# Dynamics and Equilibrium Structure of Migration-Selection Models 

Linlin Su<br>Department of Mathematics<br>Southern University of Science and Technology

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## Outline

1. A semilinear parabolic system pertaining to selection and migration
2. Theory of two-allele migration-selection models
3. The complexity of the complete dominance case
4. Various extensions of migration-selection models
5. A semilinear parabolic system pertaining to selection and migration

## Diploid Population at Single Locus



Alleles $A_{1}, A_{2}, \ldots, A_{n}$; genotypes $A_{i} A_{j}\left(=A_{j} A_{i}\right)$
E.g., At ABO locus for human blood type, there are 3 major alleles $A, B, O$; and 6 genotypes $A A, A B, A O, B O, B B, O O$

## Selection Equation by Mendel's Laws ${ }^{1}$

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\begin{equation*}
\frac{d p_{i}}{d t}=p_{i}\left[r_{i}(p)-\bar{r}(p)\right] \tag{S}
\end{equation*}
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$p_{i}(t)$ : frequency of allele $A_{i}$ at time $t, 1 \leqslant i \leqslant n$
$p=\left(p_{1}, p_{2}, \ldots, p_{n}\right)$ : gene freq. vector;
$p \in \Delta_{n}=\left\{p \in \mathbb{R}^{n}: 0 \leqslant p_{i} \leqslant 1, \sum_{i} p_{i}=1\right\}$ (n-simplex)

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Selection is relative fitness of alleles

- $p(0) \in \Delta_{n} \Rightarrow p(t) \in \Delta_{n} \forall t>0$
- $d \bar{r} / d t=2 \sum_{i} p_{i}\left(r_{i}-\bar{r}\right)^{2} \geqslant 0, \quad "="$ holds iff at equilibrium

[^0]

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British statistician and geneticist
Fisher's Fundamental Theorem of Natural Selection (1930)
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This integrates the principles of Mendelian genetics with Darwinian natural selection.

## Selection with Spatial Structure

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\end{equation*}
$$

with zero Neumann b.c.

- $\lambda>0$ is ratio of selection intensity $s$ to migration rate $d$
- $p=\left(p_{1}, \ldots, p_{n}\right), r_{i}(x, p)=\sum_{j} r_{i j}(x) p_{j}, \quad \bar{r}(x, p)=\sum_{i} r_{i} p_{i}$
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Core questions: protection/elimination of certain allele(s); existence, uniqueness, multiplicity of pos. equilibriums; stability of equilibriums; global dynamics, etc.

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Core questions: protection/elimination of certain allele(s); existence, uniqueness, multiplicity of pos. equilibriums; stability of equilibriums; global dynamics, etc.
(Lou, Nagylaki 2002, 2004, 2006 JDE; Lou, Nagylaki, Ni 2013 DCDS; Hofbauer, Su 2016 SIAP)
2. Theory of two-allele migration-selection models

## Two Alleles and Degree of Dominance

$p_{1}=u(x, t)$ : freq. of allele $A_{1}$ at location $x \in \Omega \subset \mathbb{R}^{N}$ and time $t$, $p_{2}=1-u$ : freq. of allele $A_{2}$.

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Fitness of genotype $A_{i} A_{j}: r_{i j}(x)=c_{i j} g(x)$, where

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c_{11}=1, \quad c_{12}=c_{21}=h, \quad c_{22}=-1 ;
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$h \in[-1,1]$ degree of dominance.

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Effect of selection on $A_{1}$ :

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p_{1}\left[r_{1}(x, p)-\bar{r}(x, p)\right]=g(x) \underbrace{u(1-u)[1+h-2 h u]}_{f_{h}(u)}
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- $h=0: f_{h}(u)=u(1-u)$, no dominance (as in Fisher's eq.)
- $h=-1: f_{h}(u)=2 u^{2}(1-u), A_{1}$ recessive (or $A_{2}$ completely dominant to $A_{1}$ )
- $h=1: f_{h}(u)=2 u(1-u)^{2}, A_{2}$ recessive


