

EVOLUTION UNDER MULTIALLELIC
MIGRATION-SELECTION MODELS

1. INTRODUCTION

Population genetics: Aim is to infer action of evolutionary forces from observed pattern of genetic variation.

Migration-selection models

- With spatially varying selection, they can
- (i) maintain polymorphism when selection alone cannot;
- (ii) produce stable spatial variation in phenotypes, i.e., clines.

Basic model:

DD: Discrete space, discrete time

Nonlinear difference eqs. Has simple, important special cases.

Approximations:

DC: Discrete space, continuous time

Nonlinear differential eqs. Sometimes more tractable than DD.

CD: Continuous space, discrete time

Not many results. Nonlinear integro-difference eqs.

CC: Diffusion; continuous space, continuous time

Semilinear parabolic system. Many results.

We treat DD model and then DC.

2. FORMULATION (DD)

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Assumptions

- (i) Discrete, nonoverlapping generations.
- (ii) Monoecious, diploid population.
- (iii) Pure viability selection: no fertility differences.
- (iv) K ($< \infty$) panmictic colonies (called demes) exchange adult migrants independently of genotype.
- (v) Neglect mutation and random genetic drift.
- (vi) Single locus with J alleles A_1, \dots, A_J .
- (vii) The genotypic viabilities and the backward migration rates are constant, i.e., time independent.

Notation. Alleles: h, i, j . Demes: k, l, n .

Sets of alleles and demes:

$$i \in \mathcal{I} = \{1, 2, \dots, J\}, \quad k \in \mathcal{K} = \{1, 2, \dots, K\}.$$

Simplex:

$$\Delta_J = \left\{ z \in \mathbb{R}^J : z_i \geq 0 \quad \forall i \in \mathcal{I}, \quad \sum_{j=1}^J z_j = 1 \right\}.$$

$$\Delta_J^K = (\Delta_J)^K, \quad \text{interior} = \text{int} \Delta_J, \quad \text{boundary} = \partial \Delta_J.$$

Gene frequencies:

$p_{i,k}(t)$ = freq. of A_i in zygotes in deme k
in generation t ($= 0, 1, 2, \dots$).

Freq. of A_i in each deme =

$$p_i = (p_{i,1}, \dots, p_{i,K})^T \in [0, 1]^K.$$

Gene freqs. in deme k =

$$p^{(k)} = (p_{1,k}, \dots, p_{J,k})^T \in \Delta_J.$$

All the gene freqs. =

$$p = (p^{(1)T}, \dots, p^{(K)T})^T \in \Delta_J^K.$$

Selection

$w_{ij,k}$ = constant viability of an $A_i A_j$ individual
in deme k .

Viability of A_i -individuals in deme k =

$$w_{i,k}(p^{(k)}) = \sum_j w_{ij,k} p_{j,k}.$$

Mean viability in deme k =

$$\bar{w}_k(p^{(k)}) = \sum_{i,j} w_{ij,k} p_{i,k} p_{j,k}.$$

Migration

m_{kl} = constant probability that an individual in deme k came from deme l .

$M = (m_{kl})$ = backward migration matrix ($K \times K$).

M is stochastic:

$$m_{kl} \geq 0 \quad \forall k, l; \quad \sum_l m_{kl} = 1 \quad \forall k.$$

Recursion

Prime = next generation, i.e., $t+1$.

$$p'_{i,k} = \sum_l m_{kl} p_{i,l} w_{i,l} (p^{(i)}) / \bar{w}_k (p^{(k)}). \quad (2.1)$$

Notation: $\Delta x = x(t+1) - x(t) = x' - x$.

Remarks. $p(t)$ does not always converge as $t \rightarrow \infty$ (E. Abin, personal communication). When does it?

References

L = Lou, N = Nagylaki,

NLT = Nagylaki and Lou (2007).

No Dominance

this means that $\exists v_{i,k} \geq$

$$w_{ij,k} = v_{i,k} + v_{j,k} \quad \forall i, j, k. \quad (2.2)$$

Usually the simplest case, and of much biological interest.

Theorem 2.1 (NL1). Suppose that (2.1)
and (2.2) hold. Then the number
of demes (minus any neutral
demes) is a generic upper bound
on the number of alleles present
at equilibrium.

Remark 2.2. Since $p(t)$ does not always converge, we cannot conclude that "excess" alleles are eliminated.

Remark 2.3. Note that the equilibrium may be stable or unstable.

Remark 2.4. Biological reason for theorem 2.1 is unknown. Discussed later.

3. WEAK MIGRATION (JD)

fix $\omega_{ij,k} \forall i,j,k$.

$$m_{kl} = \delta_{kl} + \epsilon \mu_{kl} \quad \forall k,l, \quad (3.1)$$

where μ_{kl} is fixed $\forall k,l$; δ_{kl} = Kronecker delta; and $\epsilon \rightarrow 0+$.

