

# Evolutionary branching in the Adaptive Dynamics framework

Theory and applications to technological change

# What does the theory of adaptive dynamics study?

---

# The origin of diversity

---

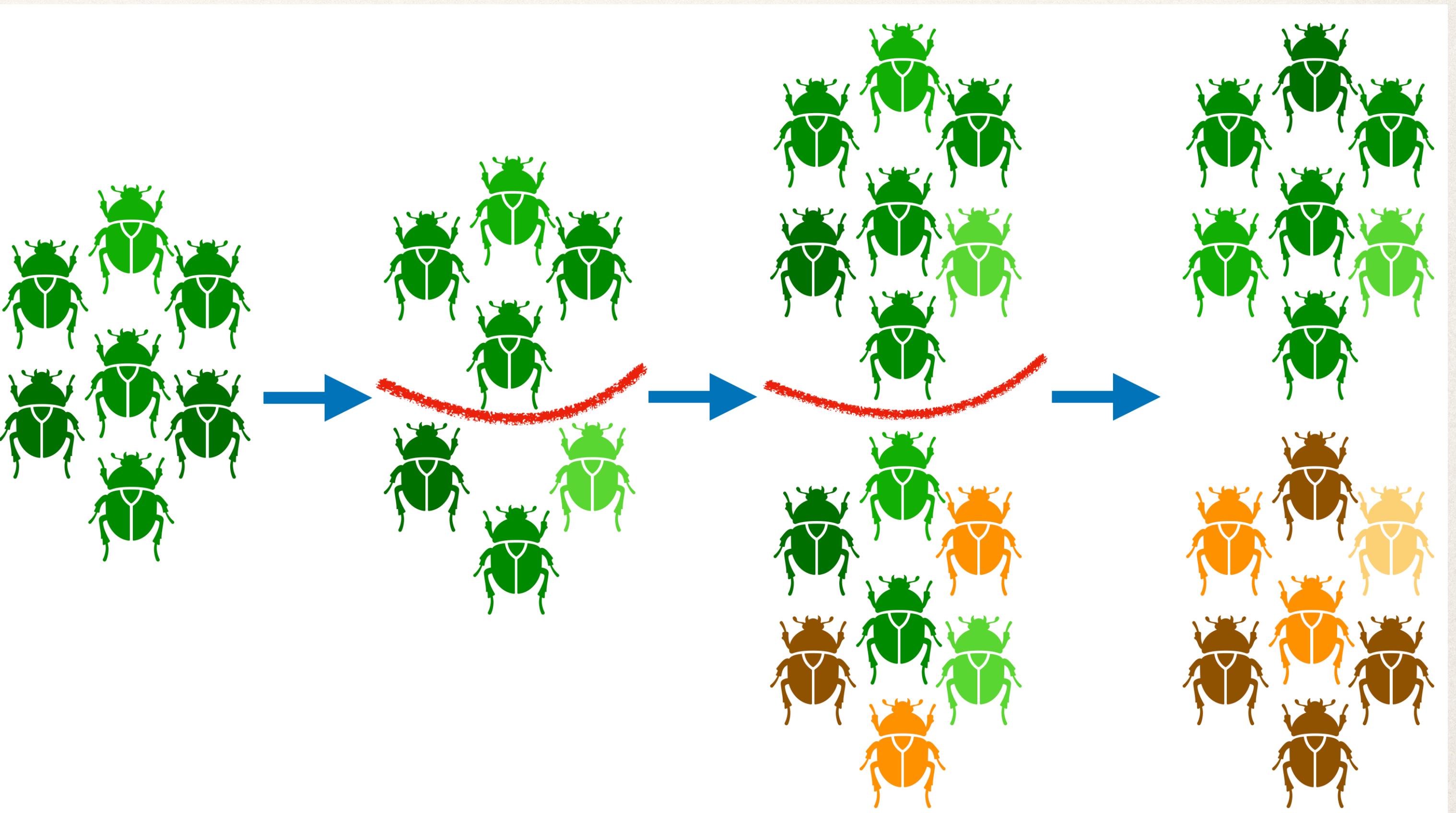
The formation of new species, called **speciation**, is one of the central themes of evolutionary theory. It occurs through the **genetic and phenotypic divergence** of populations of the same species that adapt to different environmental niches in the same or different habitats.

- ❖ **Parapatric speciation:** two populations evolve towards geographical isolation by exploiting different environmental niches of contiguous habitats.
- ❖ **Allopatric speciation:** two populations are separated geographically by natural or artificial barriers.

# The origin of diversity

**Allopatric speciation:** Different selection pressures and different genetic derivations can act in different environments, isolated populations can eventually become separate species.

Geographic isolation is an exogenous cause of speciation rather than an evolutionary consequence.



# The origin of diversity

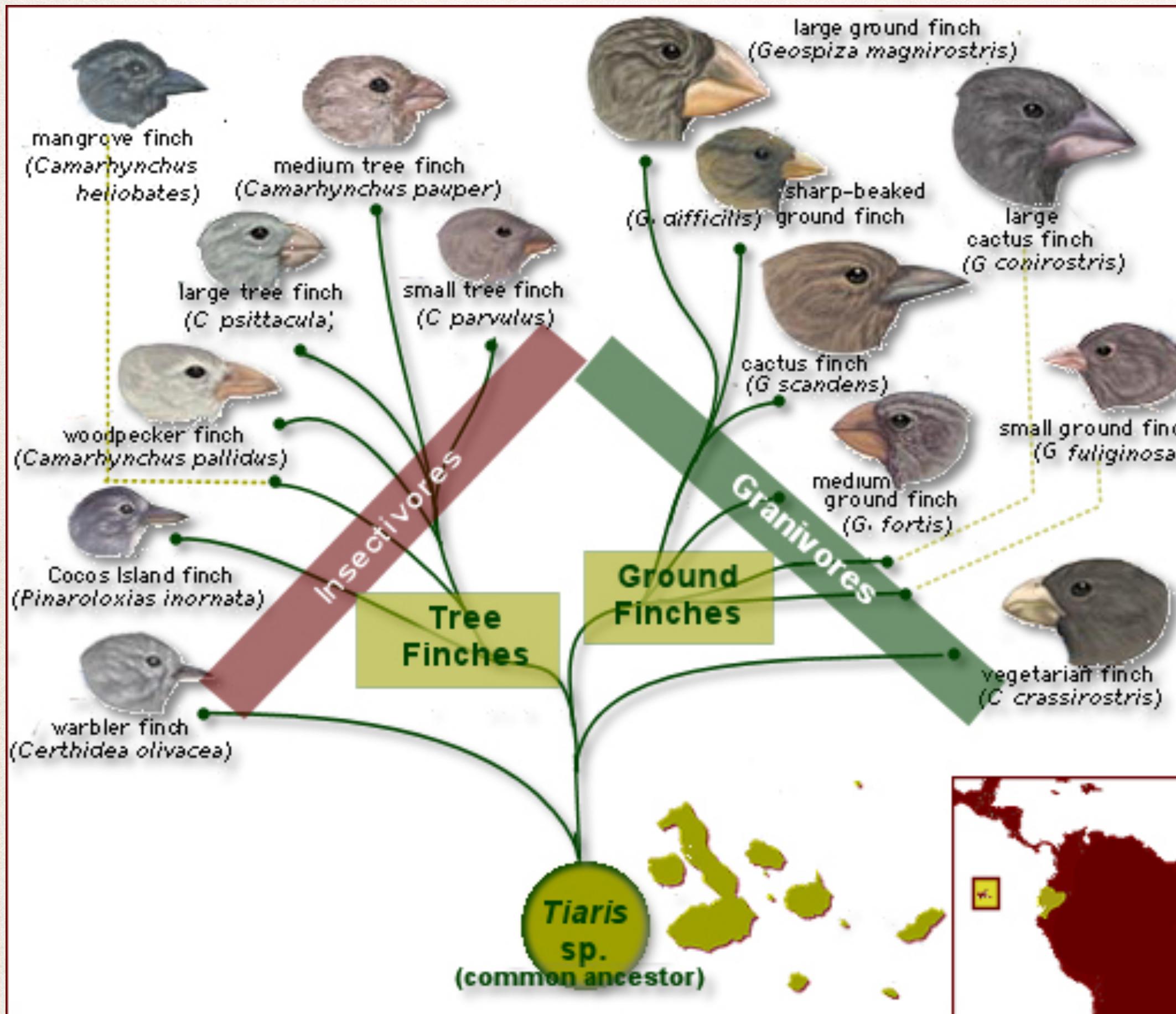
---

- ❖ Sympatric speciation: considers populations in the same geographical location.

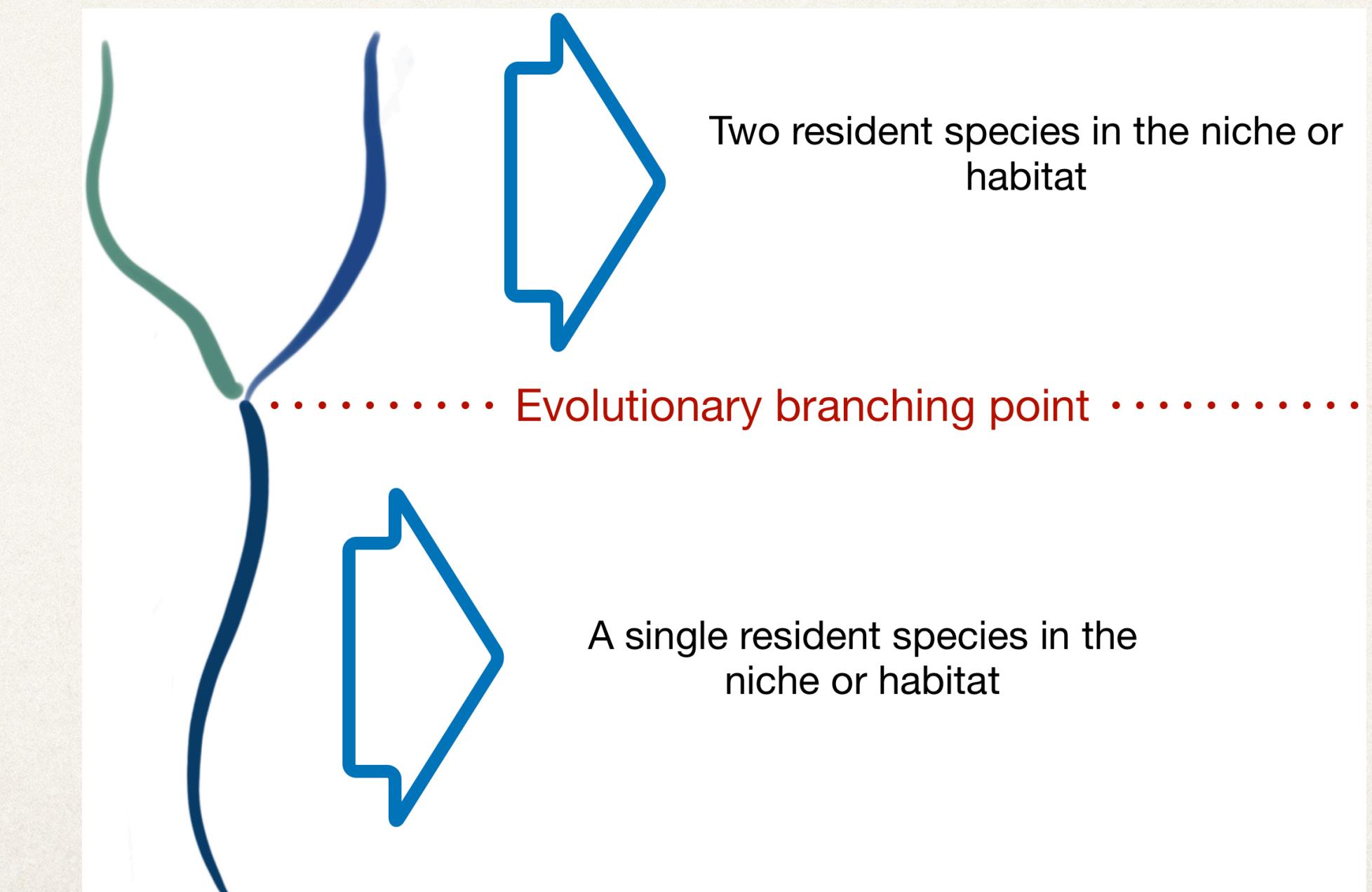
**Key ingredient (disruptive selection): it is the selection pressure favoring extreme characteristics on average characteristics**

It can result, for example, from competition for alternative environmental niches, where being a specialist can be advantageous with respect to being a generalist.

