Asymptotic Behavior of Two Interacting Pioneer/Climax Species

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Background

Assume $f : \mathbb{R}^2 \to \mathbb{R}^2$ with $f \in \mathcal{C}^1$ and

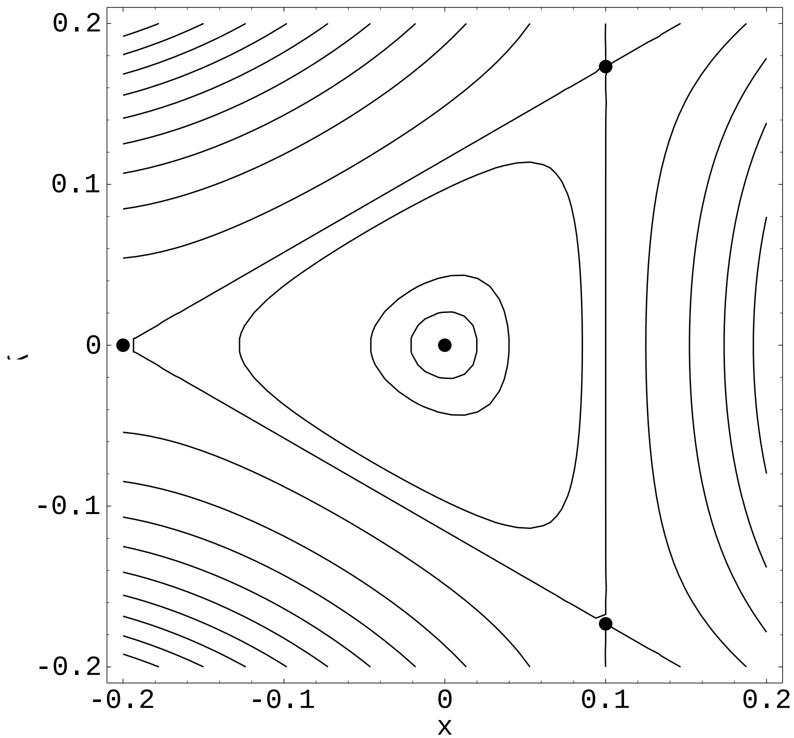
$$\begin{aligned} \frac{dx}{dt} &= f(x) \\ x(0) &= x_0. \end{aligned}$$

If $\phi(t)$ solves this IVP then we define the *orbit of* x to be

$$C(x) = \{\phi(t) | t \in \mathbb{R}\},$$

and the *omega-limit set of* x to be

$$\omega(x) = \bigcap_{t>0} Cl(\bigcup_{s \geq t} \phi(s)).$$



$\mu = 0$ and $\lambda = 0.1$

$$
\begin{aligned}
\frac{dx}{dt} &= -\mu x - \lambda y + xy \\
\frac{dy}{dt} &= \lambda x - \mu y + \frac{1}{2}(x^2 - y^2)
\end{aligned}
$$

Main Tool

Poincaré-Bendixson Theorem: If $\phi(t)$ is a bounded solution to a planar autonomous IVP, and if $\omega(x)$ contains no equilibria, then either

(a) $\phi(t)$ is a periodic solution, or

(b) $\omega(x)$ is a periodic orbit.

Introduction

Asymptotic behavior of 2 competing/cooperating species models and 3 competing Lotka-Volterra–type species models have been studied.

- For 2 competing species, ω-limit sets are single equilibria.
- For 3 competing Lotka-Volterra–type species, ω-limit sets are single equilibria except in cases allowing Hopf bifurcations. In those cases, ω-limit sets may be equilibria, nonconstant periodic orbits, or heteroclinic loops.