Pure selection ($\epsilon = 0$):

$$p'_{i,k} = p_{i,k} \omega_{i,j,k}(p^{(k)}) / \bar{\omega}_k(p^{(k)}). \quad (3.2)$$

Assumption

(A3.1). Every equilibrium of (3.2) is hyperbolic.

Theorem 3.1 (NLT). Suppose that (2.1), (3.1), and

(A3.1) hold, all the fitnesses $\omega_{ij,k}$ are fixed,
and $\epsilon > 0$ is sufficiently small.

- The set of equilibria $\Sigma_0 \subset \Delta_J^K$ of (3.2) contains only isolated points, as does the set of equilibria $\Sigma_\epsilon \subset \Delta_J^K$ of (2.1). As $\epsilon \rightarrow 0$, each equilibrium in Σ_ϵ converges to the corresponding equilibrium in Σ_0 .
- In the neighborhood of each asymptotically stable equilibrium point in Σ_0 , there exists exactly one equilibrium point in Σ_ϵ , and it is asymptotically stable. In the neighborhood of each unstable internal (i.e., in $\text{int} \Delta_J^K$) equilibrium point in Σ_0 , there exists exactly one equilibrium point in Σ_ϵ , and it is unstable. In the neighborhood of each unstable boundary (i.e., in $\partial \Delta_J^K$) equilibrium point in Σ_0 , there exists at most one equilibrium point in Σ_ϵ , and if it exists, it is unstable.
- The solution $p(t)$ of (2.1) converges to one of the equilibrium points in Σ_ϵ .

Remark 3.2 (NLT). The mean fitness (by any reasonable definition) can decrease.

Example 3.3 (NLT). Posit intermediate dominance, i.e., the absence of both underdominance and overdominance. Then, without migration, generically some allele is fixed in every deme (NL6a).

$\therefore \exists$ a globally asymptotically stable equilibrium with at most K alleles present.

\therefore Theorem 3.1 \Rightarrow (for suff. weak migration,) generically $p(t)$ converges globally to an equilibrium with exactly the same set of K alleles present.

4. STRONG MIGRATION (DD)

Fix M .

$$w_{ijk} = 1 + \epsilon \tau_{ijk} \quad \forall k, l, \quad (4.1)$$

where τ_{ijk} is fixed $\forall i, j, k$, and $\epsilon \rightarrow 0+$,
Assumption

(A4.1). M is ergodic, i.e., irreducible and aperiodic.

then M has a unique principal left eigenvector $v \in \text{int} \Delta_K \ni$

$$v^T M = v^T. \quad (4.2)$$

Average frequency of A_i :

$$P_i = v^T p_i, \quad P = (P_1, \dots, P_J)^T \in \Delta_J. \quad (4.3)$$

deviations from P :

$$q^{(k)} = p^{(k)} - P_i, \quad (4.4a)$$

$$q^{(k)} = p^{(k)} - P \in \mathbb{R}^J, \quad (4.4b)$$

$$q = (q^{(1)T}, \dots, q^{(K)T})^T \in \mathbb{R}^{JK}. \quad (4.4c)$$

Average selection coefficients

$$A_i A_j: \quad P_{ij} = \sum_k v_k \tau_{ijk}, \quad (4.5a)$$

$$A_i: \quad P_i(P) = \sum_j P_{ij} P_j, \quad (4.5b)$$

$$\text{Pop'n.}: \quad \bar{P}(P) = \sum_{ij} P_{ij} P_i P_j. \quad (4.5c)$$

Panmictic system

$$t = \lfloor \tau / \epsilon \rfloor, \quad \epsilon \rightarrow 0+.$$

$$\frac{dP_i}{d\tau} = P_i [p_i(P) - \bar{p}(P)], \quad (4.6a)$$

$$q = 0. \quad (4.6b)$$

Assumption

(A4.2). Every equilibrium of (4.6a) is hyperbolic.

Theorem 4.1 (NLT). Suppose that (2.1), (4.1), (A4.1), and (A4.2) hold, M is fixed, and $\epsilon > 0$ is sufficiently small.

- (a) The set of equilibria $\Xi_0 \subset \Delta_J^K$ of (4.6) contains only isolated points, as does the set of equilibria $\Xi_\epsilon \subset \Delta_J^K$ of (2.1). As $\epsilon \rightarrow 0$, each equilibrium in Ξ_ϵ converges to the corresponding equilibrium in Ξ_0 .
- (b) In the neighborhood of each equilibrium point in Ξ_0 , there exists exactly one equilibrium point in Ξ_ϵ . The stability of each equilibrium in Ξ_ϵ is the same as that of the corresponding equilibrium in Ξ_0 ; i.e., each pair is either asymptotically stable or unstable.
- (c) The solution $p(t)$ of (2.1) converges to one of the equilibrium points in Ξ_ϵ .

