A COUPLED MAP LATTICE MODEL OF TREE MIGRATION

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Abstract. We model tree migration with a coupled map lattice and study the dynamics of the moving front. We show that when the maximal dispersal distance is finite and the spatial redistribution pattern remains unchanged in time, the moving front will always approach an asymptotic state: a travelling wave. We also show that when the climate becomes more favorable to growth or germination, the front at any nonzero density level will have a positive acceleration. Our analysis of the model suggests that acceleration in migration happens only when the seed dispersion pattern changes.

Keywords: coupled map lattice, tree migration, travelling wave solution, acceleration in dispersion

1. Introduction: Mathematical models of tree migration

The main types of mathematical models of tree migration in literature include the deterministic model in the form of a reaction-diffusion equation [4, 12], where space and time are both continuous and the stochastic diffusion or contact process model where the space variables are often continuous but the time variable can be either continuous or discrete (e.g., the integrodifference equation model [6]). For these models, while the travelling wave solutions are proven to exist for many interesting cases, the prediction for velocities of the moving front differ significantly: the reaction diffusion equation model and the probability diffusion model with a Gaussian spatial redistribution kernel predict a velocity that is too small compared with the paleorecord and the integrodifference equation model allows a much faster velocity in the case when the seed dispersion function (i.e., the spatial redistribution kernel) has a rather fat tail. Indeed, for redistribution kernels that are not exponentially bounded, the velocity of the moving front is unbounded in time [9]. For more details on these models, we refer readers to [10, 8, 6, 2, 3] and references therein.

Another intriguing aspect of tree migration is the observation of the acceleration of the moving front in the paleorecord. While the simple diffusion model does not predict a non-zero acceleration, the integrodifference equation model with a fat-tailed redistribution kernel does. It predicts a constant acceleration for redistribution kernels just slightly fatter than an exponentially decay function. It also suggests that the shape of the redistribution
kernel is responsible for the existence of such sustained acceleration. However, one may also suspect that the large acceleration and asymptotically unbounded velocity are caused by assuming the maximal dispersal distance is infinite in this model.

In this article, under some basic assumptions on the dispersal pattern of seeds, we model the change of mature tree density with a deterministic model called coupled map lattices where both space and time variables are discrete. We assume that the maximal dispersal distance is a finite parameter depending on the environment. This maximal dispersal distance will thus determine the velocity of the moving front. By saying the moving front or simply, the front, we mean the region near the edge of the unpopulated land where the density of mature trees is above zero but yet to reach the carrying capacity of the land. Its mathematical description will be given later. If we look at the density at a fixed value, we obtain a density contour moving forward at certain velocity. One can even argue that the dispersion velocity obtained by studying fossil pollen distributions actually reflects the velocities of such contours since the exact edge where populated and unpopulated regions meet is difficult to determine. Using a coupled map lattice model, we are able to study the dynamic of this front and its asymptotic behavior as well as the acceleration of the density contours.

Coupled map lattices were first introduced by Keneko in chemistry to model spatio-temporal dynamics of chemical reaction [5]. During the past twenty years, we have seen growing interests in both its theory and applications. In this paper, we restrict our study in the one dimensional lattice case (space is of dimension one) since we are only interested in the velocity and acceleration of migration. In the more realistic two dimensional case, one needs to assume certain spatial symmetry to reduce the dimension. While the extension of the model to higher dimensions is quite straightforward, a rigorous analysis of the higher dimensional model is expected to be more difficult. In dimension one, using a coupled map lattice model for tree migration, we can easily demonstrate the existence of a travelling wave solution representing the moving front under rather general conditions. The travelling wave moves at a constant speed specified in the model. Moreover, we prove that this travelling wave solution is a global attracting fixed point of an induced finite dimensional dynamical system. Starting from any realistic initial state, any orbit of this dynamical system will be approaching this asymptotic state exponentially fast. The model also allows us to demonstrate the existence of positive acceleration of the moving front at every level of density above zero, whenever the climate becomes more favorable for trees to either grow or spread.

In what follows, we first give details of the coupled map lattice model of tree migration and its simple properties. We show the existence of a travelling wave solution representing the asymptotic state of the moving front of migration and we prove that this travelling wave solution is a global
attractor. We then define the density dependent acceleration and show it is always positive when any parameter in the model changes in favor of either growth or dispersion. We also estimate the size of the acceleration in terms of parameter changes. The technical proofs are included in the last section.

2. A Coupled Map Lattice Model of Tree Migration

We assume that the trees are migrating in one direction along a half line. The half line is divided into intervals $I_1, I_2, \cdots, I_n, \cdots$. The time variable $t$ takes integer values: $\cdots, -1, 0, 1, 2, \cdots$. At time $t$, the density of trees in interval $I_n$ is denoted by $0 \leq x_n^t \leq 1$. The density is normalized by the carrying capacity. We only count trees that are mature and bearing seeds.

The local growth function is denoted by $f(x)$. It is a monotonically increasing function on the interval $[0, 1]$. If the current tree density in certain location is $x$, then, $f(x)$ the tree density of next time period at the same location due to the local growth: any newly matured trees at this location have their parents from the same location.

The function $g(x) \geq 0$ denotes the interaction among nearby locations. Assuming that the maximal distance of dispersion will cover $r$ sites, we have the following infinite dimensional dynamical system.

$$x_{n}^{t+1} = \min\{1, f(x_{n}^{t}) + \sum_{j=-r, j\neq 0}^{r} b_{j}g(x_{n+j}^{t})\},$$

where coefficients $b_1, b_{-1}, b_{-r} > 0$, and $b_j \geq 0$ represent the strength of the interaction among neighboring sites. when $n + j \leq 0$, $b_j$ is taken to be zero. We have assumed that the maximal dispersal distances are the same in both directions and the dispersal pattern (also called, the interaction or the coupling) function $g(x)$ is the same through out the region. One can also introduce spatially nonhomogeneous interaction functions. But the analysis is similar.