References

- Survey article on n-dimensional competitive or cooperative systems — Morris W. Hirsch (1988) “Systems of differential equations which are competitive or cooperative: III. Competing species,” *Nonlinearity*, Vol. 1, pp. 51–71.
- 3-dimensional Lotka-Volterra systems — M.L. Zeeman (1993) “Hopf bifurcations in competitive three-dimensional Lotka–Volterra systems,” *Dynamics and Stability of Systems*, Vol. 8, No. 3, pp. 189–217.

Objectives

Categorize the classes of asymptotic behavior of interactions between 2 pioneer/climax species.

- pioneer/pioneer
- pioneer/climax
- climax/climax

References

- James F. Selgrade and Gene Namkoong (1990) “Stable periodic behavior in a pioneer–climax model,” *Natural Resource Modeling*, Vol. 4, No. 2, pp. 215–227.
- Suzanne Sumner (1994) “Competing Species Models for Pioneer-Climax Forest Dynamical Systems,” *Proceedings of Dynamic Systems and Applications 1*, Vol. 1, Dynamic Publishers, Inc., pp. 351–358,
- Suzanne Sumner (1996) “Hopf Bifurcation in Pioneer-Climax Competing Species Models,” *Mathematical Biosciences*, Vol. 137, pp. 1–24.
- Suzanne Sumner (1996) “Hopf Bifurcation in Competing Species Models with Linear and Quadratic Fitnesses,” *Proceedings of Dynamic Systems and Applications 2*, Vol. 2, Dynamic Publishers, Inc., pp. 535–542.

Pioneer/Climax Interactions

Mathematical model:

(1)
$$\begin{aligned}\frac{dx_1}{dt} &= x_1 f_1(c_{11}x_1 + c_{12}x_2)\\ \frac{dx_2}{dt} &= x_2 f_2(c_{21}x_1 + c_{22}x_2)\end{aligned}$$

where $c_{ij} \geq 0$.

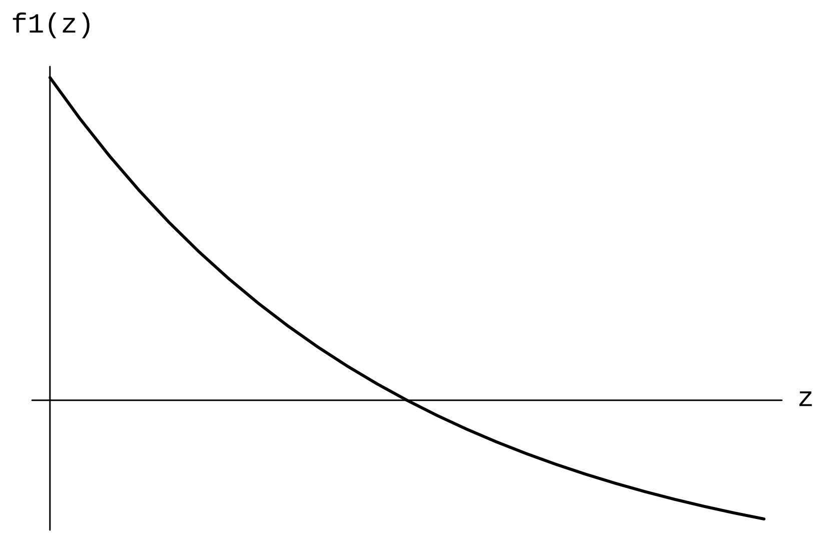
- f_i is called the *per capita fitness function*.
- $C = (c_{ij})_{i,j=1}^2$ is called the *interaction matrix*.