Remark 4.2 (NLT). \exists a smooth, globally geometrically attracting ^(invariant) manifold $\Lambda_\epsilon \ni q = \epsilon \psi(P, \epsilon)$.

$$\Lambda_0 = \{p \in \Delta_J^K : q = 0\}.$$

$\forall k_1$ is the ^{the} geometric rate, $t \geq \tilde{t} = \frac{\ln \epsilon}{\ln k_1} \Rightarrow$

$$q(t) = O(\epsilon).$$

(4.7)

Theorem 4.3 (NLT). Suppose that the assumptions of Theorem 4.1 apply. If P is bounded away from the equilibria of (4.6a) and p is within $O(\epsilon^2)$ of Λ_ϵ , then $\Delta \bar{w}(p) > 0$, where

$$\bar{w}(p) = \sum_k v_k \bar{w}_k(p^{(k)}). \quad (4.8)$$

Remark 4.4 (NLT). If $t \geq 2\tilde{t}$, then p is within $O(\epsilon^2)$ of Λ_ϵ .

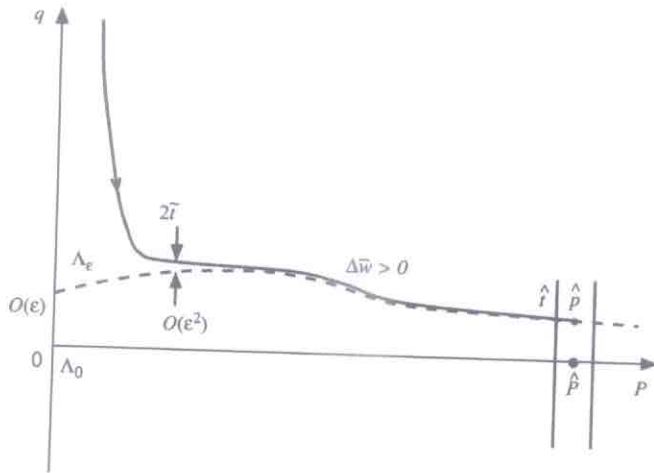
Remark 4.5 (NLT). $\Delta \bar{w} \approx$ genic variance of the panmictic population with allelic freqs. P . Fundamental Theorem of Natural Selection for strong migration.

Remark 4.6 (NLT). Can construct example \exists arbitrarily many alleles are maintained in globally asymptotically stable equilibrium in two demes with partial dominance. Holds for open set of parameters.

Example 4.7 (NLT). Two dielectric lenses.

Convergence time = $\hat{t} = O(1/\epsilon)$.

$$\tilde{t} = \frac{LW\epsilon}{LW_0}$$



5. THE LEVENE MODEL (DD)

c_k = constant proportion of adults in deme k
(after selection, but before migration).

$$c = (c_1, \dots, c_K)^T \in \text{int} \Delta_K.$$

Basic assumption: $m_{kl} = c_l \quad \forall k, l. \quad (5.1)$

An interpretation: selection occurs in each deme, but entire population mates at random, and returns to demes at random.

After one generation, gene freqs. in zygotes are deme independent.

Simplified notation

$p_i(t)$ = freq. of A_i in zygotes in generation t .

$$p = (p_1, \dots, p_I)^T \in \Delta_I.$$

Recursion

$$(5.1), (5.1) \Rightarrow$$

$$p'_i = p_i \sum_k c_k w_{i,j,k}(p) / \bar{w}_k(p), \quad (5.2)$$

where

$$w_{i,j,k}(p) = \sum_j w_{j,j,k} p_j, \quad \bar{w}_k(p) = \sum_{i,j} w_{i,j,k} p_i p_j. \quad (5.3)$$

$$\text{geometric-mean fitness} = \tilde{w}(p) = \prod_k [\bar{w}_k(p)]^{q_k}. \quad (5.4)$$

Important theorem (Li, 1955; Cunnings, 1971; N 1992):

$$\Delta \tilde{w}(p) \geq 0; \quad \Delta \tilde{w}(p) = 0 \text{ only at equilibrium.} \quad (5.5)$$

Conclusion: Generically, the equilibria of (5.2) are isolated, in which case $p(t)$ converges as $t \rightarrow \infty$.

Conjecture: $p(t)$ always converges.

Assumption

(A5.1). deme-independent degree of intermediate dominance: \exists constants $\alpha_{ij} \ni$

$$w_{ij,k} = \alpha_{ij} w_{i,i,k} + \alpha_{ji} w_{j,j,k}, \quad (5.6a)$$

where

$$0 \leq \alpha_{ij} \leq 1, \quad \alpha_{ji} = 1 - \alpha_{ij} \quad \forall i, j, k. \quad (5.6b)$$

This means that even when selection is deme-dependent, allelic interaction is not.

Theorem 5.1 (NL1, N8). Posit (5.2) and (A5.1).
Then the following hold.

- (a) There exists exactly one stable equilibrium
and it is globally attracting.
- (b) If there exists an internal equilibrium,
it is globally asymptotically stable.
- (c) The number of demes (minus any neutral
demes) is a generic upper bound
on the number of alleles present at
equilibrium.