## Migration-Selection Equation for Two Alleles

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\begin{equation*}
u_{t}=\Delta u+\lambda g(x) f(u), \quad x \in \Omega, \quad t>0 \tag{2}
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\begin{aligned}
& \quad f(0)=f(1)=0 ; f(u)>0, u \in(0,1) ; f \in C^{1}([0,1]) \\
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- $0=\int_{\Omega}[\Delta u+\lambda g f(u)] d x=\int_{\Omega} \lambda g f(u) d x$ $\Rightarrow \exists$ nontrivial equil. only if $g(x)$ changes sign
- By strong maximum principle, every nontrivial equil. $u(x) \in(0,1)$ in $\bar{\Omega}$ $u(x, 0) \in[0,1], \not \equiv 0, \not \equiv 1 \Rightarrow u(x, t) \in(0,1), \forall x \in \bar{\Omega}, t>0$


## Migration-Selection Balance

Without migration $u_{t}=\lambda g(x) f(u)$ :

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\begin{aligned}
& g(x)>0 \Rightarrow u(x, t) \rightarrow 1 \text { as } t \rightarrow \infty ; \\
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Theorem. Assume $f^{\prime}(0)>0, f^{\prime}(1)<0$ (e.g., $f_{h}$ with $|h|<1$ ).
(i) If $\int_{\Omega} g(x) d x=0$, then a nontrivial equil. always exists with migration.
(ii) If $\int_{\Omega} g(x) d x \neq 0$, then a nontrivial equil. exists if migration is not too strong (compared to selection), i.e., $\lambda>\lambda^{*}$.

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- Fleming $1975 \mathrm{JMB}(\Delta)$ : variational approach
- Hess \& Senn 1982 Math. Ann. (elliptic $L$ ): indefinite-weight eigenvalue problem with principal eigenvalue $\lambda^{*}(L \varphi+\lambda m(x) \varphi=0)$
- Senn 1983 CPDE (elliptic $L$ ): linearization at $u=0,1$, upper and lower solutions, global bifurcation w.r.t. $\lambda$


## Uniqueness of Nontrivial Equilibrium

Theorem. If $f^{\prime \prime}(u)<0$ in $(0,1)$ (e.g., $f_{h}$ with $|h| \leqslant 1 / 3$ ), then nontrivial equil. (if $\exists$ ) is unique and globally asymptotically stable.

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- Henry 1981 ( $\Delta$ )
- Lou and Nagylaki 2002 (elliptic L)


(i) $\int g=0$

(ii) $\int g<0$

(iii) $\int g>0$


## Nontrivial Equilibrium near Bifurcation.I

Theorem. (i) If $\int_{\Omega} g(x) d x=0$ and $f^{\prime}(0)>0, f^{\prime}(1)<0$, then max. (min.) points of $f$ lead to stable (unstable) branches



- Brown and Lin 1981 ( $\Delta$ with stability); Senn 1983 (elliptic $L$ )


## Nontrivial Equilibrium near Bifurcation.II

Theorem. (ii) If $\int_{\Omega} g(x) d x<0$ and $f^{\prime}(0)>0$, then



- Fleming 1975 ( $\Delta$ ), Senn 1983 (elliptic $L$ )


## Nontrivial Equilibrium near Bifurcation.II

Theorem. (ii) If $\int_{\Omega} g(x) d x<0$ and $f^{\prime}(0)>0$, then



- Fleming 1975 ( $\Delta$ ), Senn 1983 (elliptic $L$ )
(iii) The case $\int_{\Omega} g(x) d x>0$ and $f^{\prime}(1)<0$ is similar.

3. The complexity of the complete dominance case

## The Complete Dominance Case

When allele $A_{2}$ is completely dominant to allele $A_{1}, h=-1$ and

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f_{h}(u)=u(1-u)[1+h-2 h u]=2 u^{2}(1-u) .
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Thus, $\left(\mathrm{MS}_{2}\right)$ becomes

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u_{t}=\Delta u+\lambda g(x) u^{2}(1-u), \quad x \in \Omega, \quad t>0 \tag{CD}
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Difficulties

- degeneracy: $f^{\prime}(0)=0$
- $f$ is unimodal but not concave in $(0,1)$


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Conjecture of Lou-Nagylaki (2002 JDE, 2008 Tutorials in mathematical biosciences IV):

(i) $\int g=0$

(ii) $\int g<0$

(iii) $\int g>0$

## Positive Answers to LN Conjecture



- Existence: Nakashima, Ni, Su 2010 DCDS; Lou, Ni, Su 2010 DCDS
- Uniqueness for $\int g \geqslant 0: \Omega=(-1,1)$, large $\lambda, g(x) \geqslant b_{1}(x)$, Nakashima 2016, 2018 JDE


## Negative Answers to LN Conjecture

For $\Omega=(-1,1)$ and large $\lambda$,

- $\int g<0$ : Nakashima 2020 JDE ( $\exists g$ with 2 pos. nodal domains, $g(x)<b_{2}(x)$, $\exists 8$ equils. )


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- For $\lambda g^{+}-\mu g^{-}, g$ has $m$ pos. domains, $\lambda>\tilde{\lambda}, \mu>\tilde{\mu}(\lambda)$, then $\exists\left(3^{m}-1\right)$ equils. Feltrin, Sovrano 2018 Nonlinearity; Boscaggin, Feltrin, Sovrano 2020 Adv. Nonlinear Stud.