Rationale

Note:

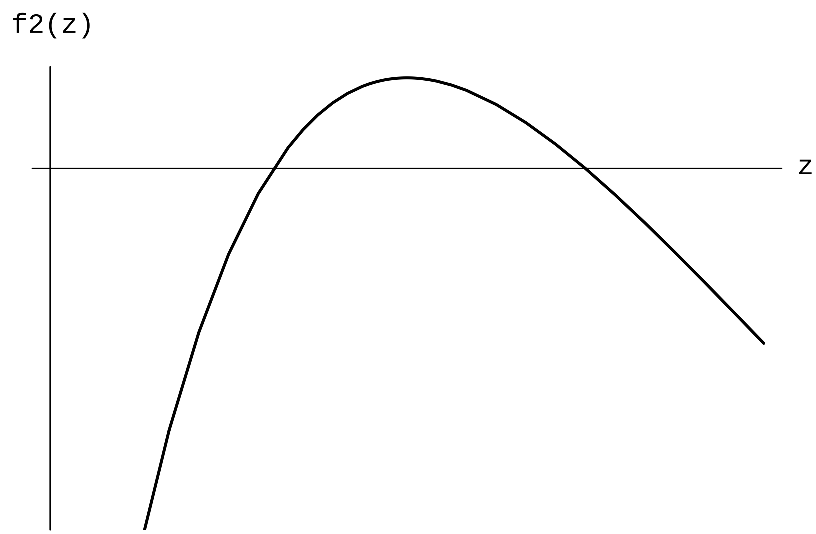
- Choosing fitness functions in this way separates a species' response to weighted density from its response to individual species' densities.
- Permits easy analysis of the system's nullclines.

Pioneer Fitness Functions



Pioneer: $f_i \in \mathcal{C}^1$, monotonically decreasing, $f_i(0) > 0$, there exists a (unique) $z > 0$ such that $f_i(z) = 0$ and $f_i'(z) < 0$.

Climax Fitness Functions



Climax: $f_j \in \mathcal{C}^1$, $f_j(0) < 0$, there exist two roots $0 < z_+ < z_-$ with $f_j'(z_-) < 0 < f_j'(z_+)$.

Classification Procedure

- Rescale variables in model so that $c_{12} = c_{21} = 1$.

(2)
$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(c_{11}x_1 + x_2) \\ \frac{dx_2}{dt} &= x_2 f_2(x_1 + c_{22}x_2) \end{aligned}$$

- If f_1 and f_2 are both pioneer fitnesses, pure competition results.
- If f_1 is a pioneer fitness and f_2 is a climax fitness, adapt the approach used by Zeeman (1993) on Lotka-Volterra models.

Note: Zeeman (1993) used the idea of equivalence classes of vector fields described by algebraic invariants.

Equivalence Classes

PC denotes the set of $\mathcal{C}^1$ vector fields on $\mathbb{R}^2_+$ such that if $F \in PC$ then $F_1(x) = x_1 f_1(c_{11}x_1 + x_2)$ and $f_1(z)$ is a pioneer fitness function, while $F_2(x) = x_2 f_2(x_1 + c_{22}x_2)$ and $f_2(z)$ is a climax fitness function.

Definition: $F, G \in PC$ are said to be *topologically equivalent* if there is a homeomorphism of $\mathbb{R}^2_+$ which maps the orbits of F onto the orbits of G while preserving orientation.

Definition: $F \in PC$ is *structurally stable* provided it has an open neighborhood of topological equivalents.

Nullclines

Non-axial nullclines are lines of the form

$$c_{ii}x_i + x_j = z_i, \quad i \neq j.$$

- x_i intercept has x_i coordinate $z_i/c_{ii} > 0$ and is an equilibrium point of (2).
- x_j intercept has x_j coordinate $z_i > 0$ and in general is not an equilibrium point.