Remark 5.2. What is the biological reason
 for Part (c)? Note that alleles that are
 nowhere the fittest can be maintained
 in ^{globally} asymptotically stable equilibrium (NL66).

6. DISCRETE SPACE, CONTINUOUS TIME (DC)

slow evolution:

$$w_{ij,k} = 1 + \epsilon \tau_{ij,k}, \quad m_{kl} = \delta_{kl} + \epsilon \mu_{kl} \quad \forall i,j,k,l, \quad (6.1)$$

where $\tau_{ij,k}$ and μ_{kl} are fixed $\forall i,j,k,l$ and $\epsilon \rightarrow 0+$.

define $p_{i,k}$, p_i , $p^{(k)}$, and \bar{p} as in general DD model (p. 3).

$$\tau_{i,k}(p^{(k)}) = \sum_j \tau_{ij,k} p_{j,k},$$

$$\bar{\tau}(p^{(k)}) = \sum_{i,j} \tau_{ij,k} p_{i,k} p_{j,k}.$$

$$(6.1) \Rightarrow \mu_{kl} \geq 0 \quad \forall k,l \ni k+l,$$

$$\sum_l \mu_{kl} = 0 \quad \forall k.$$

set $t = \lceil \tau/\epsilon \rceil$, let $\epsilon \rightarrow 0+$, and

rescale:

$$\dot{p}_{i,k} = \sum_l \mu_{kl} p_{i,l} + p_{i,k} [\tau_{i,k}(p^{(k)}) - \bar{\tau}(p^{(k)})], \quad (6.2)$$

where superior dot = d/dt .

7. LOSS OF AN ALLELE (DC)

define $u = (1, \dots, 1)^T \in \mathbb{R}^K$.

(A7.1). M is irreducible.

(A7.2). $\exists i \in J$ and constants $\gamma_{ij} \ni$

$$\gamma_{ij} \geq 0, \quad \gamma_{ii} = 0, \quad \sum_j \gamma_{ij} = 1, \quad (7.1a)$$

$$\sum_j \gamma_{ij} r_{jok}(p^{(k)}) > r_{iok}(p^{(k)}) \quad (7.1b)$$

$\forall k \in \mathcal{K}$ and $\forall p^{(k)} \in \Delta_J \ni p_{i,k} > 0$.

define

$$\Gamma_i = \{j \in J: \gamma_{ij} > 0\}, \quad (7.2a)$$

and posit that

$$p_i(0) > 0, \quad p_j(0) > 0 \quad \forall j \in \Gamma_i. \quad (7.2b)$$

Theorem 7.1 (NLT). If (6.2), (7.2), (A7.1), and (A7.2) hold, then $p_i(t) \rightarrow 0$ as $t \rightarrow \infty$.

Remark 7.2 (NLT). (A7.2) is not necessary.

There are many applications of Th'm. 7.1. We offer

Example 7.3 (NLT). Suppose that there is intermediate dominance and the homozygotes have the same order in every deme:

$$\tau_{ii,k} \geq \tau_{ij,k} \geq \tau_{jj,k} \quad (7.3)$$

$\forall i, j \in J \exists i < j$, and $\forall k \in K$.

Suppose also that

$$\tau_{ii,k} > \tau_{iik} \quad \forall i > 1, \forall k. \quad (7.4)$$

Then $p_i(t) \rightarrow u$ as $t \rightarrow \infty$; i.e., A_1 is ultimately fixed.

Remark 7.4. We do not have conditions for protecting an allele from loss for $J \geq 3$.

8. UNIFORM SELECTION

Despite the fact that most species are spatially distributed, spatial variation in gene frequencies is sometimes not observed. Possible reasons:

- (a) Strong migration almost equalizes the gene freqs. (lect. 4).
- (b) Uniform selection (see below).

8.1. Local Stability (DD)

Uniform selection:

$$(A8.1) \quad w_{ijk} = w_{ij} \quad \forall i, j, k.$$

Recall the pure-selection system

$$p'_{i,k} = p_{i,k} w_i(p^{(k)}) / \bar{w}(p^{(k)}), \quad (8.1)$$

where

$$w_i(p^{(k)}) = \sum_j w_{ij} p_{j,k}, \quad \bar{w}(p^{(k)}) = \sum_{i,j} w_{ij} p_{i,k} p_{j,k}. \quad (8.2)$$

(A8.2) Every equilibrium of (8.1) is hyperbolic.

Theorem 8.1 (NLT). Suppose that (2.1), (A8.1), and (A8.2) hold. If $\hat{p} \in \Delta_J^K$ is an equilibrium of (8.1) $\exists \hat{p}^{(k)} = \hat{p} \in \Delta_J$, independent of $k \forall k \in K$, then \hat{p} is an equilibrium of (2.1), and \hat{p} is either asymptotically stable for both (8.1) and (2.1), or unstable for both systems.

Informal paraphrase: Uniform hyperbolic equilibria persist under migration without change in stability.

