, P^*)$, where the plant 1 is excluded and the more toxic plant species 2 coexists with the herbivore. This result is both mathematically challenging and biologically interesting. Although the existence of such traveling solutions have been shown to exist in other reaction-diffusion models for prey-predator interactions (see, for example, [7, 8, 16, 21, 23]), the analysis of system (15) is more challenging due to the inclusion of multiple plant species as well as the non-monotonisity in the toxin-determined functional response $C_2(N_1, N_2)$. We managed to obtain the results for system (15) under assumptions **A1**, **A2**, and **A3'**. Future studies may focus on generalizing the results by relaxing some of these assumptions. For example, Assumption **A2** can be relaxed by allowing that the equation $\beta_2 C_2(0, N_2) - \mu = 0$ has two solutions N_2^* and $\tilde{N}_2^*$ with $0 < N_2^* < \tilde{N}_2^* < 1$, in which case the system (13) has two interior equilibria.

The results in this paper also provide insights into what ecological factors may affect the spatial vegetation composition, especially the invasion of toxic plant species. These results may have some relevance to the ecological issues mentioned in the Introduction, concerning whether climate change may be accompanied by movement of some plant species towards higher latitudes or elevations. The specific type of traveling wave solutions exhibited in the reaction-diffusion model (15) provide a more detailed description about the landscape patterns that can be formed in this plant-herbivore system. The threshold conditions identified here will allow us to explore how certain model parameters may affect the model outcomes. For example, one of the key parameters in model (15) is the toxicity level G of plant species 2. Note that the assumption **A2** is equivalent to $C_2(0, 1) > \mu/\beta_2$ or

$$\frac{\sigma_2}{1 + h_2 \sigma_2} \left[1 - \frac{\sigma_2}{4G(1 + h_2 \sigma_2)} \right] > \frac{\mu}{\beta_2},$$

which leads to a condition on G. Similarly, the assumption **A3** will also provide a condition on G as N_2^* is a solution of the equation $C_2(0, N_2^*) = \mu/\beta_2$ in which

G is involved. These conditions may determine a range for G in which the above-mentioned traveling wave solutions exist, given other parameter values. The explicit bounds for G are not presented here due to the complexity of the equations that need to be solved to determine these values.

We point out that the wave speed depends on the diffusion coefficient d. Moreover, the condition on the wave speed, $c > 2\sqrt{d(M - \mu)}$, for the existence of the traveling waves connecting E_1 and E_2 is sufficient but may not be necessary. It can be shown that a necessary condition for the existence of a nonnegative traveling wave solution is

$$c \geq 2\sqrt{d\left[\frac{\beta_1\sigma_1}{1 + h_1\sigma_1} - \mu\right]}.$$

Hence, the problem of identifying the minimum wave speed, which is important in many applications [20], remains open. Further investigation will be conducted in this direction.

We point out also that the assumption (II) on the lower growth rate for the toxic plant (i.e., $r_2 < r_1$) is not necessary for the proofs of the results in this paper. The key assumptions for the existence of traveling wave solutions are **A1** (which is equivalent to the two inequalities in Lemma 2.2), **A2** and **A3** (or the modified **A3'**). The assumption **A2** is a simplified assumption as it restricts the attention to the case of a single interior equilibrium. The analysis for the case of two interior equilibrium states can be very challenging mathematically. We have begun to consider this case and results will be published elsewhere.

5. **Appendix.** In this appendix we provide a detailed proof of Lemma 3.3. Let us begin by examning the local unstable manifold of the equilibrium point $E_1^* = (1, 0, 0, 0)$. A direct computation yields that the Jacobian matrix of (19) associated with the equilibrium $E_1^* = (1, 0, 0, 0)$ is

$$J = \begin{bmatrix} -r_1 & -r_1 a_{12} & -C_1(1,0) & 0 \\ 0 & r_2(1 - a_{21}) & 0 & 0 \\ 0 & 0 & c/d & -1/d \\ 0 & 0 & a & 0 \end{bmatrix} \tag{33}$$

with $a = \beta_1 C_1(1,0) - \mu > 0$ by the Assumption **A2**. The characteristic equation of J is

$$P(\lambda) = \det(J - \lambda I) = [r_2(1 - a_{21}) - \lambda]\left(-r_1 - \lambda\right)\left(\lambda^2 - \frac{c}{d}\lambda + \frac{a}{d}\right) = 0.$$