The *nullcline configuration* of a vector field is determined by

$$\operatorname{sgn}\left(\frac{z_1}{c_{11}} - z_{2+}\right), \quad \operatorname{sgn}\left(\frac{z_1}{c_{11}} - z_{2-}\right), \quad \operatorname{sgn}\left(\frac{z_{2+}}{c_{22}} - z_1\right), \quad \operatorname{sgn}\left(\frac{z_{2-}}{c_{22}} - z_1\right).$$

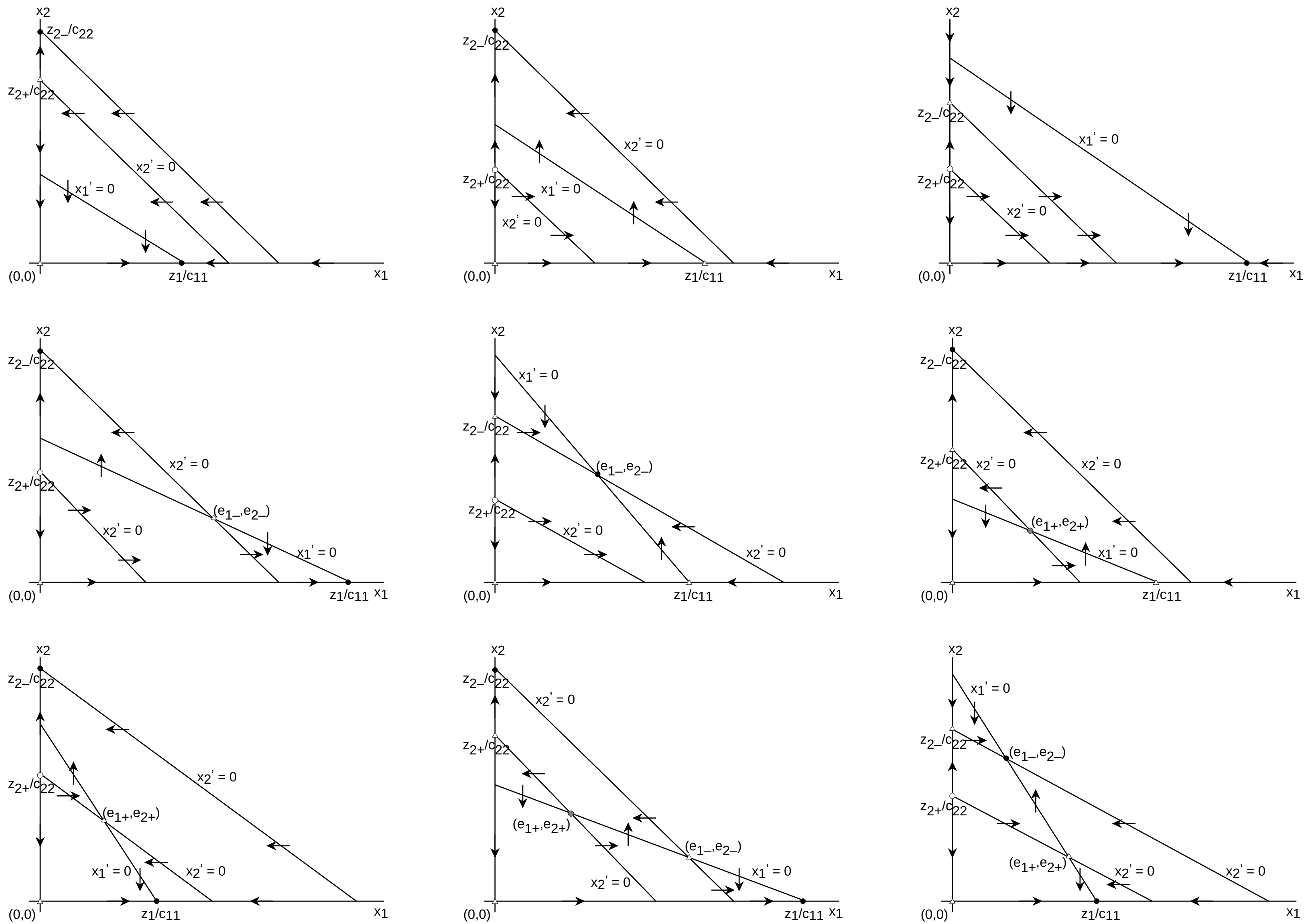
Note: Coordinate axes are invariant.
Note: Nullcline configuration is determined by the relative placement of the axial intercepts of the non-axial nullclines.