8.2. Global Convergence (DC)

Cannot do DD model. Uniform selection:

$$(A8.3) \quad r_{ij,k} = r_{ij} \quad \forall i, j, k.$$

$$r_i(p^{(k)}) = \sum_j r_{ij} p_{j,k}, \quad \bar{r}(p^{(k)}) = \sum_{i,j} r_{ij} p_{i,k} p_{j,k}$$

Pure selection:

$$\dot{p}_{i,k} = p_{i,k} [r_i(p^{(k)}) - \bar{r}(p^{(k)})]. \quad (8.3)$$

(A8.4). The system (8.3) has a uniform, globally asymptotically stable, internal equilibrium point \hat{p} .

(A8.5). $\mu_{kl} > 0 \quad \forall k, l \ni k \neq l$.

Theorem 8.2 (NL7). If $p(0) \in \text{int} \Delta_{\mathcal{I}}^K$ and (6.2), (A8.3), (A8.4), and (A8.5) hold,
then $p(t) \rightarrow \hat{p}$ as $t \rightarrow \infty$.

Remark 8.3. It should be possible to weaken (A8.5).

(A8.6). $\mu = \mu^T$.

Theorem 8.4 (NL7). If $p(0) \in \text{int} \Delta_{\mathcal{I}}^K$ and (6.2), (A8.3), (A8.4), and (A8.6) hold,
then $p(t) \rightarrow \hat{p}$ as $t \rightarrow \infty$.

Conjecture: Theorems 8.2 and 8.4 hold if $\hat{p} \in \partial \Delta_{\mathcal{I}}^K$. Corollaries in NL7 prove this when migration is either weak or strong.

9. TWO ALLELES (DC)

9.1. General Observations

Simplify notation: freq. of $A_1 =$

$$p = (p_1, \dots, p_K)^T \in [0, 1]^K.$$

$$\dot{p}_k = \sum_{\ell} \mu_{k\ell} p_{\ell} + \varphi_k(p_k). \quad (9.1)$$

The following results depend only on the fact that (9.1) is quasi-monotone (Smith, *Monotone Dynamical Systems*, 1995).

(a) If $p^{(1)}(0) > p^{(2)}(0)$, then $p^{(1)}(t) > p^{(2)}(t) \forall t$.

(b) \nexists on attracting periodic orbit.

(c) If $\mu = (\mu_{k\ell})$ is irreducible, then convergence of $p(t)$ as $t \rightarrow \infty$ is generic in the initial data.

(d) If $K=2$, then $p(t)$ converges and the convergence is ultimately monotone.

For migration and selection,

$$\begin{aligned} \dot{p}_k(p_k) = & p_k(1-p_k)[\tau_{12,k} - \tau_{22,k} \\ & + (\tau_{11,k} - 2\tau_{12,k} + \tau_{22,k})p_k]. \end{aligned} \quad (9.2)$$

If $K=3$ and (9.2) holds, an unstable limit cycle can exist (E. Akin, personal communication).

9.2. Two Demes, No Dominance

$k=1,2:$

$$\tau_{11,k} = s_k \neq 0, \quad \tau_{12,k} = 0, \quad \tau_{22,k} = -s_k;$$

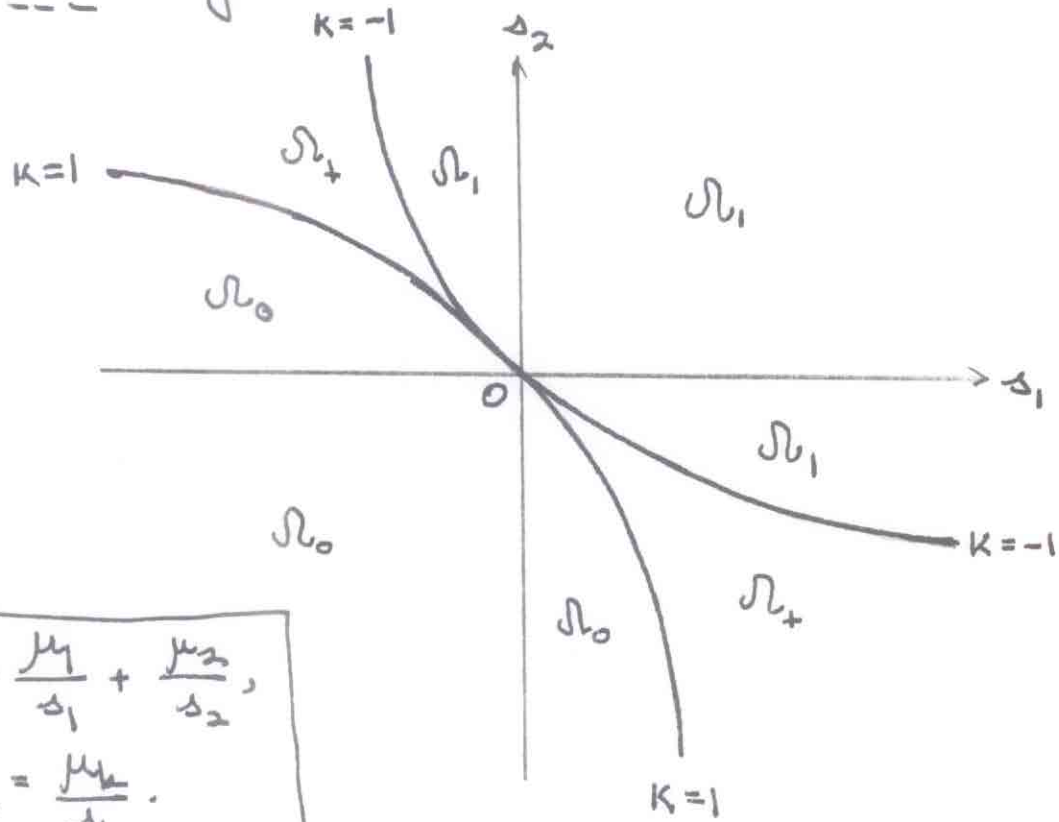
$$\mu_{12} = \mu_1 > 0, \quad \mu_{21} = \mu_2 > 0.$$