# The origin of diversity



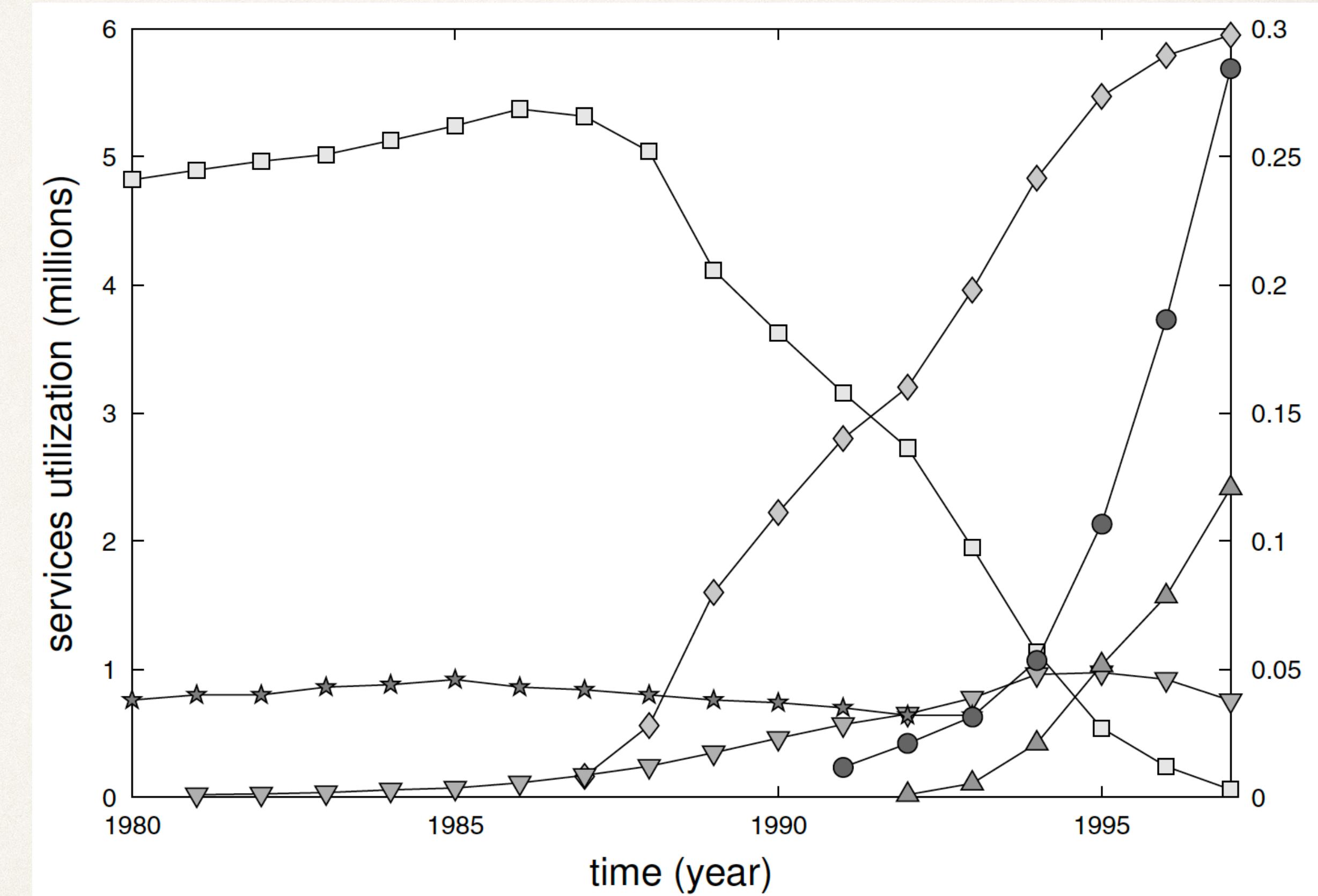
**Sympatric speciation:** The population is divided into two initially similar resident groups, which then diverge following separate evolutionary paths (branches), each driven by their own mutations, experiencing what is called **evolutionary branching**.



# Social and Technological Origin of Diversity

The arrival of digital telephones has been a successful innovation that has led to the replacement of analog telephones

Use of telecommunication services in Switzerland. **Square:** analog phones. **Diamonds:** digital phones. **Triangle below:** subscribers to analogue mobile telephony, **Triangle above:** subscribers to digital mobile telephony. **Stars:** public pay phones. **Circles:** internet host.



# What does the theory of adaptive dynamics study?

---

- ❖ Is a theoretical background originating in evolutionary biology that links demographic (**market**) dynamics to evolutionary changes.
- ❖ It allows for describing long-term evolutionary dynamics when **considering innovations as small and rare events**.
- ❖ It focuses on the long-term evolutionary dynamics of adaptive (quantitative) attributes and **ignores genetic details** through the use of **asexual models**.
- ❖ It considers interactions as the evolutionary driving force and takes into account the feedback between evolutionary change and the forces of selection that agents experience.

Dercole, F., & Rinaldi, S. (2008). *Analysis of evolutionary processes: the adaptive dynamics approach and its applications*. Princeton University Press.

Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of mathematical biology*, 34(5-6), 579-612.

Geritz, S. A., Mesze, G., & Metz, J. A. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary ecology*, 12(1), 35-57.

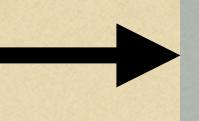
Geritz, S. A., Metz, J. A., Kisdi, É., & Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Physical Review Letters*, 78(10), 2024.

# Brief theory: Mathematical model for evolutionary competition

---

Established-Innovative Model

$$\begin{cases} \dot{n}_1 = n_1 g(n_1, n_2, \mathbf{N}, x_1, x_2, x_1) \\ \dot{n}_2 = n_2 g(n_2, n_1, \mathbf{N}, x_2, x_1, x_2) \\ \dot{\mathbf{N}} = \mathbf{G}(n_1, n_2, \mathbf{N}, x_1, x_2) \end{cases}$$



Invasion equilibrium

$$E_i = (\bar{n}_1(x_1, x_2), 0, \bar{\mathbf{N}}(x_1, x_2))$$

Local stability analysis

Before innovation  
 $n_2 = 0$

Established Model

$$\begin{cases} \dot{n}_1 = n_1 g(n_1, 0, \mathbf{N}, x_1, \cdot, x_1) \\ \dot{\mathbf{N}} = \mathbf{G}(n_1, 0, \mathbf{N}, x_1, \cdot) \end{cases}$$

Local stability analysis

Market at equilibrium  
 $E_s = (\bar{n}_1(x_1), \bar{\mathbf{N}}(x_1))$   
LAS by assumption

Market timescale

Invasion conditions - Selection gradient

$$\begin{cases} \frac{\partial \lambda}{\partial x_2}(x_1, x_1) > 0, & x_2 > x_1 \\ \frac{\partial \lambda}{\partial x_2}(x_1, x_1) < 0, & x_2 < x_1 \end{cases}$$

Stochastic Process

- Branching Point (BP): if CC and DC
- Terminal Point (TP): if CC or DC fail
- Bifurcation Branching Point (BBP): boundary region between BP and TP

Evolutionary Dynamics

Coexistence Condition - CC

$$\frac{\partial^2 \lambda}{\partial x_1 \partial x_2}(\bar{x}, \bar{x}) < 0$$

Divergence Condition - DC

$$\frac{\partial^2 \lambda}{\partial x_2^2}(\bar{x}, \bar{x}) > 0$$

Evolutionary stability  
 $f'(\bar{x}) < 0$

Canonical Equation of Adaptive Dynamics

$$\dot{x} = \frac{1}{2} \mu(x) \sigma^2(x) \bar{n}_1(x_1) \frac{\partial \lambda}{\partial x_2}(x_1, x_1) = f(x)$$

Evolutionary timescale

# Application 1

---

Hindawi  
Mathematical Problems in Engineering  
Volume 2018, Article ID 9181636, 15 pages  
<https://doi.org/10.1155/2018/9181636>



*Research Article*

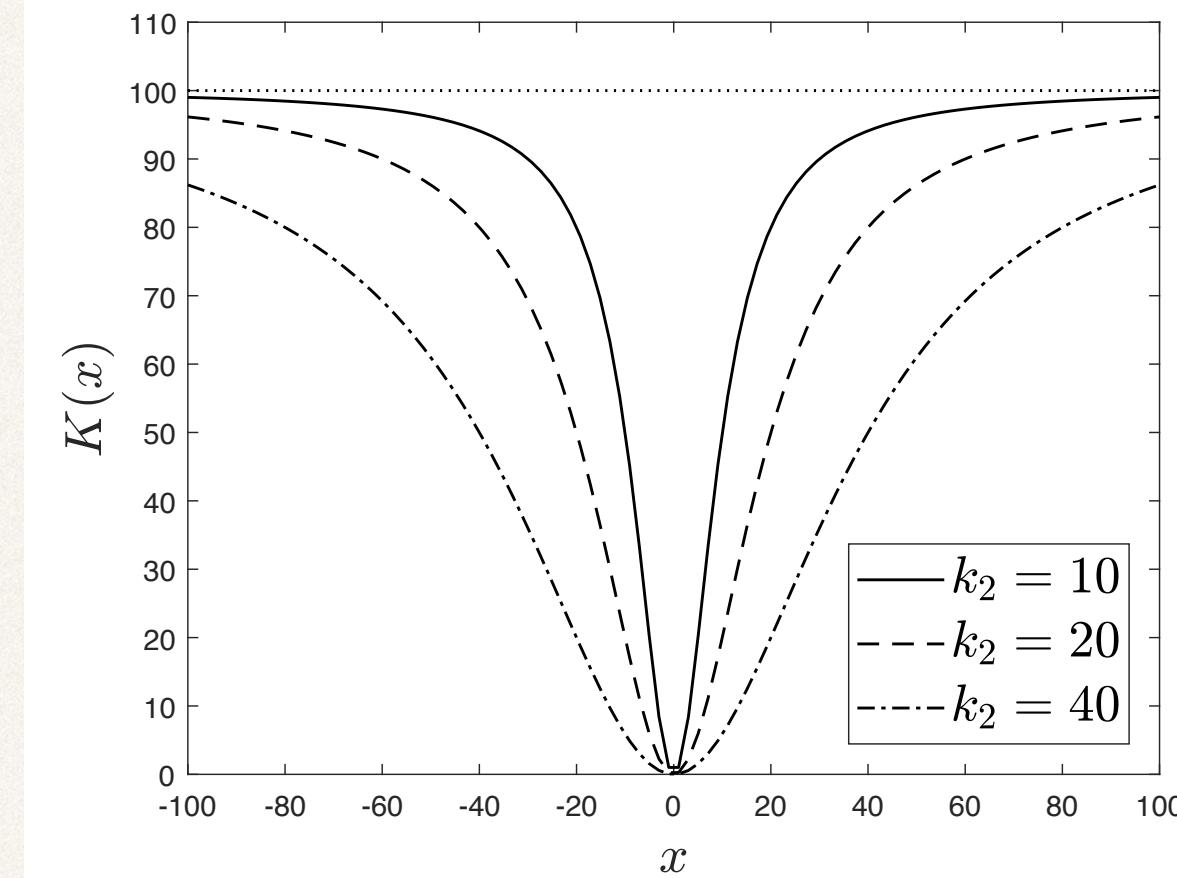
## **Conditions on the Energy Market Diversification from Adaptive Dynamics**