We shall impose more conditions on both the local growth function $f(x)$ and the interaction function $g(x)$.

For $f(x)$, we assume that i) $f(0) = 0$, (ii) $f(1) = 1$, (iii) $f'(x) > 0$, and $f(x) \geq x$.

The assumption that $f(x) \geq x$ is based on the fact that trees do not move. Once an area is populated with certain number of mature trees, it is unlikely for the density to decrease even all the neighboring sites are virgin land unless some drastic climate changes happen. Thus, our model does not apply to animal species. This assumption makes the model fundamentally different from the traditional diffusive models. This is a growth-dispersion model.

For $g(x)$, we assume that (i) $g(0) = 0$, (ii) $b_{-r}g'(0) > 1$, (iii) $g'(x) > 0$ and (iv) $g''(x) < 0$.
All these conditions are quite natural except (ii). We note that while the contribution from a neighboring site must be an increasing function of the density $x$, trees at this site will contribute to the site being observed unevenly: the seeds from trees near the edge of the site will more likely spread into the neighboring sites. In the two-dimensional case, $g(x)$ would look most likely the function $\sqrt{x}$. Thus, $g'(0) = +\infty$. We will see that this nonlinear condition plays a crucial role in our proofs of main results of this paper. Another observation is that $b_{-r}g(1) \leq 1$ since it represents the contribution to the value of the density. Thus, the equation $x = b_{-r}g(x)$ has a unique nonzero solution $0 < x^* \leq 1$.

This model, in essence, is a special case of the model Afraimovich and Pesin studied in 1993 [1]. Their model is more general because the interaction (or coupling terms) is formulated by a general multivariate function while our coupling function is a sum of single variable functions. The difference is that our coupled map is only piecewise differentiable. Indeed, the results of the paper requires only continuity, not differentiability of either $f(x)$ or $g(x)$. We use differentiability only to simplify our proofs. This coupled map lattice model can also be considered as a discretized integrodifference equation model. The connection between coupled map lattices and integrodifference equation models has been studied recently by Steven M. White and K.A. Jane White [14]. Their coupled map lattice model is different: the coupling is linear and diffusive while the coupling in our model is nonlinear and not diffusive.

In the next section we prove that the dynamical system (1) possesses a unique, up to equivalence, travelling wave solution that represents the asymptotic moving front of tree migration. We show that this travelling wave solution is a global attractor of the nonlinear operator defined by the dynamical system (1) in an invariant set of suitable initial distribution of trees.

In Section 4, we first give the precise definition of the acceleration of the moving front: the acceleration of the moving front with a fixed density. We then show that while the travelling wave solution moves at a constant speed eventually, the points on the front can have positive accelerations whenever the climate becomes more favorable to the growth of trees. We also estimate the size of this acceleration in terms of the local growth function and the coupling constants.

3. ASYMPTOTIC MOVING FRONT: THE TRAVELLING WAVE SOLUTION AND ITS STABILITY

For lattice models of this type, there are many general results on the existence of travelling wave solutions (see, e.g.,[1, 7]). Since our system is specific, we can prove the existence of such solutions using elementary arguments. We can, in fact, show that there is a unique travelling wave
solution in a reasonably large subspace of the phase space and this unique travelling wave solution is a global attractor. We first identify the phase space of the dynamical system and the invariant subspace where we will restrict our consideration.

To avoid having to consider boundary conditions, we assume the trees migrate in one direction. The other direction is bounded by a geographical barrier such as the ocean. We will see that this assumption will not affect the generality of our results on travelling wave solutions in one dimensional case. For dimension two, we need to use the spatial symmetry to reduce the dimension. We first introduce the basic components of the model.

**Phase Space:** \( M = \otimes_{i=1}^{\infty} [0, 1] \), a direct product of copies of the unit interval.

**Metric:** The phase space is equipped with the common supremum metric. For any two points in the phase space \( \bar{x} = (x_i), \bar{y} = (y_i), i \in \mathbb{N} \),

\[
d(\bar{x}, \bar{y}) = \sup_{i \in \mathbb{N}} |x_i - y_i|.
\]

We denote by \( F \) the map \( \bar{x}_t = (x_i^t) \rightarrow (x_i^{t+1}) = \bar{x}_{t+1} \) defined by the dynamics (1) on \( M \):

\[
x_{t+1}^i = F((x_i^t)) = F(\bar{x}^t).
\]

The leftward translation map on \( M \) is denoted by \( \sigma^{-1} \):

\[
(\sigma^{-1}\bar{x})_i = x_{i+1}, \quad i = 1, 2, \ldots.
\]

When we apply the rightward translation map \( \sigma \) on \( M \), we add 1 to the beginning of the sequence.

### 3.1. Existence of Travelling Wave Solutions.

We first describe the simple local dynamics of the map \( F \). It allows us to define the travelling wave solutions easily. Biologically, it means that the density will reach 1 in finite generations once a site is populated.

**Proposition 1.** Assume that \( \bar{x} = (x_i) \) and \( x_n > 0 \) for some \( n \in \mathbb{N} \).

1. There exists \( T \) such that \( (F^t\bar{x})_n = x_n^t = 1 \) for all \( t \geq T \).
2. For any fixed integer \( M_0 > 0 \), there exists \( T \) such that \( x_i^t = 1 \) for all \( t \geq T \) and \( 1 \leq i \leq n + M_0 \).

The proofs of both statements follow from the assumptions that \( f(x) \geq x, b_1 \) and \( b_{-1} \) are both positive, and the fact that \( g(x) > 0 \) for \( x > 0 \).

**Definition 1.** A travelling wave solution of (1) is defined as a fixed point of the map \( \sigma^{-c}F^k \) for some constant positive integers \( c \) and \( k \).

When \( \bar{y}^* = (y_n^*) \in M \) is such a solution, we have

\[
(\bar{y}^*) = \sigma^{-c}F^k(\bar{y}^*).
\]

Or, using coordinates, we have

\[
y_{n-c}^* = (F^k(\bar{y}^*))_n,
\]
for all $n > c$.