$$\begin{cases} \dot{p}_1 = \mu_1(p_2 - p_1) + s_1 p_1(1-p_1), & (9.3a) \end{cases}$$

$$\begin{cases} \dot{p}_2 = \mu_2(p_1 - p_2) + s_2 p_2(1-p_2). & (9.3b) \end{cases}$$

$$\sigma_k = \frac{\mu_k}{s_k}, \quad K = \sigma_1 + \sigma_2.$$

Results (Eyland 1971; NL8)



$$K = \frac{\mu_1}{s_1} + \frac{\mu_2}{s_2},$$

$$\sigma_k = \frac{\mu_k}{s_k}.$$

$$\left\{ \begin{array}{l} \Omega_0 = \{ (s_1, s_2)^T : s_k < 0 \forall k, \text{ or } s_1 s_2 < 0 \text{ and } |K| > 1 \}, \\ \Omega_1 = \{ (s_1, s_2)^T : s_k > 0 \forall k, \text{ or } s_1 s_2 < 0 \text{ and } |K| < -1 \}, \\ \Omega_+ = \{ (s_1, s_2)^T : s_1 s_2 < 0 \text{ and } |K| < 1 \}. \end{array} \right.$$

Ω_0 : $p(t) \rightarrow 0$ as $t \rightarrow \infty$ (A_1 lost).

Ω_1 : $p(t) \rightarrow (1, 1)^T$ as $t \rightarrow \infty$ (A_1 fixed).

Ω_+ : $p(t) \rightarrow \hat{p} > 0$ as $t \rightarrow \infty$ (polymorphism).
If $s_2 < 0 < s_1$, and $|K| < 1$, then

$$\hat{p}_1 = \frac{1}{2}(1+B) - \sigma_1, \quad \hat{p}_2 = \frac{1}{2}(1-B) - \sigma_2,$$

where $B = (1 - 4\sigma_1\sigma_2)^{1/2}$.

9.3. Two Demes, Complete Dominance (N8)

$$\begin{cases} r_{11,1} = \sigma_1, & r_{12,1} = r_{22,1} = 0, & \sigma_1 > 0, \\ r_{11,2} = -\sigma_2, & r_{12,2} = r_{22,2} = 0, & \sigma_2 > 0. \end{cases}$$

$\therefore A_1$ is recessive in both demes, favored in deme 1, and deleterious in deme 2.

$$\mu_{12} = m_1 > 0, \quad \mu_{21} = m_2 > 0.$$

$$\begin{cases} p_1 = p = \text{freq. of } A_1 \text{ in deme 1,} \\ p_2 = q = \text{ " " " " " " 2.} \end{cases}$$

$$\begin{cases} \dot{p} = m_1(q-p) + \sigma_1 p^2(1-p), & (9.4a) \end{cases}$$

$$\begin{cases} \dot{q} = m_2(p-q) - \sigma_2 q^2(1-q). & (9.4b) \end{cases}$$

define

$$r = \frac{\sigma_1}{m_1}, \quad s = \frac{\sigma_2}{m_2}, \quad \theta = \frac{r}{s}. \quad (9.5)$$

Qualitative behavior is fully determined by \underline{r} and $\underline{\theta}$.

Internal equilibria satisfy a polynomial eq. of degree 6.