**Hernán Darío Toro-Zapata,<sup>1</sup> Gerard Olivar-Tost<sup>2</sup> and Fabio Dercole<sup>3</sup>**

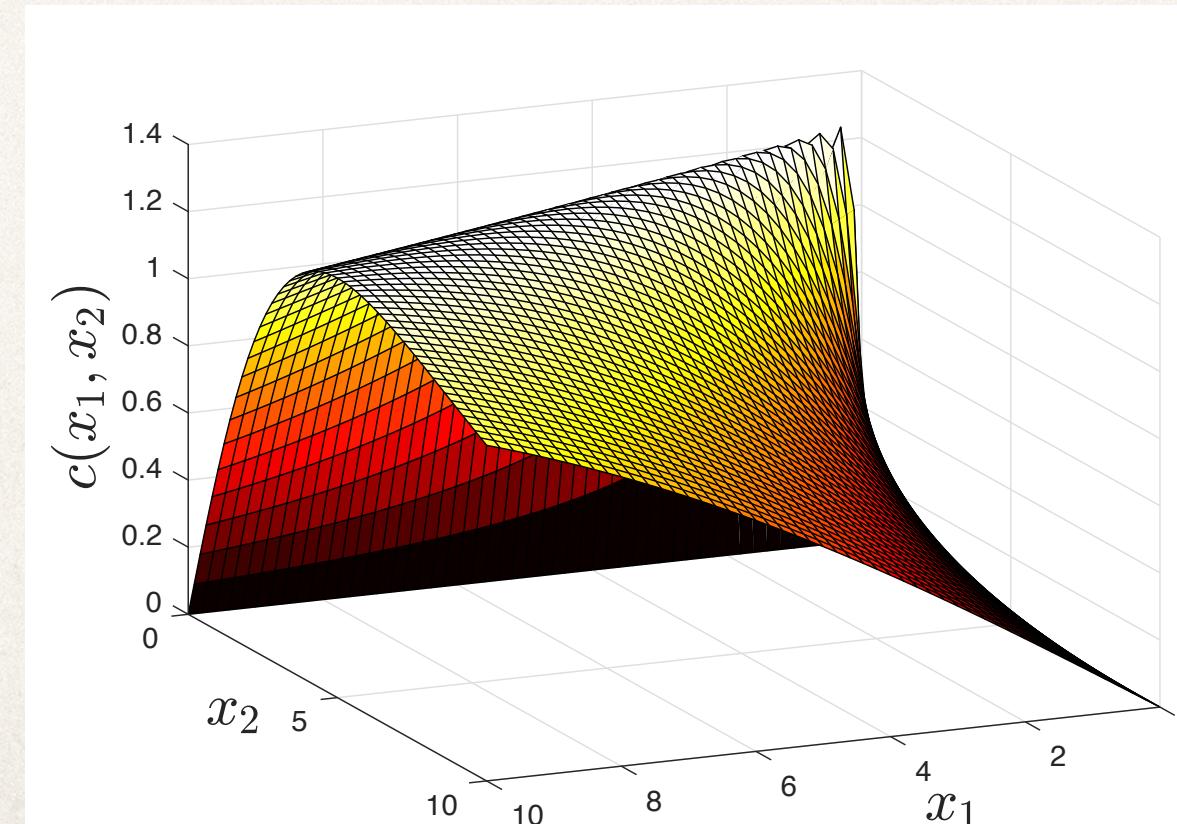
# Conditions on the energy market diversification from adaptive dynamics

## Established - Innovative Model

$$\begin{cases} \dot{n}_1 = n_1 r(x_1) \left( 1 - \frac{n_1 + c(x_1, x_2)n_2}{K(x_1)} \right) = n_1 g(n_1, n_2, x_1, x_2, x_1) \\ \dot{n}_2 = n_2 r(x_2) \left( 1 - \frac{n_2 + c(x_2, x_1)n_1}{K(x_2)} \right) = n_2 g(n_1, n_2, x_1, x_2, x_2) \end{cases}$$



$$K(x) = \frac{k_1 x^2}{k_2^2 + x^2}$$



$$c(x_1, x_2) = \frac{(c_1^2 + c_2^2)x_1x_2}{c_1^2x_1^2 + c_2^2x_2^2}$$

Table 1: Description of state variables and coefficients with their corresponding ranges.

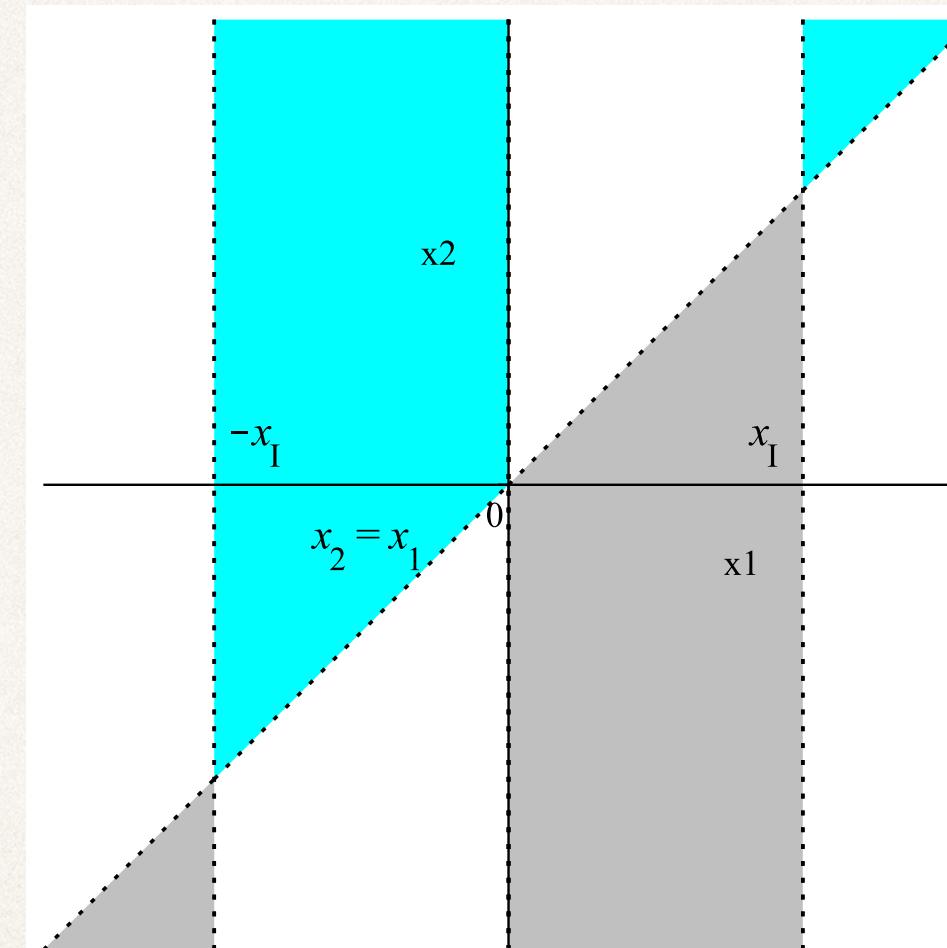
| State variables description |   | Units                |
|-----------------------------|---|----------------------|
| $n_1(t)$                    | CGC* for Standard Energy, characterized by $x_1$                          | MW                   |
| $n_2(t)$                    | CGC for Innovative Energy, characterized by $x_2$                         | MW                   |
| Parameter description       |   | Ranges               |
| $x_1$                       | Quantitative continuous characteristic trait defining SE                  | $x_1 \in \mathbb{R}$ |
| $x_2$                       | Quantitative continuous characteristic trait defining IE                  | $x_2 \in \mathbb{R}$ |
| $r(x_i)$                    | CGC growing rate as a function of $x_i$ , for $i = 1, 2$                  | $r > 0$              |
| $K(x_i)$                    | Maximum CGC as function of $x_i$ , for $i = 1, 2$                         | $K > 0$ MW           |
| $c(x_1, x_2)$               | Interaction coefficient between both CGC as a function of $x_1$ and $x_2$ | $c \in \mathbb{R}$   |

\*CGC: cumulative generation capacity. \*\*GT's: generation technologies.

# Conditions on the energy market diversification from adaptive dynamics

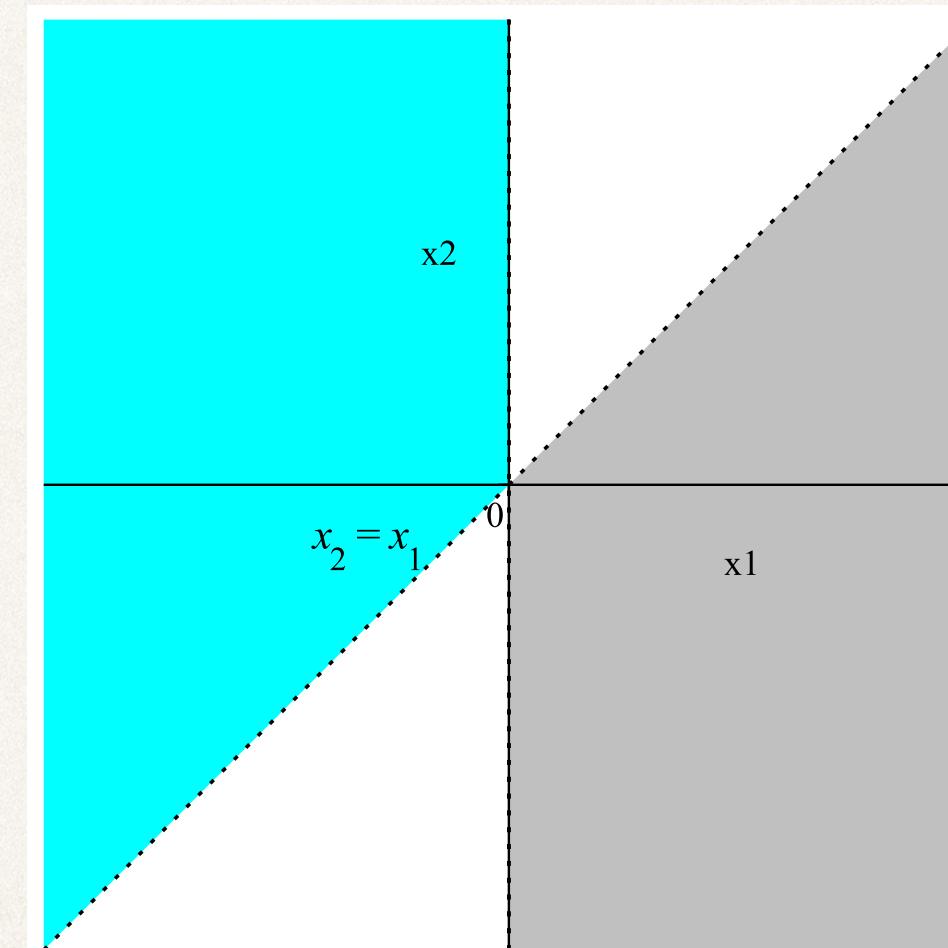
Selection Gradient and invasion conditions:

Different regions in the established-innovative plane where invasion conditions given are satisfied. Blue regions above the diagonal correspond to negative selection gradients, and gray regions below that line correspond to positive selection gradients.