Two simplest travelling wave solutions are trivial solutions $\bar{y}^*_0 = (0, 0, \cdots)$ and $\bar{y}^*_1 = (1, 1, \cdots)$. We are interested in finding travelling wave solutions representing the front of the migration moving into previously unpopulated region. Our investigation is thus restricted to an invariant subspace of $\mathcal{M}$: $\mathcal{B}$. This invariant subspace consists of all sequences with finitely many none zero entries.

$$
\mathcal{B} = \{ \bar{x} = (x_1, x_2, \cdots, x_n, 0, 0, \cdots) : 0 \leq x_i \leq 1, n \in \mathbb{N} \}
$$

We look for sequences in the form of

$$
\bar{y} = (1, \cdots, 1, y_{m-1}, \cdots, y_1, y_0, 0, 0, \cdots),
$$

where $1 > y_{m-1}, \cdots, y_0 > 0$ that satisfy the equation in the definition.

**Theorem 1.** For the dynamical system defined in (1),

1. there exist travelling wave solutions for $k = 1$ in the form of
   $$
   \bar{y}^* = (1, \cdots, 1, y_{m-1}, \cdots, y_1, y_0, 0, 0, \cdots);
   $$
   the velocity $c$ of travelling wave solutions is equal to $r$.
2. there is a unique solution for $k = 1$ in the form of
   $$
   \bar{y} = (1, \cdots, 1, y_{m-1}, \cdots, y_1, y_0, 0, 0, \cdots)
   $$
   satisfying the monotonicity condition $1 > y_{m-1} \geq \cdots \geq y_1 \geq y_0 > 0$;
3. the travelling wave solution is unique if $b_j > 0$ for all $j = -r, -r + 1, \cdots, -1$;
4. there are no travelling wave solutions when $k > 1$.

The uniqueness is understood up to equivalence: different numbers of 1’s at the beginning of the solution represent the same solution. Without specifying how many 1’s at the beginning, we denote the unique monotonically decreasing solution by

$$
\bar{y}^* = (1, \cdots, 1, \beta_{m-1}, \cdots, \beta_1, \beta_0, 0, 0, \cdots),
$$

where $\beta_0 > 0$ satisfies $\beta_0 = b_{-r}g(\beta_0)$.

### 3.2. Stability of Travelling Wave Solutions.

To determine the stability of travelling wave solutions, we note that the map $x \to b_{-r}g(x)$ has two fixed points: the origin is an unstable fixed point while the unique nonzero fixed point $x^* = b_{-r}g(x^*) \neq 0$ is a stable one. In fact, we must have $0 < b_{-r}g(x^*) < 1$ since $b_{-r}g(x) = 1$ for some point $x < x^*$.

Since the travelling wave solutions are fixed points of the nonlinear map $\sigma^{-c}\mathcal{F}$, the natural approach to investigate the stability of these fixed points is to linearize the map near these fixed points and study the spectra of linear operators. But this approach has two disadvantages in our case. First, because the map $\mathcal{F}$ is only piecewise differentiable, the linearization is difficult to carry out, if not impossible. Second, this approach can, at best,
obtain local stability. On the other hand, our rather explicit formula of the dynamical system enables us to study the stability directly and globally. We summarize the stability results in the following theorem.

**Theorem 2.**

1. When $b_j > 0$, $j = -r, -r+1, \cdots, -1$, the unique travelling wave solution is globally asymptotically stable in the following sense:
   
   For any given initial condition $\bar{x} = (x_n, \cdots, x_1, x_0, 0, 0, \cdots)$ with $x_0 \neq 0$, there exists an integer $\alpha$ such that
   
   $$\lim_{k \to \infty} \sigma^{-ck+\alpha}(\mathcal{F})^k \bar{x} = \bar{y}^*.$$  

2. Any travelling wave solution in the form of
   
   $$\bar{y} = (1, \cdots, 1, y_{k_1}, \cdots, y_{k_2}, 0, 0, \cdots)$$
   
   with $y_k = 0$ for some $k_2 \geq k \geq k_1$ is unstable.

3. The unique monotonically decreasing travelling wave solution
   
   $$\bar{y}^* = (1, \cdots, 1, \beta_{m-1}, \cdots, \beta_1, \beta_0, 0, 0, \cdots)$$
   
   is globally asymptotically stable in the following sense:

   For any given initial condition $\bar{x} = (x_n, \cdots, x_1, x_0, 0, 0, \cdots)$ with $x_i \neq 0, i = 0, 1, \cdots, n$ and $n \geq r$, there exists an integer $\alpha$ such that
   
   $$\lim_{k \to \infty} \sigma^{-ck+\alpha}(\mathcal{F})^k \bar{x} = \bar{y}^*.$$  

The proof of the stability results is divided into several steps.

First, we show that the dynamics that we are interested in is essentially of finite dimensional: there is a finite dimensional subspace which contains all travelling wave solutions and is invariant under $\sigma^{-c}\mathcal{F}$. It means that the depth of the moving front is always bounded by a fixed length $(l+1)c$ for all times.

**Lemma 1.**

1. There exist a sequence of constants $\delta_1 < \delta_2 < \cdots < \delta_l < 1$ such that the following set $S$ is invariant under the map $\sigma^{-c}\mathcal{F}$:

   $$S = \{ \bar{x} = (x_1)_{i=1}^\infty : x_1 = \cdots = x_c = 1; x_{ic+1}, \cdots, x_{ic+c} \geq \delta_{l-i+1}, i = 1, \cdots, l; x_i = 0, i > (l+1)c \}.$$  