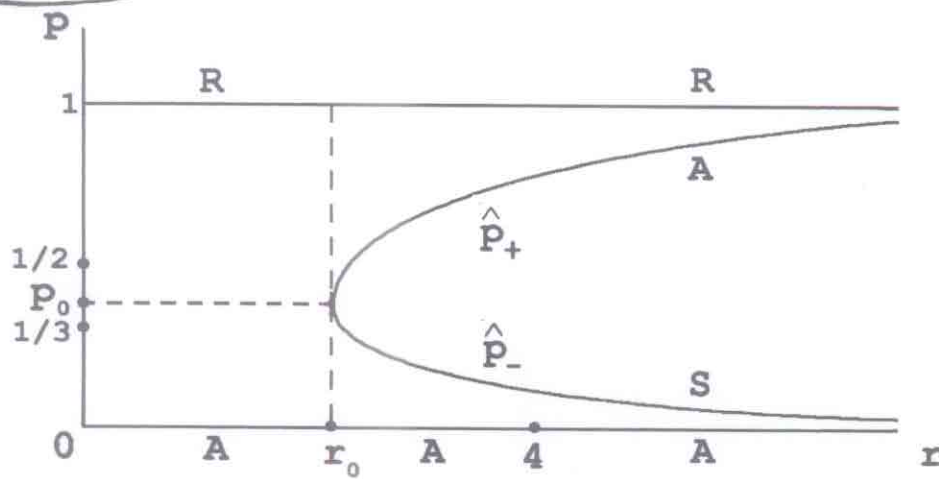
There are 3 cases. Results from N8. At equil., p uniquely determines q .

A = asymptotically stable

R = repelling

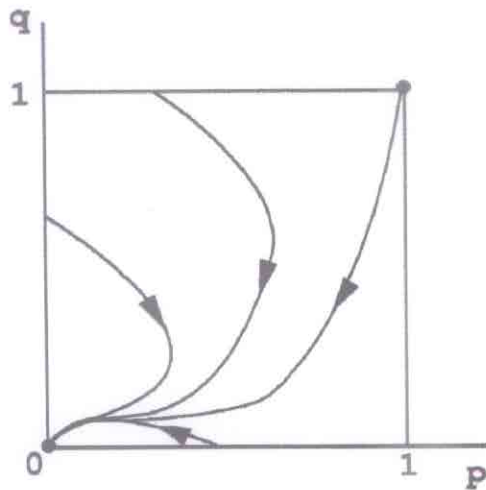
S = saddle point

(a) $\theta < 1$

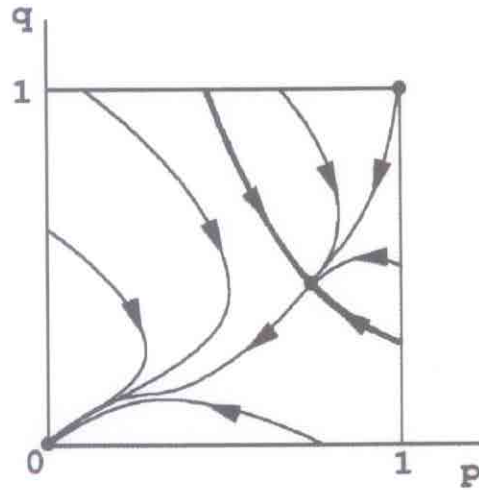


$r_0 = r_0(\theta)$
 $p_0 = p_0(r)$
 $\hat{p}_{\pm} = \hat{p}_{\pm}(r, \theta)$
 saddle-node bifurcation