Recall that $c^2 > 4d(M - \mu) \geq 4da$. From this inequality, it can be shown that the last equation results in J having one negative eigenvalue $-r_1$ and three positive eigenvalues

$$\lambda_1 = r_2(1 - a_{21}), \quad \lambda_2 = \frac{c + \sqrt{c^2 - 4da}}{2d}, \quad \lambda_3 = \frac{c - \sqrt{c^2 - 4da}}{2d}.$$

Hence, the unstable manifold of the equilibrium E_1^* is three dimensional. A further computation shows that the eigenvectors $\mathbf{h_i}$ corresponding to eigenvalues λ_i, for

$i = 1, 2, 3$, are respectively given by

$$\mathbf{h_1} = \left(-\frac{r_1 a_{12}}{r_1 + \lambda_1}, \, 1, \, 0, \, 0 \right)^T$$

$$\mathbf{h_2} = \left(-\frac{C_1(1,0)}{r_1 + \lambda_2}, \, 0, \, 1, \, \frac{a}{\lambda_2} \right)^T = \left(-\frac{C_1(1,0)}{r_1 + \lambda_2}, \, 0, \, 1, \, \frac{c - \sqrt{c^2 - 4da}}{2} \right)^T \qquad (34)$$

$$\mathbf{h_3} = \left(-\frac{C_1(1,0)}{r_1 + \lambda_3}, \, 0, \, 1, \, \frac{a}{\lambda_3} \right)^T = \left(-\frac{C_1(1,0)}{r_1 + \lambda_3}, \, 0, \, 1, \, \frac{c + \sqrt{c^2 - 4da}}{2} \right)^T.$$

From the unstable manifold theorem and (34) it follows that there are a small neighborhood $\mathcal{O}$ of the origin in $\mathbb{R}^3$ and a smooth (twice continuously differentiable) function $\Phi = (\Phi_1, \cdots, \Phi_4) : \mathcal{O} \to \mathbb{R}^4$ such that the local unstable manifold E_1^{*U} of E_1^* can be expressed as

$$E_1^{*U} = \Big\{ k_1 \mathbf{h_1} + k_2 \mathbf{h_2} + k_3 \mathbf{h_3} + E_1^* + \Phi(k_1, k_2, k_3) : (k_1, k_2, k_3) \in \mathcal{O} \Big\}$$

$$= \Big\{ \big(u_1(k_1, k_2, k_3), u_2(k_1, k_2, k_3), v(k_1, k_2, k_3), w(k_1, k_2, k_3) \big), (k_1, k_2, k_3) \in \mathcal{O} \Big\}$$

with

$$\begin{aligned}
u_1(k_1, k_2, k_3) &= -k_1 h_{11} - k_2 h_{12} - k_3 h_{13} + 1 + \Phi_1(k_1, k_2, k_3), \\[6pt]
u_2(k_1, k_2, k_3) &= k_1 + \Phi_2(k_1, k_2, k_3), \\[6pt]
v(k_1, k_2, k_3) &= k_2 + k_3 + \Phi_3(k_1, k_2, k_3), \\[6pt]
w(k_1, k_2, k_3) &= k_2 h_{32} + k_3 h_{33} + \Phi_4(k_1, k_2, k_3),
\end{aligned} \qquad (35)$$

where

$$h_{11} = \frac{r_1 a_{12}}{r_1 + \lambda_1} > 0, \qquad h_{12} = \frac{C_1(1,0)}{r_1 + \lambda_2} > 0, \qquad h_{13} = \frac{C_1(1,0)}{r_1 + \lambda_3} > 0,$$

$$h_{32} = \frac{c - \sqrt{c^2 - 4da}}{2} < \frac{c}{2} = \gamma_1, \qquad \gamma_2 > h_{33} = \frac{c + \sqrt{c^2 - 4da}}{2} > \frac{c}{2} = \gamma_1. \qquad (36)$$

Moreover, the function $\Phi_i(k_1, k_2, k_3)$ satisfies

$$\Phi_i(0,0,0) = \frac{\partial \Phi_i(0,0,0)}{\partial k_j} = 0, \quad i = 1, \cdots, 4, \, j = 1, 2, 3. \qquad (37)$$

Lemma 5.1. *There are an interval $[s_2, s_1]$ with $s_1 > |s_2|$ and a continuous function $p : [s_2, s_1] \to \mathbb{R}^4$ such that*

1. $p(s) \in E_1^{*U}$ for $s \in [s_2, s_1]$,
2. $p(s_i) \in S_i$ for $i = 1, 2$, and $p(s) \in \text{Int } \Omega$ for $s \in (s_2, s_1)$.