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Fig. 1 in F-S 2018, $\lambda=20, \mu=500, g=\sin (\pi t), \Omega=(0,3)$

- $\int g \geqslant 0$ : Nakashima, Su 2020 JDE ( $\exists g$ with 2 pos. domains, $g(x)<b_{3}(x), 3$ equils.)


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- $\int g \geqslant 0$ : Nakashima, Su 2020 JDE ( $\exists g$ with 2 pos. domains, $g(x)<b_{3}(x), 3$ equils.)



## Some Open Problems

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- Dynamics and euqil. structure of system (SM) for multiple alleles?
(Many open problems in Lou-Nagylaki-Ni 2013 DCDS)

4. Various extensions of migration-selection models

## (MS) + Long-Distance Migration



In Nagylaki 2012a TPB, long-distance migration was approximated by panmixia:

$$
\frac{\partial p_{i}}{\partial t}=\Delta p_{i}+p_{i}\left[r_{i}(x, p)-\bar{r}(x, p)\right]+b\left[\bar{p}_{i}(t)-p_{i}\right], \quad x \in \Omega, \quad t>0
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with zero Neumann b.c., where

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(Nagylaki 2012b TPB; Lou, Nagylaki, Su 2013 JDE; Su, Nagylaki 2015 DCDS; Li, Nakashima, Ni 2017 Eur. J. Appl. Math., etc.)

## (MS) + Long-Distance Migration + Geographical Barrier



Nagylaki (2016 TPB) proposed

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with zero Neumann b.c. on $\partial \Omega$ and transition condition

$$
\begin{equation*}
\nabla_{\nu} p_{i}(x \pm, t)=\gamma_{ \pm}\left[p_{i}(x+, t)-p_{i}(x-, t)\right], \quad x \in \Gamma, \quad t>0 . \tag{TC}
\end{equation*}
$$

Here $\Gamma$ barrier, $\Omega=\Omega_{-} \cup \Gamma \cup \Omega_{+}, \Omega_{-} \cap \Omega_{+}=\emptyset, \nu$ unit normal vector along $\Gamma$ from $\Omega_{-}$to $\Omega_{+}, x \pm$ limit of $x$ as $x \rightarrow \Gamma$ from $\Omega_{ \pm}$, $\gamma_{+}$and $\gamma_{-}$rescaled rightward and leftward transmissivities.

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- Question: Can (TC) be derived by the method of effective boundary conditions? Yes, if $\gamma_{+}=\gamma_{-}$(Li and Wang 2017 Nonlinearity).


## $(\mathrm{MS})+$ Recombination

Locus $\mathcal{A}$ : alleles $A, a$; locus $\mathcal{B}$ : alleles $B, b$ 4 types of gametes: $A B, A b, a B, a b$ Recombination of two loci during meiosis


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Freqs. of gametes $p=\left(p_{1}, \ldots, p_{4}\right) \in \Delta_{4}$ and obey

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\partial_{t} p_{i}=d \Delta p_{i}+\lambda S_{i}(x, p)-\eta_{i} \rho D, \quad x \in \Omega, \quad t>0 \tag{MS+R}
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$D=p_{1} p_{4}-p_{2} p_{3}$ (linkage disequilibrium),
$\eta_{1}=\eta_{4}=-\eta_{2}=-\eta_{3}=1$,
$S_{1}(x, p)=p_{1}\left[\alpha(x)\left(p_{3}+p_{4}\right)+\beta(x)\left(p_{2}+p_{4}\right)\right], \cdots$ (selection)

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(Slatkin 1975 Genetics, Barton 1986 Heredity, Bürger 2017 TPB, Su-Lam-Bürger 2019 JDE)

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- Yuan Lou, The Ohio State Univ. \& Renmin Univ. of China
- Thomas Nagylaki ${ }^{\dagger}$, The Univ. of Chicago
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[^0]:    ${ }^{1}$ Nagylaki 1992, Chap. 4.10