   The leftward shift map $\sigma^{-c}$ and the map $\mathcal{F}$ commute on the set $S$:

   $$\mathcal{F} \sigma^{-c} = \sigma^{-c} \mathcal{F}.$$  

2. If $b_j > 0$ when $j = -r, \cdots, -1$, then, for any given initial point $\bar{x} = (x_n, \cdots, x_0, 0, 0, \cdots)$ with $x_0 \neq 0$, there exist constant integers $\alpha, k_0$ such that

   $$\sigma^{-\alpha}(\mathcal{F})^{k_0} \bar{x} \in S.$$  

3. For any given initial point $\bar{x} = (x_n, \cdots, x_0, 0, 0, \cdots)$ with $n \geq r$ and $x_i \neq 0$ for all $i, 0 \leq i \leq n$, there exist constant integers $\alpha, k_0$ such that

   $$\sigma^{-\alpha}(\mathcal{F})^{k_0} \bar{x} \in S.$$
To show the global stability of fixed points, we directly estimate the distance between $\sigma^{-ck}(F)^k\bar{x}$ and $\bar{y}^*$ for $\bar{x} \in S$. Note that the set $S$ can be imbedded in a subspace of dimension $(l+1)c$. The stability problem becomes a finite dimensional one. The convergence of $\sigma^{-ck}(F)^k\bar{x}$ to $\bar{y}^*$ is then proved by induction showing that each coordinate converges.

**Theorem 3.** For every $\bar{x} \in S$,
\[
\lim_{k \to \infty} \sigma^{-ck}(F)^k\bar{x} = (\sigma^{-c}F)^k\bar{x} = \bar{y}^*.
\]

**Remark.** The existence and global stability of the unique travelling wave solution imply that one should be able to see a distinct moving front of certain well-defined shape in the absence of climate change. This well-defined shape, which represents density variation in this moving front, is determined by patterns of seed dispersion. Because the asymptotic moving front is described by a travelling wave solution, acceleration of this front is always zero. The acceleration we discuss in next section occurs before the moving front reaches its asymptotic state.

## 4. Acceleration in Tree Migration

Paleorecords of tree migration shows the existence of periods of accelerated migration. For mathematical models aforementioned in the introduction, while travelling wave solutions representing the moving front were proved to exist, little can be said about the existence of acceleration and its magnitude corresponding to climate changes. For reaction diffusion equation models, one needs to introduce time dependent coefficients and nonlinear reaction terms in order to incorporate the climate change into the model. This change makes the model difficult to analyze. The situation with integrodifference model is even more subtle. The model shows that in the absence of a climate change, the front can move at a constant acceleration when the dispersal function has a moderately fat tail ($e^{-a\sqrt{x}}$). The velocity of the moving front becomes unbounded in time for dispersal functions of the type $e^{-ax^\beta}$, $0 < \alpha, 1 > \beta > 0$ [6].

In this section, we use the results on the existence of travelling wave solutions and their stability to study the acceleration of the moving front corresponding to climate changes. Our basic assumptions are that a climate change occurs within a short period of time: in one generation and the maximal dispersal distance is not affected by the climate change. Before a rather abrupt change of the climate, the moving front of trees is almost at its equilibrium: the travelling wave solution. When the climate becomes more favorable to germination and/or growth, this moving front falls out of equilibrium and it will seek the new equilibrium defined by the travelling wave solutions for the new system. Acceleration then occurs during this period of time because the rate of approaching this new equilibrium is exponential. To be more specific, assume that the density function at time $t$ and at the
location \( x \geq 0 \) is \( u(x, t), \) \( 1 \geq u(x, t) \geq 0 \). We may assume it is a strictly decreasing function in \( x \) and increasing in \( t \). At any moment \( t \), the front is defined by a segment of the graph of this function 
\[
\{(u, x) : 1 > u > 0\}.
\]
When \( u(x, t) \) is not a travelling wave solution, the points in the front are generally, moving at different speed. The speed of the point \((u, x)\) with a fixed density level \( 0 < u_0 < 1 \) is \( \frac{dx(t, u_0)}{dt} \) where \( x(t, u_0) \) is defined implicitly by the equation
\[
(2) \quad u_0 = u(x(t, u_0), t).
\]
The acceleration of the moving front at any given density level \( u_0 \) is thus, defined naturally by \( \frac{d^2 x(t, u_0)}{dt^2} \).

Since our model is discrete in both space and time, this definition needs to be modified.

4.1. Acceleration of the moving front: its definition. We define the set of initial profiles of the moving front where the acceleration will be considered.

\[
D = \{\bar{y} | \bar{y} = (1, \ldots, 1, y_{k_1}, y_{k_1+1}, \ldots, y_{k_2}, 0, \ldots), y_i \geq y_j, k_1 \leq i < j \leq k_2\}.
\]
The number of 1’s in any sequence in \( D \) is at least \( c \) and \( 1 > y_{k_1-1} \geq y_{k_2} > 0 \).
The set \( D \) is clearly invariant under \( \mathcal{F} \). Note that the last nonzero entry of \( \bar{y} \) moves by \( c \) units every time \( \mathcal{F} \) is applied. This indicates that the very tip of the moving front is moving at a constant velocity at \( c \) per unit time. But other points on this moving front can have different velocities. To determine the velocities of points on this moving front, we need to make its profile look like a continuous curve: connecting the discrete dots representing the moving front. We denote this piecewise linear curve by \( u(x, \bar{y}) \) with \( k_1 - 1 \leq x \leq k_2 + 1 \). For any positive integer \( k_1 - 1 \leq i \leq k_2 \), we have for,
\[
u(x, \bar{y}) = (y_{i+1} - y_i)(x - i) + y_i, \quad i \leq x \leq i + 1
\]
Note that \( u(k_1 - 1, \bar{y}) = 1 \) and \( u(k_2 + 1, \bar{y}) = 0 \).