Proof. Recall that a point $p = \big(u_1(k_1, k_2, k_2), u_2(k_1, k_2, k_3), v(k_1, k_2, k_3), w(k_1, k_2, k_3) \big) \in S_1 \, (S_2)$ if and only if $0 < u_i(k_1, k_2, k_2) < 1$, $i = 1, 2$ and

$$\frac{w(k_1, k_2, k_3)}{v(k_1, k_2, k_3)} = \frac{k_2 h_{32} + k_3 h_{33} + \Phi_4(k_1, k_2, k_3)}{k_2 + k_3 + \Phi_3(k_1, k_2, k_3)} = \gamma_1 \, (\gamma_2).$$

To this end, let $\bar{s}_1 = 1$ and $\bar{s}_2 = -\dfrac{\gamma_2 - h_{33}}{\gamma_2 - h_{32}}$. Then, in view of (36), we have $-1 < \bar{s}_2 < 0$. Upon a straightforward calculation and with the use of definitions of h_{32} and h_{33} one obtain

$$\begin{aligned}
\frac{\bar{s}_2 h_{32} + h_{33}}{\bar{s}_2 + 1} &= \gamma_2, \\
\frac{\bar{s}_1 h_{32} + h_{33}}{\bar{s}_1 + 1} &= \gamma_1.
\end{aligned} \tag{38}$$

Next, for $i = 1, \cdots, 4$ we define functions

$$\begin{aligned}
\psi_i(s, \theta) &= \frac{\Phi_i(\theta, s\theta, \theta)}{\theta} \\
&= \int_0^1 \left[\frac{\partial \Phi_i(\theta\tau, s\theta\tau, \theta\tau)}{\partial k_1} + s\frac{\partial \Phi_i(\theta\tau, s\theta\tau, \theta\tau)}{\partial k_2} + \frac{\partial \Phi_i(\theta\tau, s\theta\tau, \theta\tau)}{\partial k_3} \right] d\tau.
\end{aligned} \tag{39}$$

From (37) and (39) it follows that

$$\psi_i(s, \theta) = O(\theta), \qquad \frac{\partial \psi_i(s, \theta)}{\partial s} = O(\theta) \qquad \text{as } \theta \to 0 \tag{40}$$

uniformly for s in a bounded interval. Hence, $\psi_i(s, \theta)$ is well defined and is differentiable with respect to s for all small θ, including $\theta = 0$. Define a function

$$\begin{aligned}
\chi(s, \theta) &= \frac{sh_{32} + h_{33} + \psi_4(s, \theta)}{s + 1 + \psi_3(s, \theta)} \\
&= \frac{sh_{32} + h_{33}}{s + 1} + \frac{(s+1)\psi_4(s, \theta) - (sh_{32} + h_{33})\psi_3(s, \theta)}{[s + 1 + \psi_3(s, \theta)][s + 1]}.
\end{aligned} \tag{41}$$

Then, with the use of (36),(40), (41) and following a direct computation we obtain

$$\frac{\partial \chi(s, \theta)}{\partial s} = \frac{h_{32} - h_{33}}{\left[s + 1\right]^2} + O(\theta) = -\frac{\sqrt{c^2 - 4da}}{\left[s + 1\right]^2} + O(\theta). \tag{42}$$