$c_2^2 - c_1^2 = 0.1025 > 0$  ( $c_1 = 1$  and  $c_2 = 1.05$  were used)

$$\frac{\partial \lambda}{\partial x_2}(x_1, x_1) = \frac{[k_2^2(3c_1^2 + c_2^2) - (c_2^2 - c_1^2)x_1^2] r}{x_1(k_2^2 + x_1^2)(c_1^2 + c_2^2)}$$



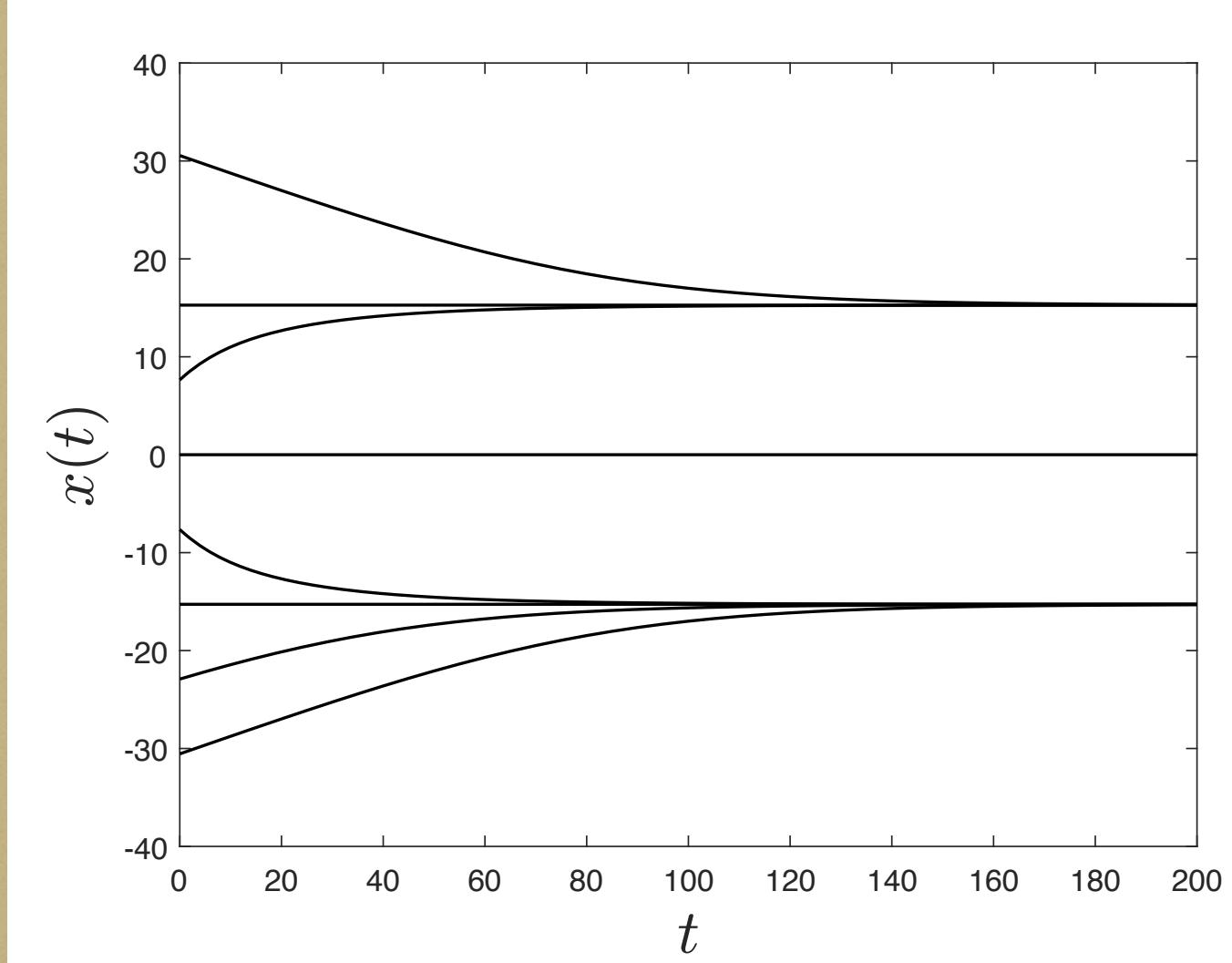
Note that a big innovation is required to have a cooperative market just after an innovation in a market dominated by SE generation technology

$c_2^2 - c_1^2 = -0.1025 < 0$  (with  $c_1 = 1.05$  and  $c_2 = 1$ )

# Conditions on the energy market diversification from adaptive dynamics

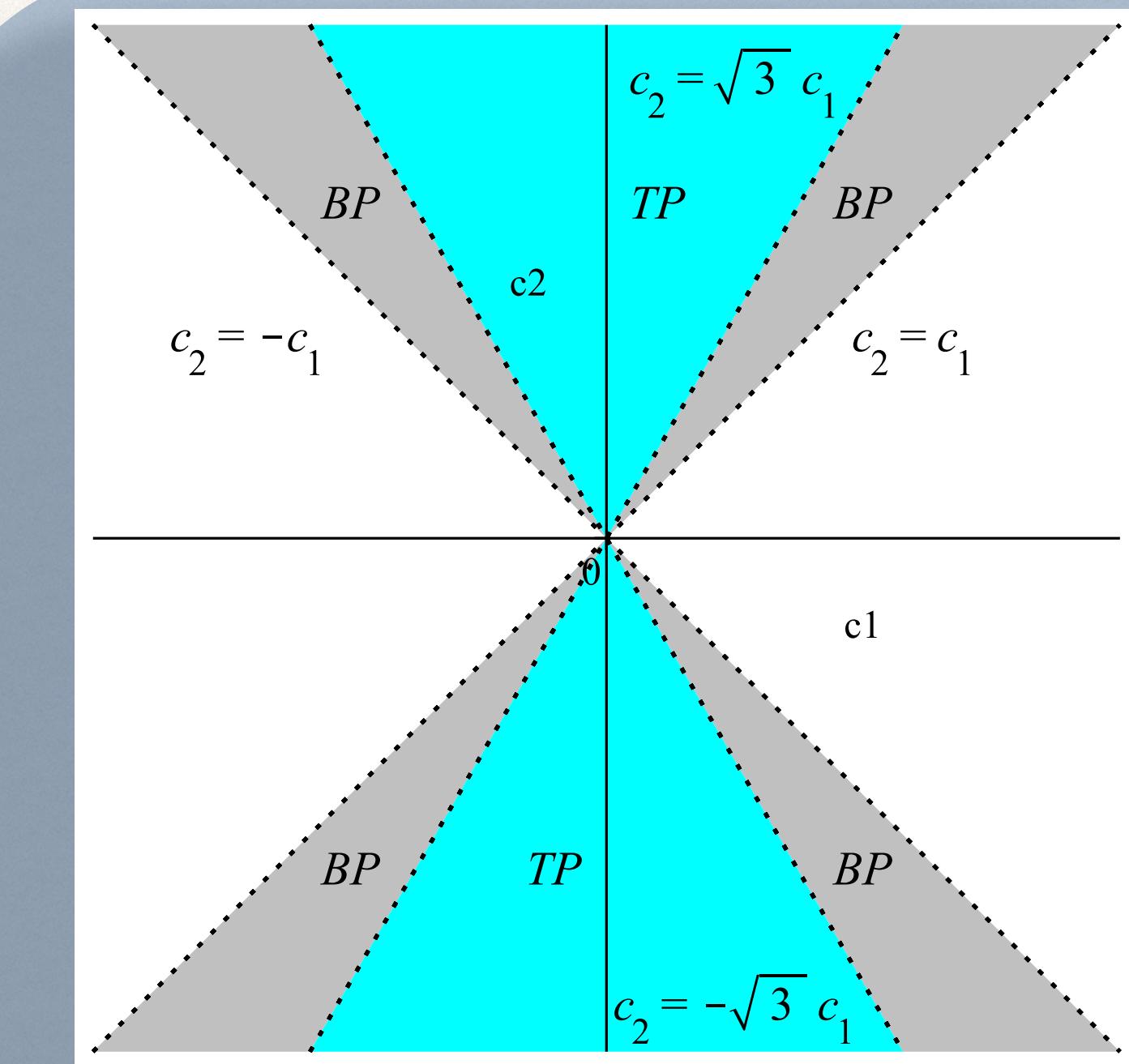
## Canonical Equation of Adaptive Dynamics and classification of evolutionary equilibria

$$\dot{x}_1 = \frac{1}{2}\mu(x_1)\sigma^2(x_1)\bar{n}(x_1)\frac{\partial\lambda}{\partial x_2}(x_1, x_1)$$



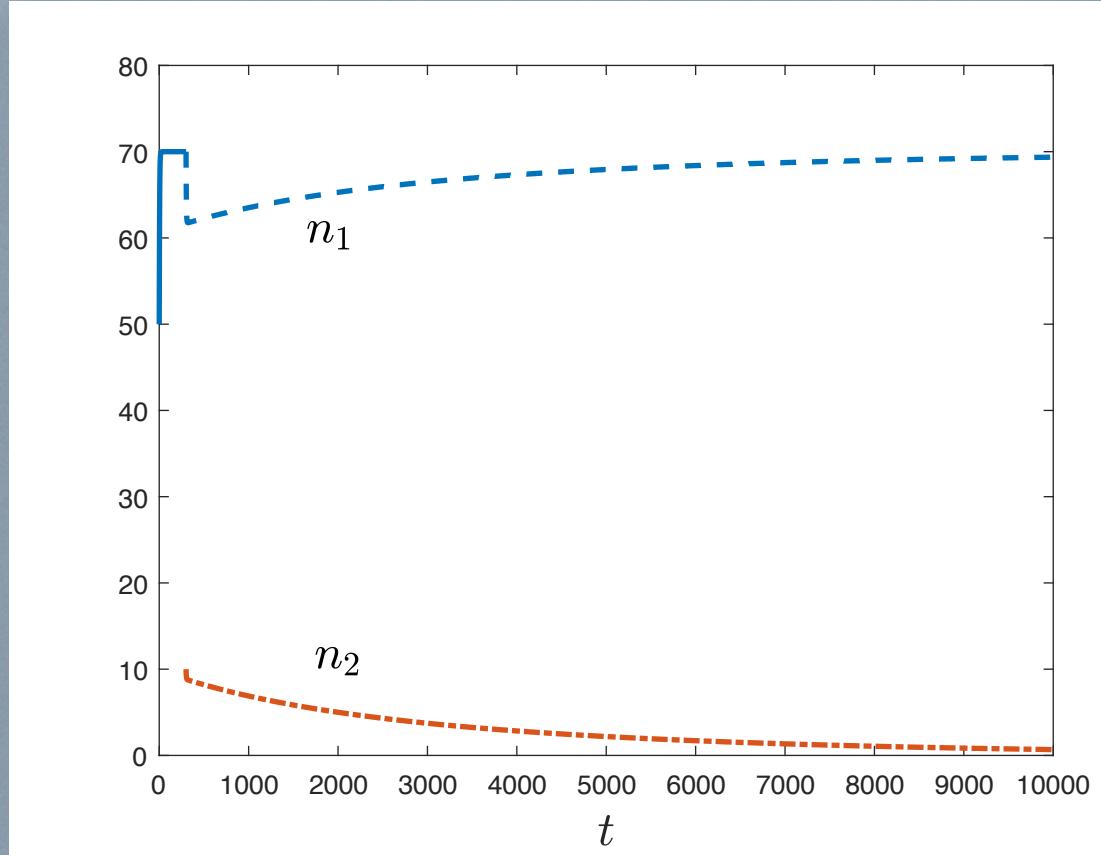
Numeric simulation of evolutionary dynamics of the characteristic trait described by the Canonical Equation

$$r = 0.3, c_1 = 1, c_2 = 2, k_1 = 100, k_2 = 10, \mu = 1, \text{ and } \sigma = 1$$



Classification of stable evolutionary equilibria as BP, TP or BBP.