For any given number \( 0 < y \leq 1 \), the velocity of the moving front at the density level \( y \) at time \( t \) is naturally defined by
\[
v(t, y) = \max\{x : u(x, \mathcal{F}^{t+1}(\bar{y})) \geq y\} - \max\{x : u(x, \mathcal{F}^t(\bar{y})) \geq y\}.
\]
The acceleration of the moving front at the density level \( y \) at time \( t \) is defined by
\[
A(t, y) = v(t, y) - v(t - 1, y).
\]
When \( y = 0 \), we simply have \( v(t, 0) = c \) for all \( t \) and thus, \( A(t, 0) = 0 \). In the case when the travelling wave solution is asymptotically stable, we must have \( \lim_{t \to \infty} v(t, y) = c \) and \( \lim_{t \to \infty} A(t, y) = 0 \).
4.2. Positivity of Acceleration. In general, the sign of $A(t, y)$ is not positive for all $0 < y \leq 1$ and $t \geq 0$. Indeed, since the travelling wave solution is an asymptotically stable fixed point of the map $\sigma^{-c}F$, the sign of the acceleration $A(t, y)$ depends on whether $v(t, y)$ is bigger or smaller than $c$. We show that in a particular situation of interest, the acceleration is positive when $t = 0$ for all $0 < y \leq 1$. We will also briefly discuss the implication of this positive acceleration in the context of tree migration.

In the following theorem, we assume that $b_j > 0, j = -r, \ldots, -1$. We assume that the climate becomes more favorable for trees to grow in a very short period of time and stays favorable afterwards. We show that the acceleration is positive at all positive density levels at $t = 0$ when the climate changes for better. We first make precise the meaning of one system being more favorable to growth than the other.

**Definition 2.** For two systems $F^{(a)}, F^{(b)}$ in the form of (1), we say that $F^{(a)}$ is more favorable to growth than $F^{(b)}$ if for any $n \geq 1$ and any $\bar{y} \in D$,

$$F^{(a)}_n(\bar{y}) \geq F^{(b)}_n(\bar{y}).$$

$F^{(a)}$ is said to be strictly more favorable to growth than $F^{(b)}$ if for for any $n \geq 1$ and any $\bar{y} \in D$,

$$F^{(a)}_n(\bar{y}) > F^{(b)}_n(\bar{y}),$$

whenever $F^{(b)}_n(\bar{y}) > 0$.

**Remark** When $F^{(a)}$ is said to be strictly more favorable to growth than $F^{(b)}$ and both systems have the same maximal dispersal distance $r$, the travelling wave solutions for these two systems keep the same order. Assume that $\bar{x}^* = (1, \ldots, 1, \alpha_{m-1}, \ldots, \alpha_0, 0, \ldots)$ and $\bar{y}^* = (1, \ldots, 1, \beta_{m-1}, \ldots, \beta_0, 0, \ldots)$ are the unique travelling wave solutions of these two systems. We have $\alpha_i > \beta_i, i = m - 1, \ldots, 0$.

**Theorem 4.** Assume that $F^{(a)}$ is strictly more favorable to growth than $F^{(b)}$. Before time $t = 0$, the dynamics is governed by $F^{(b)}$ and the system is at equilibrium, i.e., the front is moving along the travelling wave solution of $F^{(b)}$. Assume that at $t = 0$, the dynamics is changed to $F^{(a)}$. Then, for every $y$ with $0 < y < 1$ the acceleration $A(0, y) > 0$.

In the absence of climate change, for small $y > 0$, the sign of the acceleration $A(t, y)$ depends on whether $v(t, y)$ is bigger or smaller than $c$.

**Theorem 5.** Let $\bar{y}_0 = (1, \ldots, 1, y_{k_1}, \ldots, y_{k_2}, 0, \ldots), y_{k_2} > 0$ be the initial position of the moving front and $\bar{y}^t = (1, \ldots, 1, \beta_{m-1}, \ldots, \beta_0, 0, \ldots)$ is the travelling wave solution of the system. Then, for all $t \geq 1$ and $0 < y \leq |y_{k_2} - \beta_0|$, the sign of the acceleration $A(t, y)$ is the same as that of $y_{k_2} - \beta_0$. 

4.3. **Magnitude of the positive acceleration.** It is easy to see that when some coefficient $b_j$ increases or the local growth function $f$ becomes bigger, the system becomes more favorable to growth. In these cases, it is possible to estimate the magnitude of the acceleration. When $y$ is small, $A(t, y)$ could be approximately what a field biologist would actually measure. Its magnitude can also be estimated easily since the velocity is determined by $\beta_0$ and $b_{-c}$ (see the proof of Theorem 4). Assume that the last nonzero entries of the travelling wave solutions of two systems are $\alpha_0 > \beta_0 > 0$, respectively. Then, a simple calculation shows that for $0 < y \leq \beta_0$, the acceleration $A(0, y)$ is bounded by

$$ \left( \frac{y}{\beta_0} - \frac{y}{\alpha_0} \right) < \frac{y}{\beta_0} \left( 1 - \frac{\beta}{\alpha} \right) < 1. $$

This indicates that this type of acceleration is quite small and a large acceleration can only appear when the maximal dispersion distance also increases.

Another simple yet interesting property of this model is that a change in the local growth function $f$ will not affect the numbers $\beta_0, \cdots, \beta_c$ in the travelling wave solution $\bar{y}^* = (1, \cdots, 1, \beta_{n-1}, \cdots, \beta_1, \beta_0, 0, \cdots)$ if the dispersion parameters $\{b_j\}$ remain unchanged. This indicates that the type of acceleration we consider in this paper relies more on the dispersion pattern and less on the life history of the tree. This property is consistent with what was observed in the paleorecord [3].

4.4. **Conclusion.** The deterministic coupled map lattices allow us to model tree (or other plant) migration differently from the traditional diffusive models. By studying the dynamics of a one dimensional coupled map lattice, we gain insight into the asymptotic behavior and the nature of acceleration of the moving front. Our model suggests that as long as the climate remains unchanged, the moving front will approach its asymptotic state: a travelling wave, regardless of the differences in dispersion patterns. Acceleration happens only when the seed dispersion pattern changes. If the faster migration velocity is sustained after an accelerating period or the magnitude of acceleration is large, it indicates an increase in the maximal dispersal distance of seeds.