Nullcline Equivalence

Definition: $F, G \in PC$ are *nullcline equivalent* if they have the same nullcline configuration.

Definition: $F \in PC$ is *nullcline stable* provided it has an open neighborhood of nullcline equivalents.

Proposition 1 *There are nine stable nullcline classes of* PC *and they have open dense union in* PC*.*


x2
z2–/c22
z2+/c22
x2' = 0
x1' = 0
(0,0)
z1/c11
x1
x2
z2–/c22
x2' = 0
z2+/c22
x1' = 0
x2' = 0
(0,0)
z1/c11
x1
x2
x1' = 0
z2–/c22
z2+/c22
x2' = 0
(0,0)
z1/c11
x1
x2
z2–/c22
x2' = 0
z2+/c22
(e1–,e2–)
x2' = 0
x1' = 0
(0,0)
z1/c11
x1
x2
x1' = 0
z2–/c22
(e1–,e2–)
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x2' = 0
x2' = 0
(0,0)
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x2
z2–/c22
z2+/c22
x2' = 0
x2' = 0
(e1+,e2+)
x1' = 0
(0,0)
z1/c11
x1
x2
z2–/c22
z2+/c22
x2' = 0
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x1
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x1' = 0
z2–/c22
(e1–,e2–)
z2+/c22
(e1+,e2+)
x2' = 0
x2' = 0
(0,0)
z1/c11
x1

Notes

- 3 classes with no interior fixed points
- 4 classes with 1 interior fixed point
- 2 classes with 2 interior fixed points
- In unbounded region outside of nullclines the model is that of competition and the system is monotone by Kamke's comparison principle. Hence the system is *dissipative*.

Nullcline Classes

$\frac{z_1}{c_{11}} - z_{2+}$	$\frac{z_1}{c_{11}} - z_{2-}$	$\frac{z_{2+}}{c_{22}} - z_1$	$\frac{z_{2-}}{c_{22}} - z_1$	$\det C$
$-$	$-$	$+$	$+$	$\pm$
$+$	$-$	$-$	$+$	$\pm$
$+$	$+$	$-$	$-$	$\pm$
$+$	$+$	$-$	$+$	$-$
$+$	$-$	$-$	$-$	$+$
$+$	$-$	$+$	$+$	$-$
$-$	$-$	$-$	$+$	$+$
$+$	$+$	$+$	$+$	$-$
$-$	$-$	$-$	$-$	$+$

Axial Equilibria

Fixed Point	Eigenvalues	Eigenvectors
$(0,0)$	$\lambda_1 = f_1(0)$ $\lambda_2 = f_2(0)$	$\Lambda_1 = (1,0)^*$ $\Lambda_2 = (0,1)^*$
$(\frac{z_1}{c_{11}}, 0)$	$\lambda_1 = f_2(\frac{z_1}{c_{11}})$ $\lambda_2 = z_1 f_1'(z_1)$	$\Lambda_1 = (\frac{z_1 f_1'(z_1)}{c_{11}(f_2(\frac{z_1}{c_{11}}) - z_1 f_1'(z_1))}, 1)^*$ $\Lambda_2 = (1,0)^*$
$(0, \frac{z_{2\pm}}{c_{22}})$	$\lambda_1 = f_1(\frac{z_{2\pm}}{c_{22}})$ $\lambda_2 = z_{2\pm} f_2'(z_{2\pm})$	$\Lambda_1 = (\frac{c_{22}(f_1(\frac{z_{2\pm}}{c_{22}}) - z_{2\pm} f_2'(z_{2\pm}))}{z_{2\pm} f_2'(z_{2\pm})}, 1)^*$ $\Lambda_2 = (0,1)^*$

Notes

- Origin is always a saddle point with stable manifold along the climax axis and unstable manifold along the pioneer axis.
- No orbit remains in region near origin for all time. Orbits cross any vertical line near the origin transversely.
- Stability of $(\frac{z_1}{c_{11}}, 0)$ and $(0, \frac{z_{2\pm}}{c_{22}})$ are determined by the algebraic invariants.