(a) $\theta < 1$



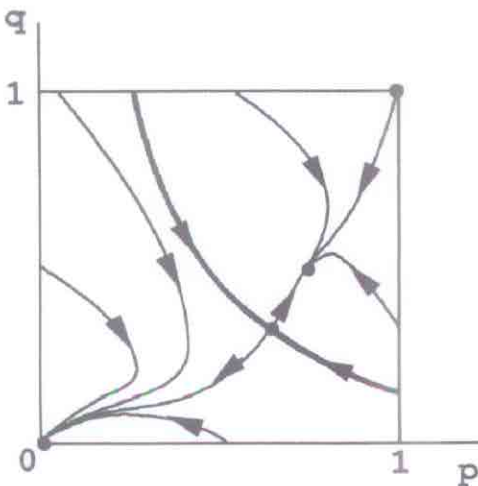
(a₁) $\theta < 1, r < r_0$



(a₂) $\theta < 1, r = r_0$

• = equilibrium

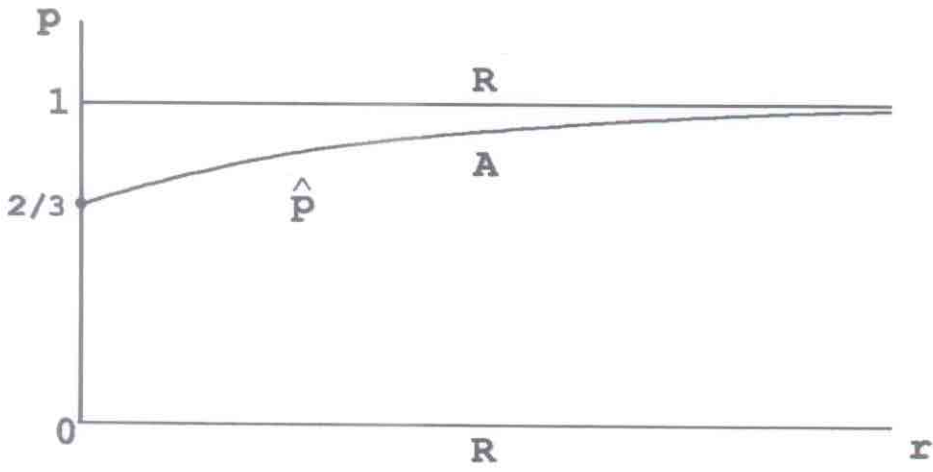
saddle-node $(p_0, q_0)^T$



(a₃) $\theta < 1, r > r_0$

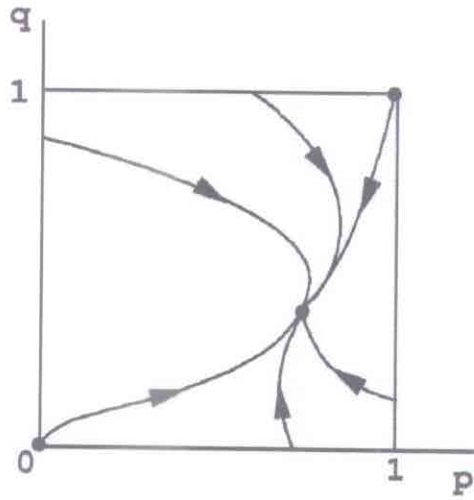
In both cases (a₂) and (a₃),
 \exists 3 other possible phase portraits where the separatrix emanates from different sides. It must separate $(0,0)^T$ and $(1,1)^T$ from each other.

(b) $\theta=1$



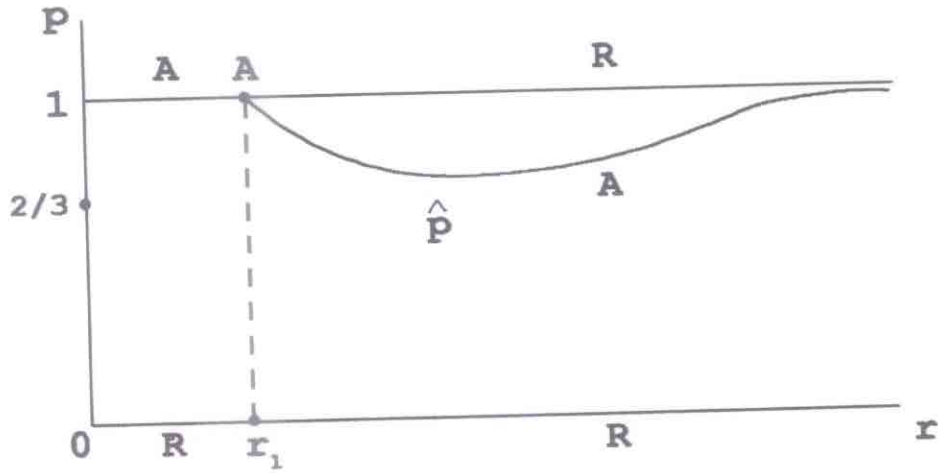
$$\hat{p} = \hat{p}(r, 1).$$

(b) $\theta=1$



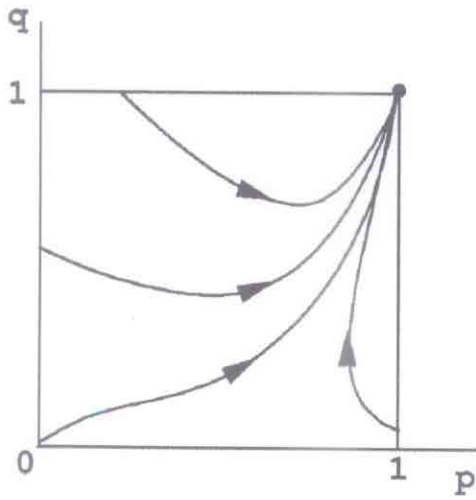
(b) $\theta=1, r>0$

(c) $\theta > 1$

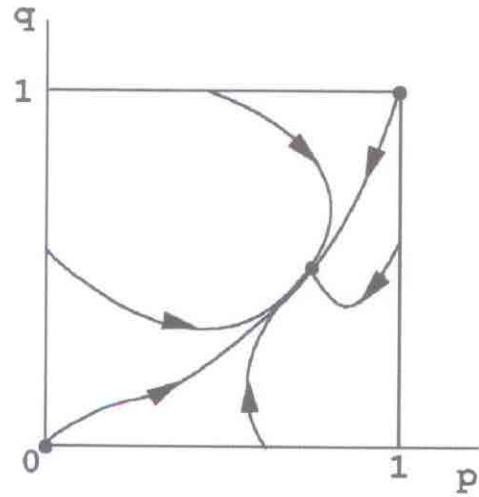


$r_1(\theta) = \theta - 1,$
 $\hat{p} = \hat{p}(r, \theta).$
 transcritical
 bifurcation
 = exchange
 of stability

(c) $\theta > 1$



(c₁) $\theta > 1, r \leq r_1$



(c₂) $\theta > 1, r > r_1$