# Conditions on the energy market diversification from adaptive dynamics

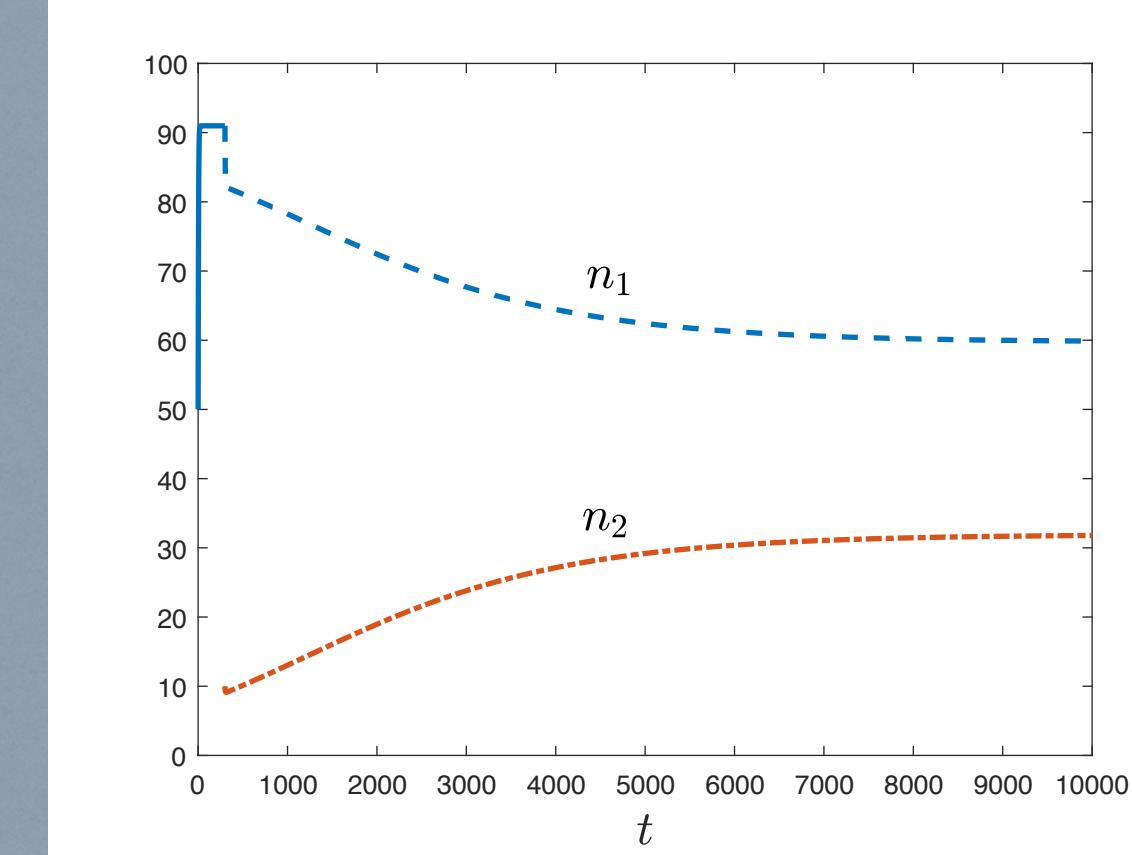


$$c_1 = 1, c_2 = 2$$



Terminal Point

Diversification is not possible

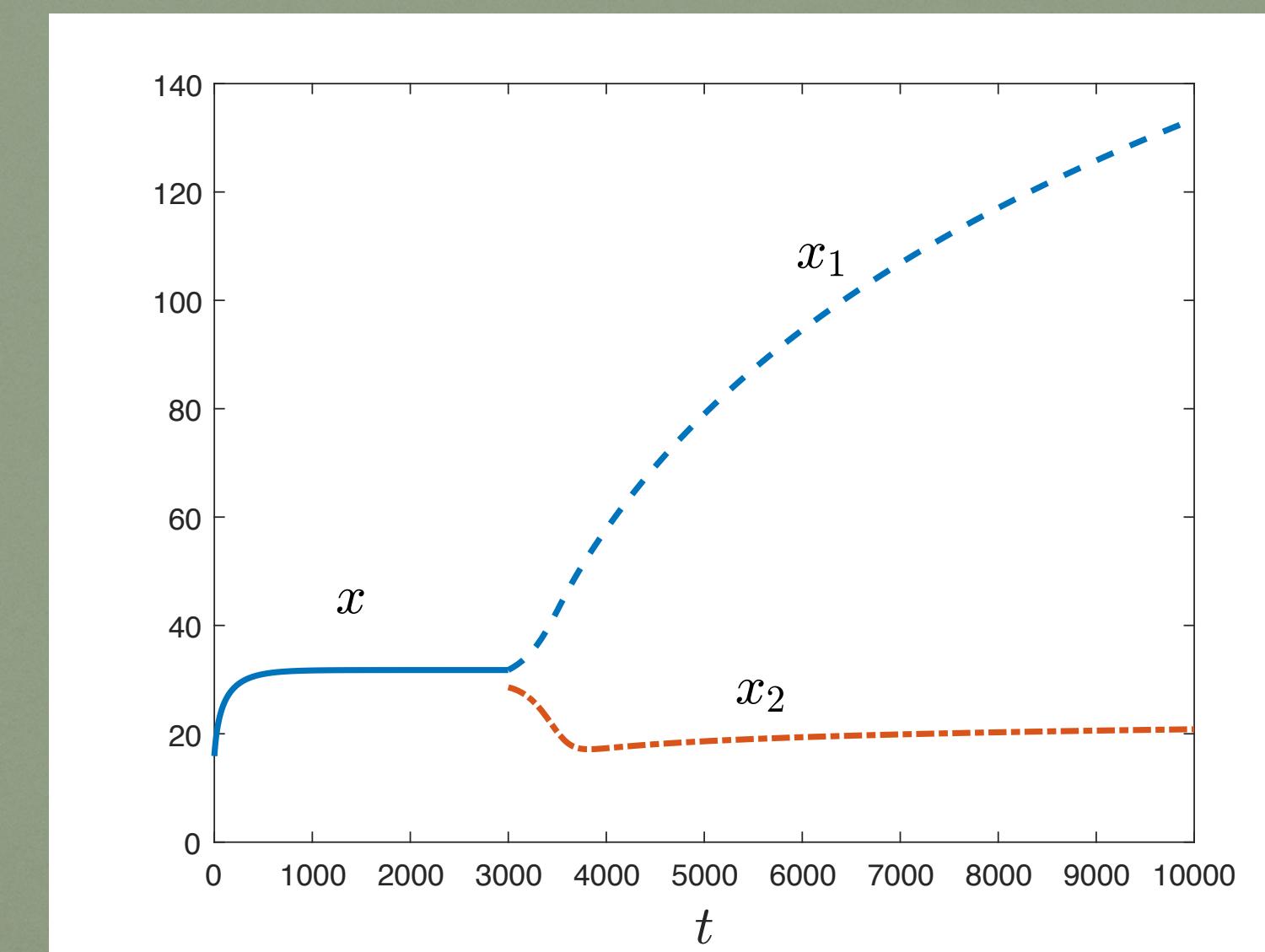


$$c_1 = 1, c_2 = 1.2$$



Branching Point  
Energy market diversifies

**Diversification.** Trait dynamics after branching: two established densities will coexist in the market



# Results and Conclusions from the application

---

- ❖ Local stability analysis of Established-innovative model helps to answer the question of **under what conditions can IE spread into the market and interact or even substitute SE.**
- ❖ Energy market will not crash under any circumstances.
- ❖ The instability of invasion equilibria is related to the possibility for an IE to invade the market
- ❖ The existence and stability of equilibria in presence of both, SE and IE, are related to the coexistence, leading to diversification.

- ❖ The interaction dynamics in the market model is well defined for both competition and cooperation market configurations.
- ❖ Invasion conditions determine specific regions of the trait plane under which the invasion of the innovative attribute is possible, and configurations that lead to its disappearance.
- ❖ It was proven that under convenient configurations of subsidies awarded (or taxes imposed), it is possible to determine scenarios in order to evolutionary equilibria to exist and to be locally asymptotically stable.
- ❖ It was shown that evolutionary stability implies coexistence.
- ❖ Evolutionary equilibria can be terminal points, where no marginal innovation can invade into the market. Or can also be branching points, where innovative energy can penetrate, coexist and diversify the market.

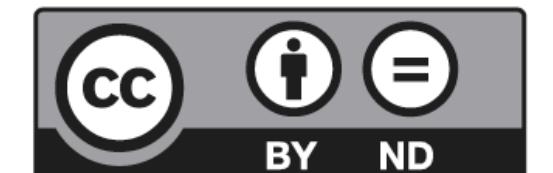
- ❖ Both parameters (subsidies/taxes) describe the dynamics in the market timescale, but they finally make a difference in the evolutionary time scale.  
**In deed, the expressions in the selection gradient controlling the sign, are a measure of the strength of diversification through innovation.**
- ❖ Diversification occurs in markets that are at least slightly asymmetric and in which IE is stimulated over SE, either by the allocation of subsidies or by the imposition of lower taxes.
- ❖ Finally note that repeated process of innovation can give origin to a rich variety of different and complex kinds of technological evolution.
- ❖ Specific situations should be studied in greater depth and detail in order to achieve an informed decision making.