Interior Equilibria

(3) $$(e_1, e_2) = \left(\frac{-c_{22}(\frac{z_2}{c_{22}} - z_1)}{\det C}, \frac{-c_{11}(\frac{z_1}{c_{11}} - z_2)}{\det C}\right)$$

- If (e_1, e_2) lies at the intersection of nullclines where

  $$f_1'(z_1) f_2'(z_2) > 0$$

  then this fixed point behaves like an interior equilibrium of a competitive or cooperative system.
- The eigenvalues and eigenvectors of the linearized system indicate the stability properties of the interior equilibria.

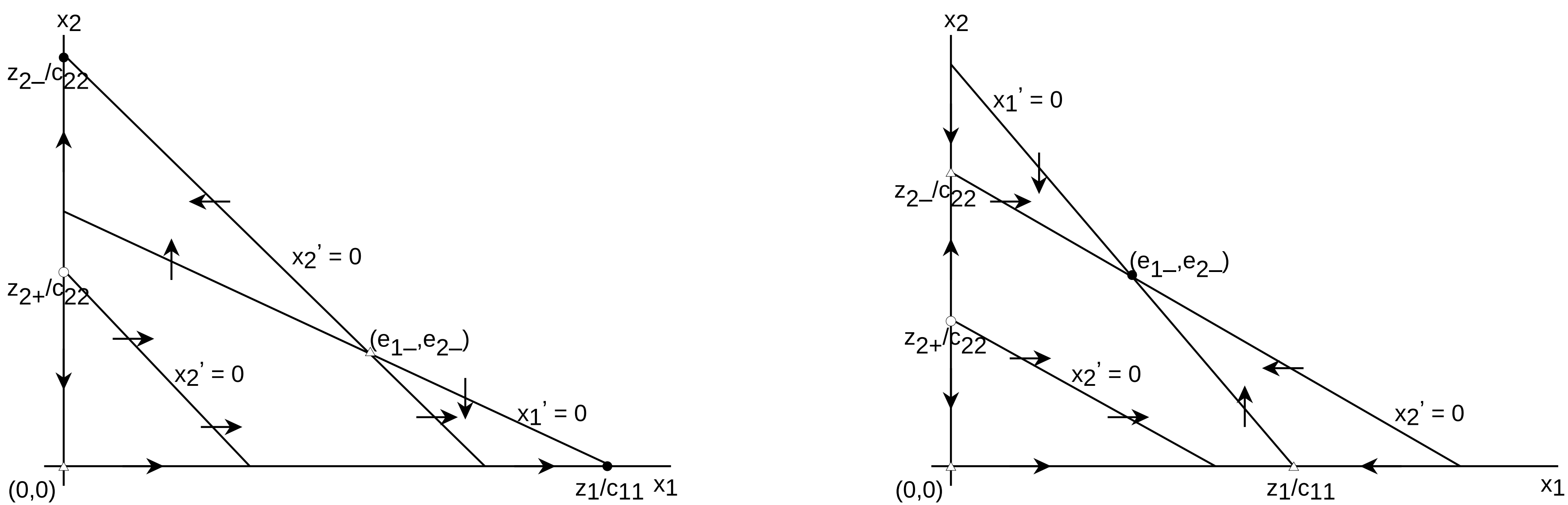
Cases of $f_1'(z_1)f_2'(z_2) > 0$

Proposition 2 *If* (e_1, e_2) *lies at the intersection of nullclines where* $f_i'(z_i) < 0$ *for* $i = 1, 2$ *and if this is the only non-axial fixed point, then the region in* $\mathbb{R}^2_+$ *between these nullclines is positively invariant.*

proof: (Briefly) On a nullcline for species i,

$$\frac{dx_j}{dt} > 0 \Longleftrightarrow (x_i - e_i)(\det C) > 0.$$

Stability of the unique interior fixed point is determined by the stability of its neighboring axial fixed points.