(42) implies

$$\frac{\partial \chi(s, \theta)}{\partial s} < 0 \tag{43}$$

if θ is sufficiently small. Moreover, (38) and (41) imply that $\chi(\bar{s}_i, 0) = \gamma_i$ for $i = 1, 2$. Hence, from the Implicit Function Theorem it follows that for each small $\theta > 0$, there are $s_i(\theta) \approx \bar{s}_i$ such that $\chi(\bar{s}_i(\theta), \theta) = \gamma_i$ for $i = 1, 2$. Since $\bar{s}_1 = 1$ and $\bar{s}_2 > -1$, we can choose a sufficiently small $\theta_0 > 0$ such $s_1(\theta_0) \approx 1$ and $s_1(\theta_0) > -s_2(\theta_0)$. Now let $s_i = s_i(\theta_0)$. Then (43) yields that $\chi(s, \theta_0)$ is strictly decreasing on s for $s \in [s_2, s_1]$ and hence we have

$$\gamma_2 = \chi(s_2(\theta_0), \theta_0) = \chi(s_2, \theta_0) > \chi(s, \theta_0) > \chi(s_1(\theta_0, \theta_0) > \chi(s_2, \theta_0) = \gamma_1 \tag{44}$$

for $s \in (s_2, s_1)$. Now let

$$p(s) = \big(u_1(\theta_0, s\theta_0, \theta_0), u_2(\theta_0, s\theta_0, \theta_0), v(\theta_0, s\theta_0, \theta_0), w(\theta_0, s\theta_0, \theta_0) \big), \quad s \in [s_2, s_1].$$

Then $p(s) \in E_1^{*U}$. Moreover (35) yields that

$$
\begin{aligned}
u_1(\theta_0, s\theta_0, \theta_0) &= \theta_0\big[-h_{11} - sh_{12} - h_{13} + \psi_1(s, \theta_0)\big] + 1, \\
u_2(\theta_0, s\theta_0, \theta_0) &= \theta_0\big[1 + \psi_2(s, \theta_0)\big],
\end{aligned}
\tag{45}
$$

$$
\frac{w(\theta_0, s\theta_0, \theta_0)}{v(\theta_0, s\theta_0, \theta_0)} = \chi(s, \theta_0).
$$

From (40), (44), and (45) it follows that, for sufficiently small $th_0 > 0$,

$$
0 < u_i(\theta_0, s\theta_0, \theta_0) < 1, \quad s \in [s_2, s_1], \quad i = 1, 2
\tag{46}
$$

and

$$
\gamma_1 = \frac{w(\theta_0, s_1\theta_0, \theta_0)}{v(\theta_0, s_1\theta_0, \theta_0)} < \frac{w(\theta_0, s\theta_0, \theta_0)}{v(\theta_0, s\theta_0, \theta_0)} < \frac{w(\theta_0, s_2\theta_0, \theta_0)}{v(\theta_0, s_2\theta_0, \theta_0)} = \gamma_2, \quad s \in (s_2, s_1).
\tag{47}
$$

In view of (46) and (47) we conclude that $p(s_i) \in S_i$ for $i = 1, 2$ and $p(s) \in \operatorname{Int}\Omega$ for $s \in (s_2, s_1)$. This completes the proof of Lemma 5.1. $\qquad\square$

We are now in the position to prove Lemma 3.3.

Proof. Let $\Gamma = \{p(s) : s \in [s_2, s_1]\}$, where $p(s)$ is defined as in Lemma 5.1. Then $\Gamma \subset E_1^{*U}$. For $p \in \Gamma$, let $\Psi(t, p)$ be the solution of (19) with $\Psi(0, p) = p$. We define

$$
\Gamma_i = \{p \in \Gamma : \text{ there is a } t_p \geq 0 \text{ such that } \Psi(t_p, p) \in S_i\}, \quad i = 1, 2.
$$

By Lemma 5.1, $p(s_i) \in S_i \cap \Gamma$ for $i = 1, 2$. Hence, Γ_i is not empty for $i = 1, 2$. It is obvious that, by the continuity of solutions on the initial value, both Γ_1 and Γ_2 are open relative to Γ. Hence,

$$
\Gamma_1 \cup \Gamma_2 \neq \Gamma
$$

since Γ is closed and connected. That is, there is a point

$$
p_* \in \Gamma \setminus (\Gamma_1 \cup \Gamma_2).
$$

It follows from the definition that $\Psi_*(t) = \Psi(t, p_*) \notin S_1 \cup S_2$ for all $t \geq 0$. Therefore, Lemma 15 yields that $\Psi_*(t) \in \operatorname{Int}\Omega$ for all $t \geq 0$. $\qquad\square$

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E-mail address: zfeng@math.purdue.edu
E-mail address: huang@math.uah.edu
E-mail address: don_deangelis@usgs.gov