# Application 2

**Copernican Journal of Finance & Accounting**

**2018, volume 7, issue 2**

Toro-Zapata, H.D., & Olivar-Tost, G. (2018). Mathematical model for the evolutionary dynamics of innovation in city public transport systems. *Copernican Journal of Finance & Accounting*, 7(2), 77–98. <http://dx.doi.org/10.12775/CJFA.2018.010>



e-ISSN 2300-3065

p-ISSN 2300-1240

**HERNÁN DARÍO TORO-ZAPATA\***

Universidad del Quindío  
Universidad Nacional de Colombia – Manizales

**GERARD OLIVAR-TOST\*\***

Universidad Nacional de Colombia – Manizales

**MATHEMATICAL MODEL FOR THE EVOLUTIONARY DYNAMICS  
OF INNOVATION IN CITY PUBLIC TRANSPORT SYSTEMS**

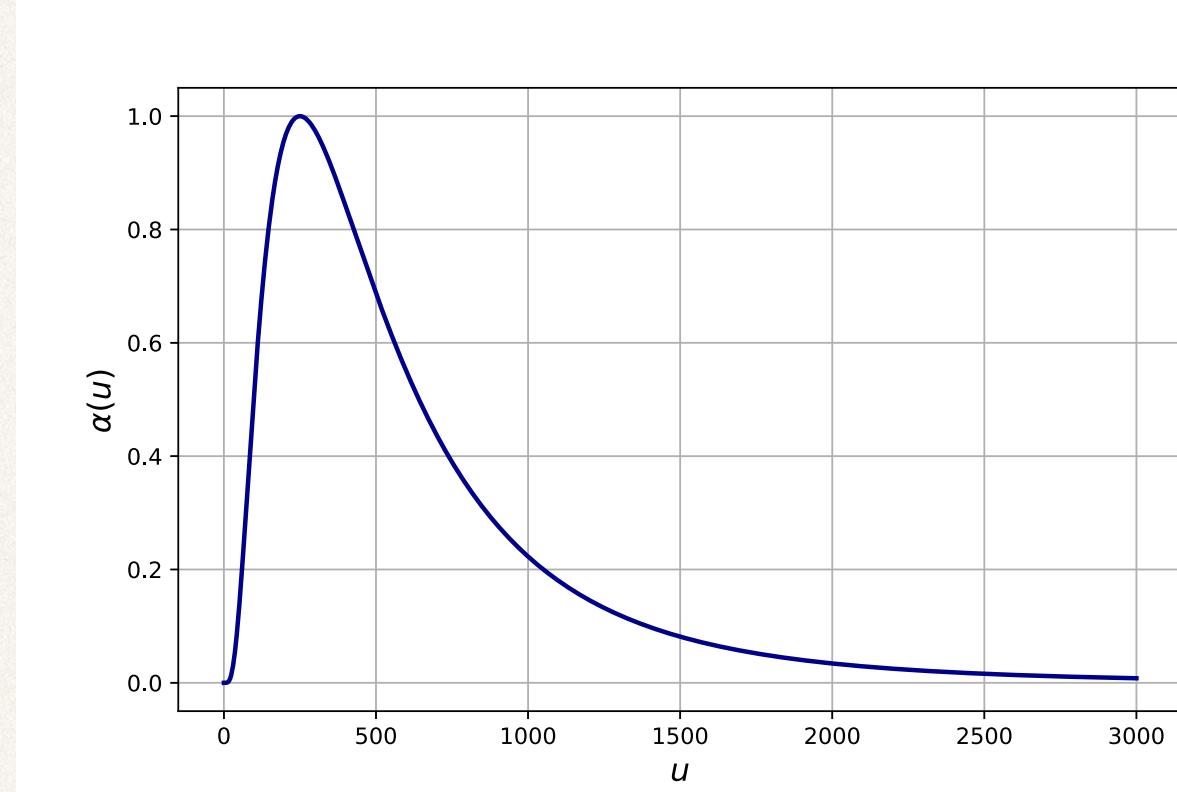
# Mathematical model for the evolutionary dynamics of innovation in public transportation systems

## Established - Innovative Model

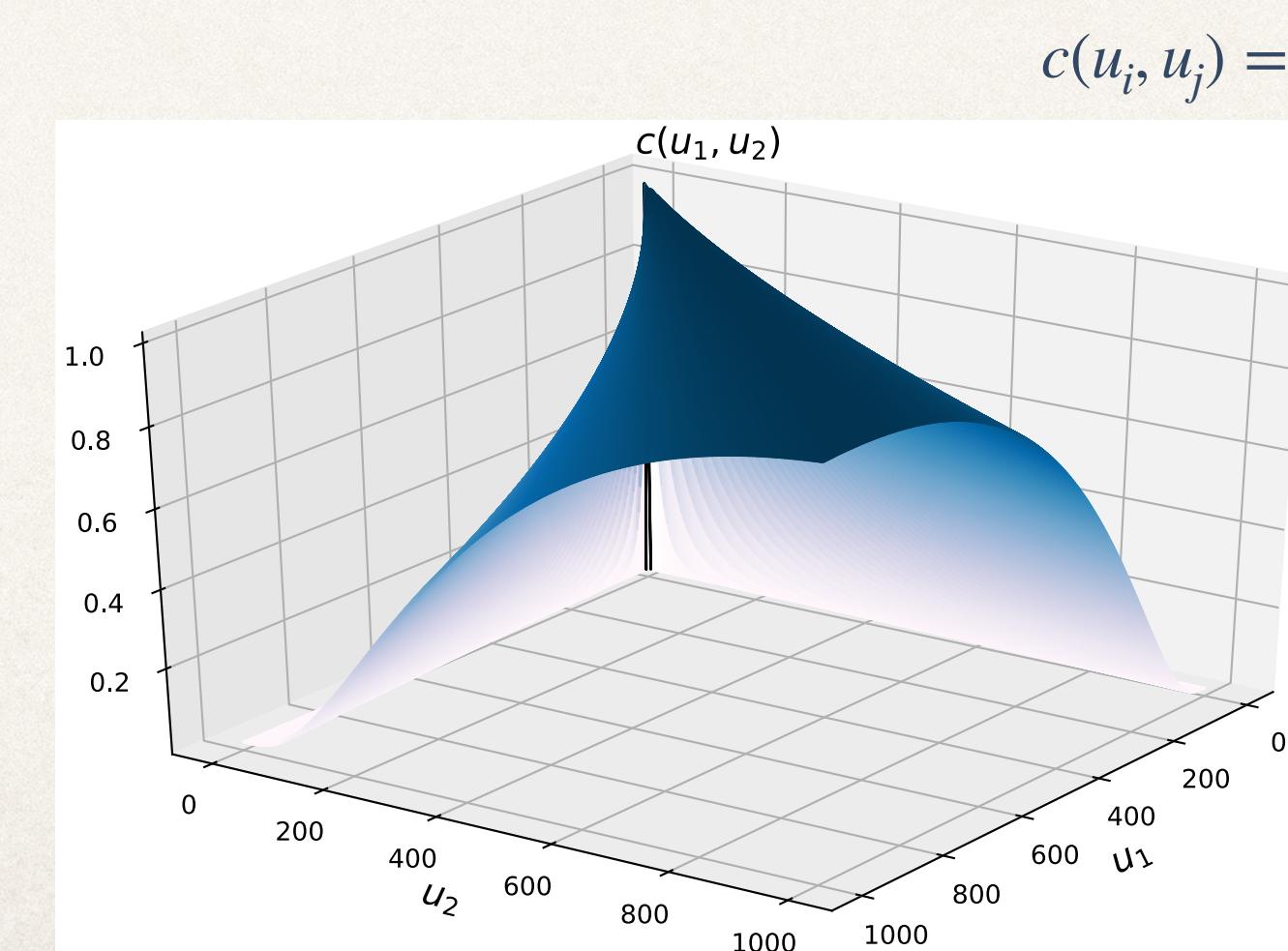
$$\begin{aligned}\dot{x}_i &= (\alpha(u_i)y_i - \delta(u_i)) \left[ 1 - \text{sign}(\alpha(u_i)y_i - \delta(u_i)) \left( x_i + \sum_{k=1, k \neq i}^N c(u_i, u_k)x_k \right) \right] x_i \\ \dot{y}_i &= l(u_i)(1 - y_i) - \epsilon(u_i)\alpha(u_i)x_iy_i,\end{aligned}$$

Table 1: Description of state variables and parameters

| Description of the states |  | Value |
|---------------------------|--|-------|
|                           |  |       |
| $x_i$                     | Proportion of people using the $i$ -th TS                                | -     |
| $y_i$                     | Budget destined to the expansion of the $i$ -th TS                       | -     |
| Parameter Description     |  | Value |
| $u_i$                     | Characteristic attribute describing the $i$ -th TS                       | -     |
| $\alpha(u_i)$             | Instant rate of adoption of the $i$ -th TS                               | -     |
| $\delta(u_i)$             | Rate at which the $i$ -th TS is abandoned by users                       | -     |
| $l(u_i)$                  | Rate at which new resources are invested for expansion of the $i$ -th TS | -     |
| $\epsilon(u_i)$           | Efficiency of the $i$ -th TS in converting the investment in new users   | -     |
| $c(u_i, u_k)$             | Interaction rate between $i$ -th and $k$ -th TS's                        | -     |



$$\alpha(u) = a \exp\left(-\frac{1}{2a_1^2} \ln^2\left(\frac{u}{a_2^2}\right)\right)$$

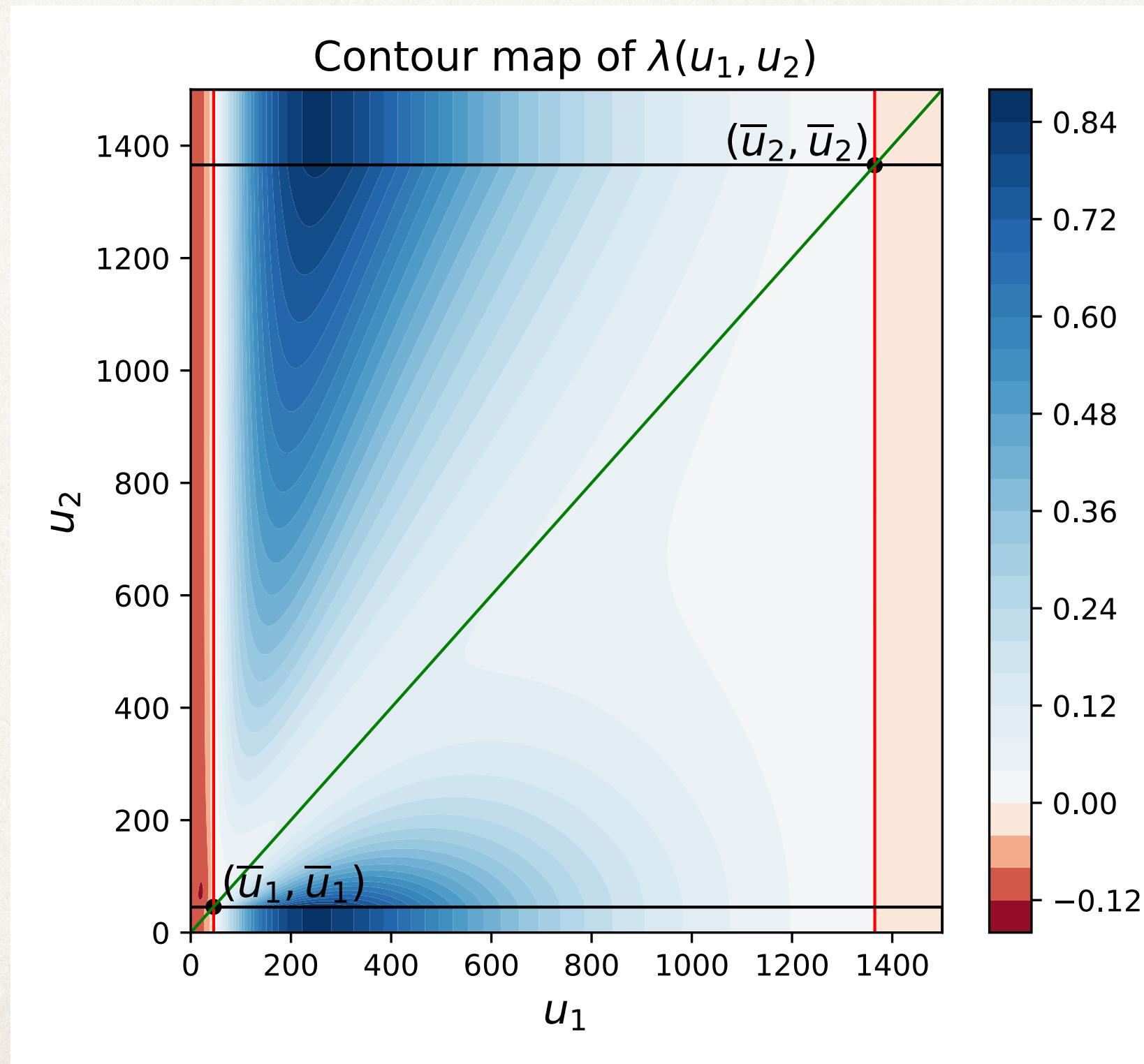


$$c(u_i, u_j) = \exp\left(\frac{\ln^2 f_1}{2f_2^2}\right) \exp\left(-\frac{1}{2f_2^2} \ln^2\left(\frac{f_1 u_i}{u_j}\right)\right)$$