Remark: A similar result holds for a unique interior equilibrium lying at the intersection of nullclines where $f_i'(z_i) > 0$ for $i = 1, 2$.

Hopf Bifurcations

Characteristic polynomial of $DF(e_1, e_2)$:

$$\lambda^2 - (\operatorname{tr} DF(e_1, e_2))\lambda + \det DF(e_1, e_2)$$

where

$$\begin{aligned}
\operatorname{tr} DF(e_1, e_2) &= \frac{-c_{11}c_{22}}{\det C}\Big((\frac{z_2}{c_{22}} - z_1)f_1'(z_1) + (\frac{z_1}{c_{11}} - z_2)f_2'(z_2)\Big) \\
\det DF(e_1, e_2) &= \frac{c_{11}c_{22}}{\det C}(\frac{z_1}{c_{11}} - z_2)(\frac{z_2}{c_{22}} - z_1)f_1'(z_1)f_2'(z_2)
\end{aligned}$$

Lemma 3 *A necessary condition for a Hopf bifurcation to occur about an interior equilibrium* (e_1, e_2) *is that* (e_1, e_2) *lie at the intersection of nullclines where* $f_1'(z_1)f_2'(z_2) < 0$*.*

Lemma 4 *If* $\det C > 0$ *then no Hopf bifurcation can occur around any interior equilibrium.*

Eigenvalues

- For Hopf bifurcations eigenvalues are a complex conjugate pair.
- $\operatorname{tr} DF(e_1, e_2)$ is the sum of the eigenvalues of the system.
- $\det DF(e_1, e_2)$ is the product of the eigenvalues of the system.

Bifurcation Values

$\operatorname{tr} DF(e_1, e_2) = 0$ and $\det DF(e_1, e_2) > 0$ when

$$\hat{c}_{ii} = \frac{z_i f_j'(z_j)}{z_j f_j'(z_j) - (\frac{z_j}{c_{jj}} - z_i) f_i'(z_i)},$$

for $i = 1, 2$ and $i \neq j$. Under these conditions

$$\frac{d\alpha}{dc_{ii}}\bigg|_{\hat{c}_{ii}} = \frac{c_{jj}\Big(z_j f_j'(z_j) - (\frac{z_j}{c_{jj}} - z_i) f_i'(z_i)\Big)^2}{2(\frac{z_j}{c_{jj}} - z_i)(f_i'(z_i) - c_{jj} f_j'(z_j))} \neq 0.$$

Note: α is the real part of the eigenvalue.

Main Result

Theorem 5 *If $F \in PC$ the ω-limit sets of all orbits are single equilibria except in cases which permit a Hopf bifurcation.*

Remark: Seven of the 9 stable nullcline classes coincide with stable topological classes.

Stability Summary

$(\frac{z_1}{c_{11}}, 0)$	$(0, \frac{z_{2+}}{c_{22}})$	$(0, \frac{z_{2-}}{c_{22}})$	(e_{1+}, e_{2+})	(e_{1-}, e_{2-})
sink	saddle	sink		
saddle	source	sink		
sink	source	saddle		
sink	source	sink		saddle
saddle	source	saddle		sink
saddle	saddle	sink	Hopf	
sink	source	sink	saddle	
sink	saddle	sink	Hopf	saddle
sink	source	saddle	saddle	sink

Future

- Details of the climax/climax interaction (18 stable nullcline classes exploiting symmetry).
- Generalize procedure to any fitness function $f(z)$, having non-degenerate roots ($f(z) = 0$ and $f'(z) \neq 0$).
- Extend procedure to interactions of 3 pioneer and climax species.