5. **Proofs**

5.1. **Proof of Proposition 1.** (1) Since $b_{-1} > 0$, we have

$$ x_{n+1}^1 \geq f(x_{n+1}^0) + b_{-1}g(x_n^0) > 0. $$

Thus,

$$ x_{n}^2 \geq f(x_{n}^1) + b_{1}g(x_{n+1}^1) \geq x_{n}^1 + b_{1}g(x_{n+1}^1). $$

Denote $\delta = b_{1}g(x_{n+1}^1)$. In general, we have, for $t = 1, 2, \cdots$,

$$ x_{n}^{t+1} \geq f(x_{n}^{t}) + b_{1}g(x_{n+1}^{t}) \geq x_{n}^{t} + b_{1}g(x_{n+1}^{t}) = x_{n}^{t} + \delta. $$
Let $T = \text{the integer part of } (1/\delta) + 2$. Then, $x_T^t = 1$, for all $t \geq T$.

(2) The proof is similar to (1) using the fact that $b_{-1}, b_1 > 0$ and $g(x) > 0$ for $x > 0$.

5.2. **Proof of Theorem 1, the Existence of Travelling Wave Solutions.** We proceed directly to a constructive proof of the second statement. In the proof, we explain how it is possible to have non-monotonic solutions. Other statements follow easily.

We start with a sequence in the form of

$$
y^* = (y_{n-1}, \ldots, y_i, \ldots, y_1, y_0, 0, 0, \ldots)
$$

We assume that the entry at lattice site $n$, $(y^*)_n = \bar{y}^*_n = y_0$ is the last non-zero entry (the tip of the moving front) in the sequence. After we apply the map $F$ to $\bar{y}^*$, the last nonzero entry is at the lattice site $n + r$:

$$(F(\bar{y}^*))_{n+r} = f(y_{n+r}) + b_{-r}g(y_0) + b_{-r+1}g(0) + \cdots = b_{-r}g(y_0).$$

The fixed point condition for the map $\sigma^{-c}F$,

$$\bar{y}^*_{n-c} = (F(\bar{y}^*))_n$$

implies that we must have

$$c = r \text{ and } (F(\bar{y}^*))_{n+r} = y_0 = b_{-r}g(y_0),$$

i.e., $y_0$ is a nonzero fixed point of the one variable map $x \mapsto b_{-r}g(x)$. We denote this unique value by $\beta_0$. This also implies that for $k > 1$, there is not fixed points of $\sigma^{-c}F^k$ in the form of $\bar{y}^* = (y_n, \ldots, y_i, \ldots, y_1, y_0, 0, 0, \ldots)$ because the map $x \mapsto b_{-r}g(x)$ does not have any non-trivial periodic point.

We now can find $y_i$, $i = 1, \ldots, n - 1$, successively. We assume that $r = c$ is typically much larger than 1. We have

$$y_1 = (F(\bar{y}^*))_{n-1+c} = f(\bar{y}^*_{n-1+r}) + b_{-r}g(y_1) + b_{-r+1}g(y_0).$$

In this equation, the sum

$$C_1 = f(\bar{y}^*_{n-1+r}) + b_{-r+1}g(y_0) \geq 0$$

is known number, so, $y_1$ is a solution to the equation

$$x = b_{-r}g(x) + C_1.$$ 

There are two possible solutions to this equation when $C_1 = 0$: $y_1 = 0$ and $y_1 = y_0 = \beta_0$. Note that when $b_{-r+1} > 0$, $C_1 > 0$, the equation $x = b_{-r}g(x) + C_1$ has a nonnegative unique solution $y_1 > y_0 = \beta_0$.

Assume that we have solved $y_{k-1}, \ldots, y_0$ and all of them are smaller than 1. To determine $y_k$, we use again the fixed point condition

$$y_k = \bar{y}^*_{n-k} = (F(\bar{y}^*))_{n-k+c} = f(\bar{y}^*_{n-k+c}) + b_{-r}g(\bar{y}^*_{n-k}) + \cdots + b_{r}g(\bar{y}^*_{n-k-2c}).$$
Let $C_k = f(y_{n-k+c}^*) + b_{-r+1} g(y_{n-k+1}^*) + \cdots + b_r g(y_{n-k-2c}^*)$. We have

$$y_k = b_r g(y_k) + C_k.$$ 

The solution always exists. If the solution is bigger than 1, we must have $y_k = 1$.

If we have chosen previous solutions $y_{k-1}, \ldots, y_1, y_0$ in a decreasing order, then we have $C_k \geq C_{k-1} \geq \cdots \geq C_1 \geq 0$. Thus, we have $y_k \geq y_{k-1}$. We see also that this $y_k$ is unique. If we assume all $b_{\pm j} > 0$, $j = 1, 2, \ldots, r$, then, we must have $y_n > \cdots > y_1 > y_0 > 0$.

We are left to show that when $k$ is sufficiently large, $y_k = 1$. Note that the limit must exist $\lim_{k \to \infty} y_k = L \leq 1$. Because of continuity of $f$ and $g$, this limit must be 1 since

$$f(L) + b_{-r} g(L) + \cdots + b_r g(L) > L.$$ 

This also implies that $y_k = 1$ when $k$ is large enough.

**Remark.** Note that the uniqueness of the fixed point is understood up to equivalence. If $(1, y_n, \ldots, y_1, y_0, 0, \cdots)$ is a fixed point, then $(1, \cdots, 1, y_n, \cdots, y_1, y_0, 0, \cdots)$ is also a fixed point. We do not distinguish these fixed points when we consider these fixed points as travelling wave solutions.

5.3. Proof of Stability of Travelling Wave Solutions.

**Proof of Lemma 1.**

(1) Let $\bar{x} = (x_i)_{i=1}^\infty \in S$. We show that $\sigma^{-c} \mathcal{F} \bar{x} \in S$. Let $\delta_1$ be any positive number between 0 and $\beta_0$, the nonzero fixed point of the map $x \to b_{-c} g(x)$. Since $x_{lc+c}, \ldots, x_{lc+c} \geq \delta_1$, we have

$$(\mathcal{F} \bar{x})_{lc+c+j} = b_{-c} g(x_{lc+c+j}) + \text{some nonnegative terms} \geq b_{-c} g(\delta_1) > \delta_1$$

for all $j = 1, \cdots, c$. Indeed, this argument implies that

$$(\mathcal{F} \bar{x})_i > \delta_1$$

for all $i, 1 \leq i \leq (l+2)c$. Note also that $(\mathcal{F} \bar{x})_i = 0$ for $i > (l+2)c$.