# Mathematical model for the evolutionary dynamics of innovation in public transportation systems

Fitness function:  $\lambda(u_1, u_2) = \lambda_2 = (\alpha(u_2) - \delta(u_2))[(1 - sign(\alpha(u_2) - \delta(u_2))c(u_2, u_1)\bar{x}_1(u_1))]$

Contour map of the fitness function with the values of the parameters  $d = 0.1$ ,  $l = 0.01$ ,  $\epsilon = 0.1$ ,  $a = 95$ ,  $a_1 = 0.8$ ,  $a_2 = \sqrt{250}$ ,  $f_1 = 1.1$ ,  $f_2 = 1$ . The color range allows for establishing the regions in the  $(u_1, u_2)$ -plane where the fitness function is positive (blue regions), and therefore where the invasion of the innovative TS is possible. The solid green line correspond to  $u_2 = u_1$ , the black solid line to  $l(u_1) = l^*(u_1)$  and the solid red line correspond to the switching curve where  $\alpha(u_2) = \delta(u_2)$ .

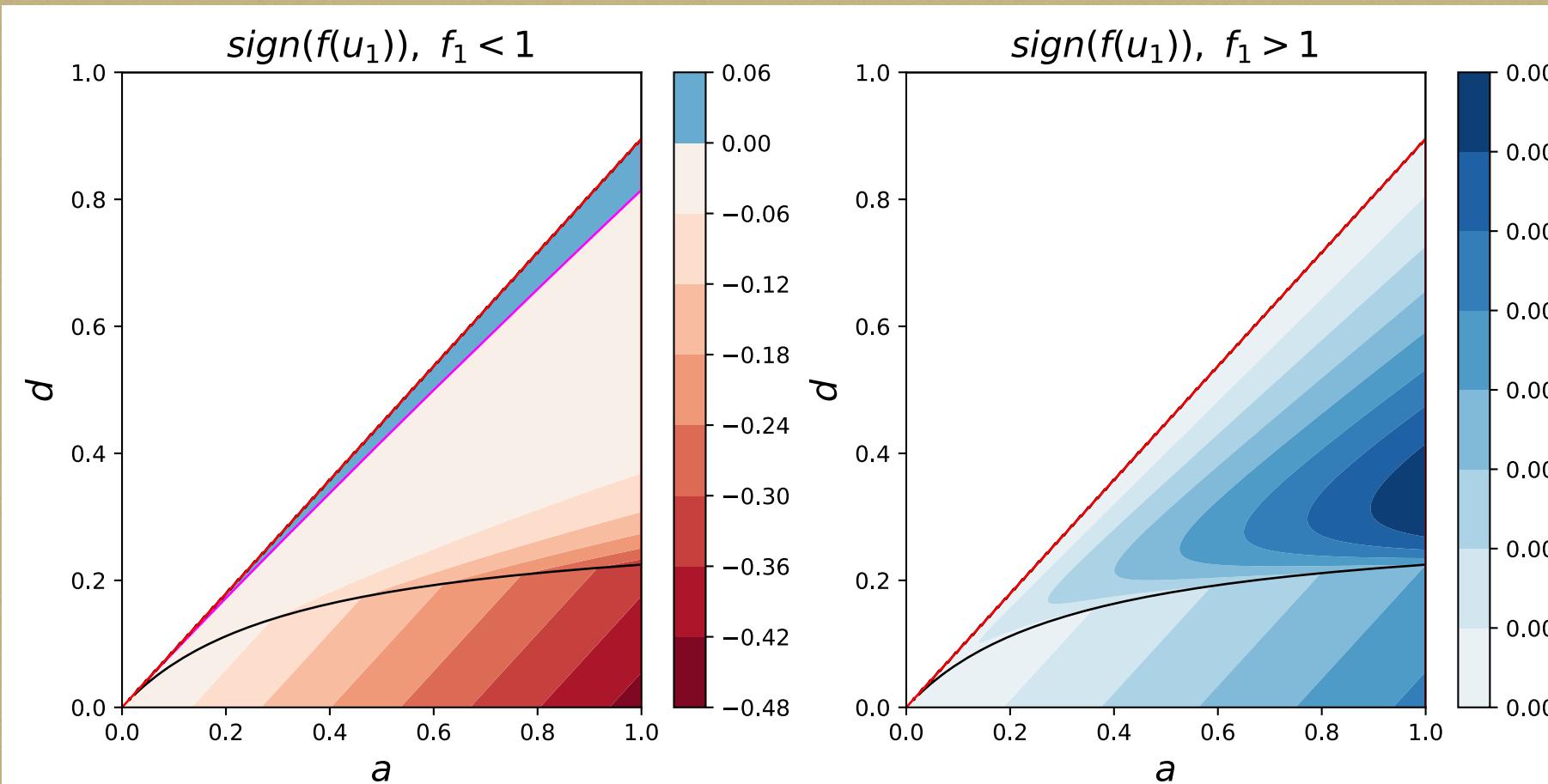


Through the study of the sign of this function for specific  $u_1$  and  $u_2$ , the possibility of innovative TS invasion may be established.

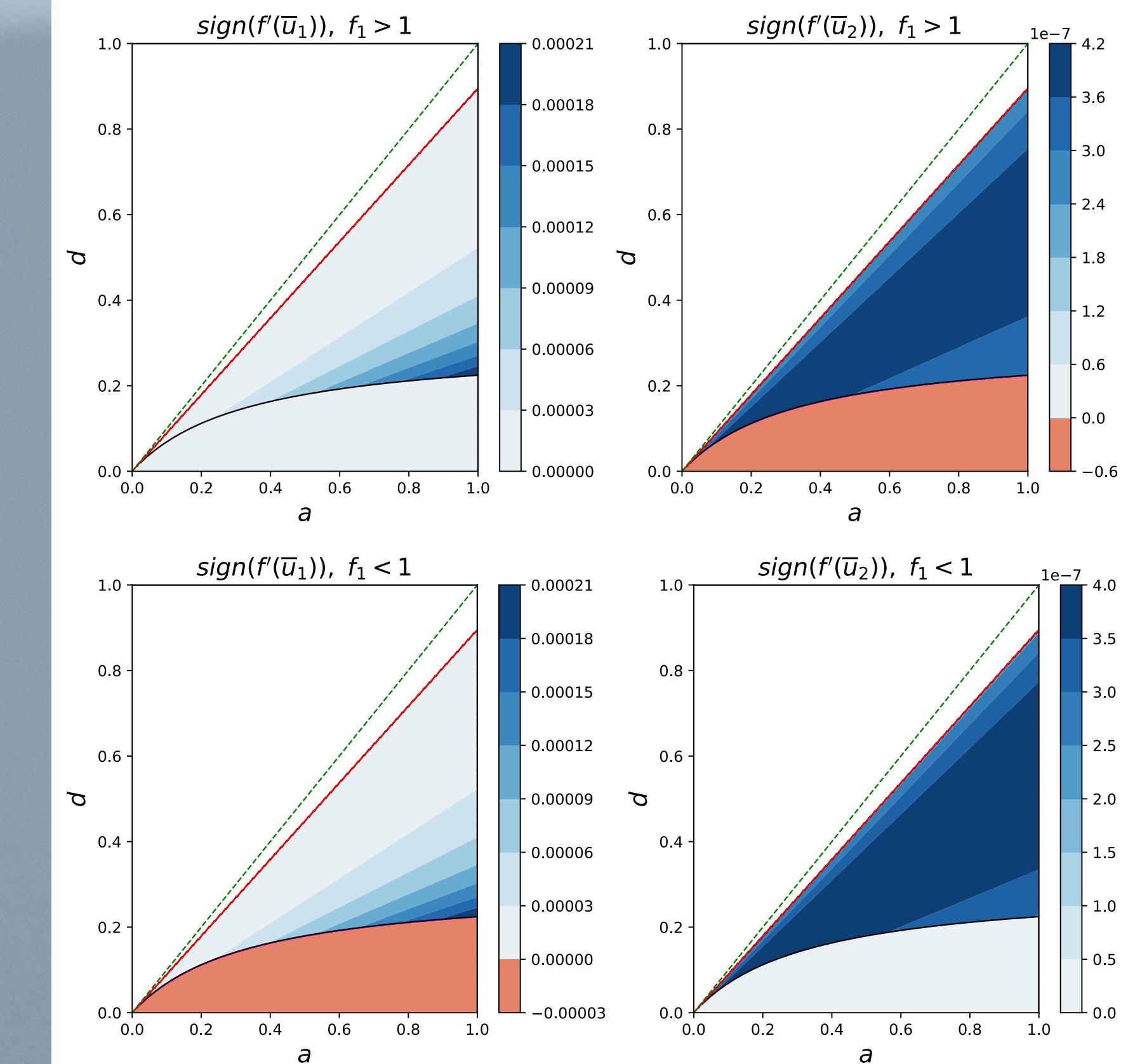
# Mathematical model for the evolutionary dynamics of innovation in public transportation systems

## Canonical Equation of Adaptive Dynamics and local stability of evolutionary equilibria

$$\dot{x}_1 = \frac{1}{2} \mu(x_1) \sigma^2(x_1) \bar{n}(x_1) \frac{\partial \lambda}{\partial x_2}(x_1, x_1)$$