Choose

$$\delta_2 = f(\delta_1) + [b_{-c} + \cdots + b_{-1}] g(\delta_1) > \delta_1.$$ 

We have that, for $j = 1, \cdots, c$,

$$(\mathcal{F} \bar{x})_{lc+c+j} = f(x_{lc+c+j}) + b_{-c} g(x_{(l-1)c+j}) + \cdots + b_{-1} g(x_{(l-1)c+j}) + \cdots + b_c g(x_{(l+1)c+j})$$ 

$$\geq f(\delta_1) + [b_{-c} + \cdots + b_{-1}] g(\delta_1) = \delta_2.$$ 

If we have already chosen $\delta_{k-1} > \cdots > \delta_1 > 0$, we let

$$\delta_k = f(\delta_{k-1}) + [b_{-c} + \cdots + b_{-1}] g(\delta_{k-1}) > \delta_{k-1}.$$ 

Since $x_i \geq \delta_{k-1}$ for $i \leq (l-k+3)c$, we have subsequently,

$$(\mathcal{F} \bar{x})_{(l-k+2)c+j} = f(x_{(l-k+2)c+j}) + b_{-c} g(x_{(l-k+1)c+j}) + \cdots + b_{-1} g(x_{(l-k+2)c+j}) + \cdots$$
\[ \geq f(\delta_{k-1}) + [b_{-c} + \cdots + b_{-1}]g(\delta_{k-1}) = \delta_k. \]

We observe that the sequence \( \delta_1, \ldots, \delta_k, \ldots \) is determined by the system only and it must end with \( \delta_l < 1 \) and \( \delta_i = 1 \) for all \( i > l \) for some positive integer \( l \). Thus, we have \( \sigma^{-c}FS \subset S \). A direct consequence of the invariance of \( S \) under \( \sigma^{-c}F \) is that by adding a fixed number of 1’s to each sequence in \( S \), we obtain another set invariant under \( \sigma^{-c}F \).

(2) When \( b_j > 0 \) for all \( j = -r, \ldots, -1 \), there exists \( k \geq 1 \) such that

\[ (F^k \bar{x})_i > \delta_1 \]

for all \( i \leq (n + 1) + kc \) and

\[ (F^k \bar{x})_i = 0 \]

for all \( i > (n + 1) + kc \).

Let \( k_0 = k + l \). We have

\[ (F^{k+l} \bar{x})_i > \delta_1, \text{ for } (n + 1) + (k + l - 1)c < i \leq (n + 1) + (k + l)c \]

\[ (F^{k+l} \bar{x})_i > \delta_2, \text{ for } (n + 1) + (k + l - 2)c < i \leq (n + 1) + (k + l - 1)c \]

\[ \ldots \]

\[ (F^{k+l} \bar{x})_i > \delta_m, \text{ for } (n + 1) + (k + l - m)c < i \leq (n + 1) + (k + l - m + 1)c \]

\[ \ldots \]

\[ (F^{k+l} \bar{x})_i = 1, \text{ for } 1 \leq i \leq (n + 1) + kc. \]

So, if we set \( \alpha = (n + 1) + k - 1c \), we have

\[ \sigma^{-\alpha}F^{k_0} \bar{x} \in S. \]

(3) The conditions allow to have a \( k \geq 1 \) such that

\[ (F^k \bar{x})_i > \delta_1 \]

for all \( i \leq (n + 1) + kc \) and

\[ (F^k \bar{x})_i = 0 \]

for all \( i > (n + 1) + kc \). The rest of the arguments is identical to those in the proof of (2).

Proof of Theorem 3.

We take any element \( \bar{y} \in S \). We write \( \bar{y} = (1, \ldots, 1, y_{n-1}, \ldots, y_1, y_0, 0, \ldots) \) with \( y_0 > 0 \) and the total number of nonzero entries of \( \bar{y} \) being \( (l + 1)c \). We will show that

\[ \lim_{k \to \infty} [\sigma^{-ck}F^k \bar{y}]_i = (\bar{y}^*)_i, \]

for all \( 1 \leq i \leq (l + 1)c \), where \( \bar{y}^* = (1, \ldots, 1, \beta_{m-1}, \ldots, \beta_1, \beta_0, 0, \ldots) \) and we add 1’s to the front of the sequence of \( \bar{y}^* \) so that it has exactly \( (l + 1)c \) nonzero entries.

The strategy of the proof is that we use the special structure of the dynamical system. We notice that the coordinate \([\sigma^{-c}F \bar{y}]_i\) depends on
If we denote this map by $f$, we have $(y, y_0) \to$

$$\left( f(y_{n-1}) + b_{c}g(y_n) + b_{c+1}g(y_{n-1}) + \cdots + b_{c}g(y_{n-2c}), \right.$$

$$\left. \cdots, b_{c}g(y_1) + b_{c+1}g(y_0), b_{c}g(y_0) \right).$$

If we denote this map by $G_n$, we have

$$G_n(y_n, \ldots, y_0) = (b_{c}g(y_n) + C_{n,1}, G_{n-1}(y_{n-1}, \ldots, y_0)),$$

where $C_{n,1} = f(y_{n-1}) + b_{c+1}g(y_{n-1}) + \cdots + b_{c}g(y_{n-2c})$ is a function of $(y_{n-1}, \ldots, y_0)$.

If we iterate the map $G_n$ $k$ times, we have

$$(y_n^k, \ldots, y_0^k) = G_k^n(y_n, \ldots, y_0) = G_n(y_{k-1}^n, C_{n-1}^{k-1}(y_{n-1}, \ldots, y_0))$$

$$= (b_{c}g(y_{k-1}^n) + C_{n,k}, G_{n-1}^{k-1}(y_{n-1}, \ldots, y_0)),$$

where

$$C_{n,k} = f(y_{n-1}^{k-1}) + b_{c+1}g(y_{n-1}^{k-1}) + \cdots + b_{c}g(y_{n-2c}^{k-1}).$$

We need to show for each $n$,

$$\lim_{k \to \infty} y_{n}^{k} = \beta_n.$$

The assertion is certainly true when $n = 0$ since $\beta_0$ attracts every positive point under the iteration of the map $x \to b_{c}g(x)$.

Now we assume that $y_{n}^{k}$ converges to $\beta_i$ for all $0 \leq i \leq n - 1$. To see that $y_{n}^{k}$ converges to $\beta_n$, we first observe the following facts:

1. $\beta_n = b_{c}g(\beta_n) + C_{n}^{*}$, where

$$C_{n}^{*} = f(\beta_{n-1}) + b_{c+1}g(\beta_{n-1}) + \cdots + b_{c}g(\beta_{n-2c}).$$

(When $n$ is small, the expressions are different: $C_{0}^{*} = 0$, $C_{1}^{*} = b_{c+1}g(\beta_0)$, etc. We are giving here the general formula.)

2. For every $n, k, n \geq 1$, $C_{n,k} \geq 0$ and the limit

$$\lim_{k \to \infty} C_{n,k} = C_{n}^{*}$$

because of our assumption on convergence for $0 \leq i \leq n - 1$ and the continuity of functions $f$ and $g$.

Now we estimate the distance between $y_{n}^{k}$ and $\beta_n$.

$$y_{n}^{k} - \beta_n = (b_{c}g(y_{n}^{k-1}) - b_{c}g(\beta_n)) + (C_{n,k} - C_{n}^{*}).$$

Because of the convergence of $(b_{c}g)^k(\delta_1)$ to $\beta_0$ and $y_i \geq \delta_1$ for all $i \leq i \leq (l+1)c$, we have that

$$y_{i}^{k} > (b_{c}g)^k(\delta_1)$$
for all \( k \geq 1 \) and \( 1 \leq i \leq (l + 1)c \). Since \( \beta_n > \beta_0 \), we have that there exist \( \lambda < 1 \) and \( k_0 \) such that for any \( \xi \) between \( y_n^k \) and \( \beta_n \), and \( k \geq k_0 \),
\[
|b_{-c}g'(\xi)| < \lambda
\]
and
\[
|C_{n,k} - C_n^a| < \epsilon.
\]

Thus, we have
\[
|y_n^k - \beta_n| < \lambda|y_n^{k-1} - \beta_n| + \epsilon.
\]

Iterating this recursive relation, we have
\[
|y_n^k - \beta_n| < \lambda^2|y_n^{k-2} - \beta_n| + \lambda \epsilon + \epsilon < \cdots
\]
\[
\cdots < \lambda^{k-k_0}|y_n^{k_0} - \beta_n| + \lambda^{k-k_0-1}\epsilon + \cdots + \epsilon
\]
\[
= \lambda^{k-k_0}|y_n^{k_0} - \beta_n| + \epsilon - \frac{\lambda^{k-k_0}}{1 - \lambda}.
\]

This implies that \( \lim_{k \to \infty} y_n^k = \beta_n \). It seems that we are using the differentiability here. But the differentiability is not necessary as long as the curve \( y = b_{-c}g(x) \) satisfies some Lipschitz condition.

**Remark.** Here we only prove the convergence of \( y_n^k \) as \( k \to \infty \). A similar analysis can show that this convergence is actually exponentially fast when \( k \) is sufficiently large. The travelling wave solution can also be proven to be stable in the rigorous mathematical sense when the initial value is restricted to the subspace \( \mathcal{B} \).

5.4. **Proof of positive acceleration.**

**Proof of Theorem 4.**

Since the front was moving according to the travelling wave solution of \( \mathcal{F}(b) \) before time \( t = 0 \), we have \( v(-1, y) = c \) for all \( y, 0 \leq y \leq 1 \). Since \( A(0, y) = v(0, y) - v(-1, y) = v(0, y) - c \), we just need to show \( v(0, y) > c \) for all \( y, 0 < y \leq 1 \). Let the density sequence at \( t = 0 \) be \( \bar{x} = (1, \cdots, 1, x_1, x_2, \cdots, x_n, 0, \cdots) \), where \( 1 > x_1 > x_2 > \cdots > x_n > 0 \) and \( \bar{x} = \sigma^{-c}\mathcal{F}(b)\bar{x} \). To show \( v(1, y) > c \), it suffices to show that the image of \( \bar{x} \) under \( \sigma^{-c}\mathcal{F}(a) \), \( \bar{y} = (1, \cdots, 1, y_1, y_2, \cdots, y_n, 0, \cdots) = \sigma^{-c}\mathcal{F}(a)\bar{x} \) satisfies conditions \( y_i > x_i \) for all \( i, 1 \leq i \leq n \).

Assume that we have \( m \) 1’s at the beginning of the sequence \( \bar{x} \). Note that
\[
y_i = [\mathcal{F}(a)\bar{x}]_{m+i+c}
\]
and that
\[
x_i = [\mathcal{F}(b)\bar{x}]_{m+i+c}
\]
because \( \bar{x} \) is a fixed point of \( \sigma^{-c}\mathcal{F}(b) \). Since \( \mathcal{F}(a) \) is strictly more favorable to growth than \( \mathcal{F}(b) \), we have \( y_i > x_i \) for all \( i \) between 1 and \( n \).

**Proof of Theorem 5.**

For \( 0 < y < \min\{y_{k_2}, \beta_0\} \), the acceleration is determined by the sequence \( \{b_{-c}g[y_{k_2}]\} \). Because the sequence converges to \( \beta_0 \) exponentially, the acceleration has the same sign as the displacement \( y_{k_2} - \beta_0 \).
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**REFERENCES**


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