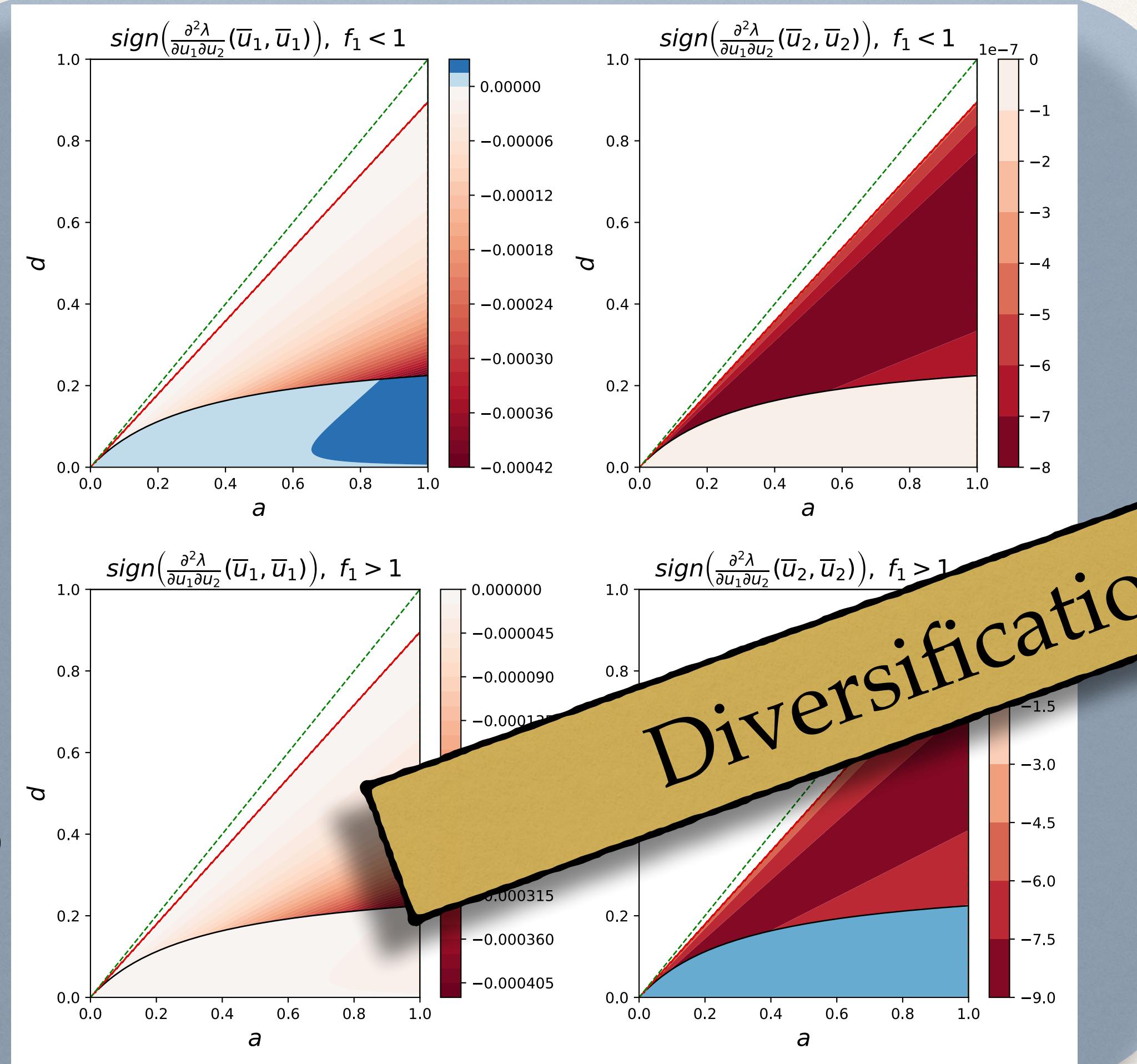


The contour map of  $\dot{x}_1$  as a function of  $a$  and  $d$  is shown for  $u_1 = 160$  and  $f_1 = 0.9$  (left panel) and for  $f_1 = 1.1$  (right panel).



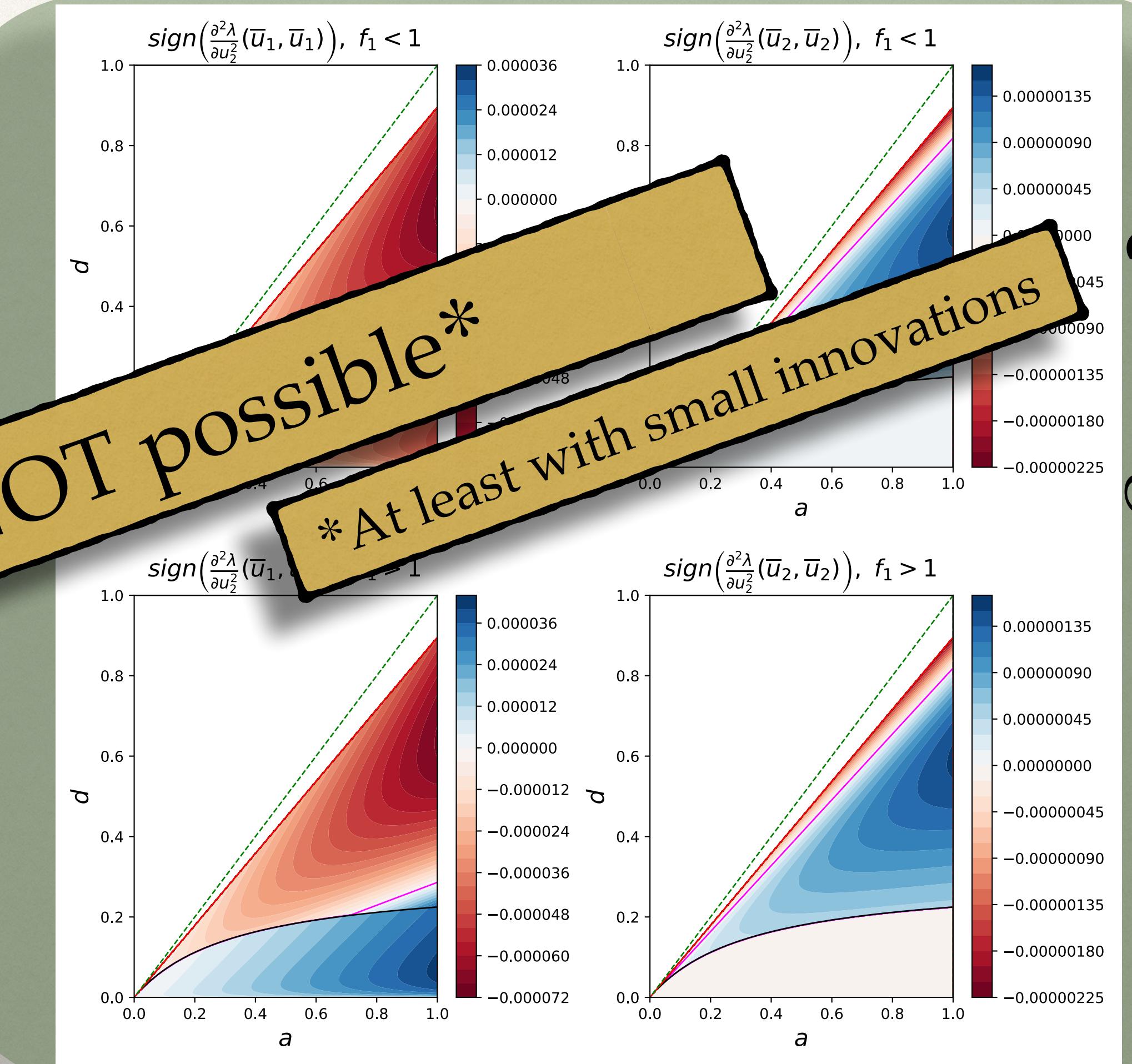
# Mathematical model for the evolutionary dynamics of innovation in public transportation systems

¿Coexistence < 0?



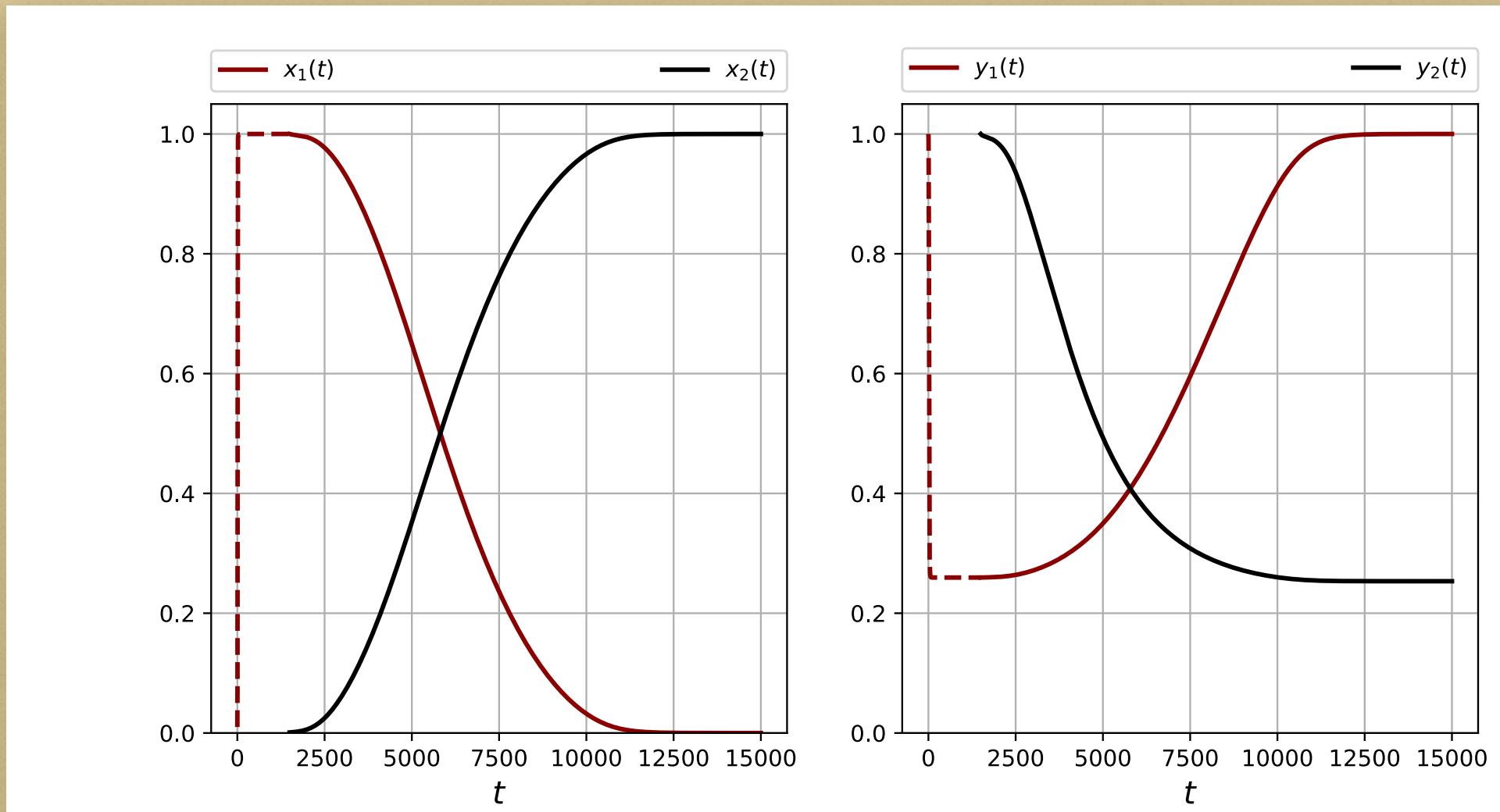
Diversification is NOT possible\*

\*At least with small innovations

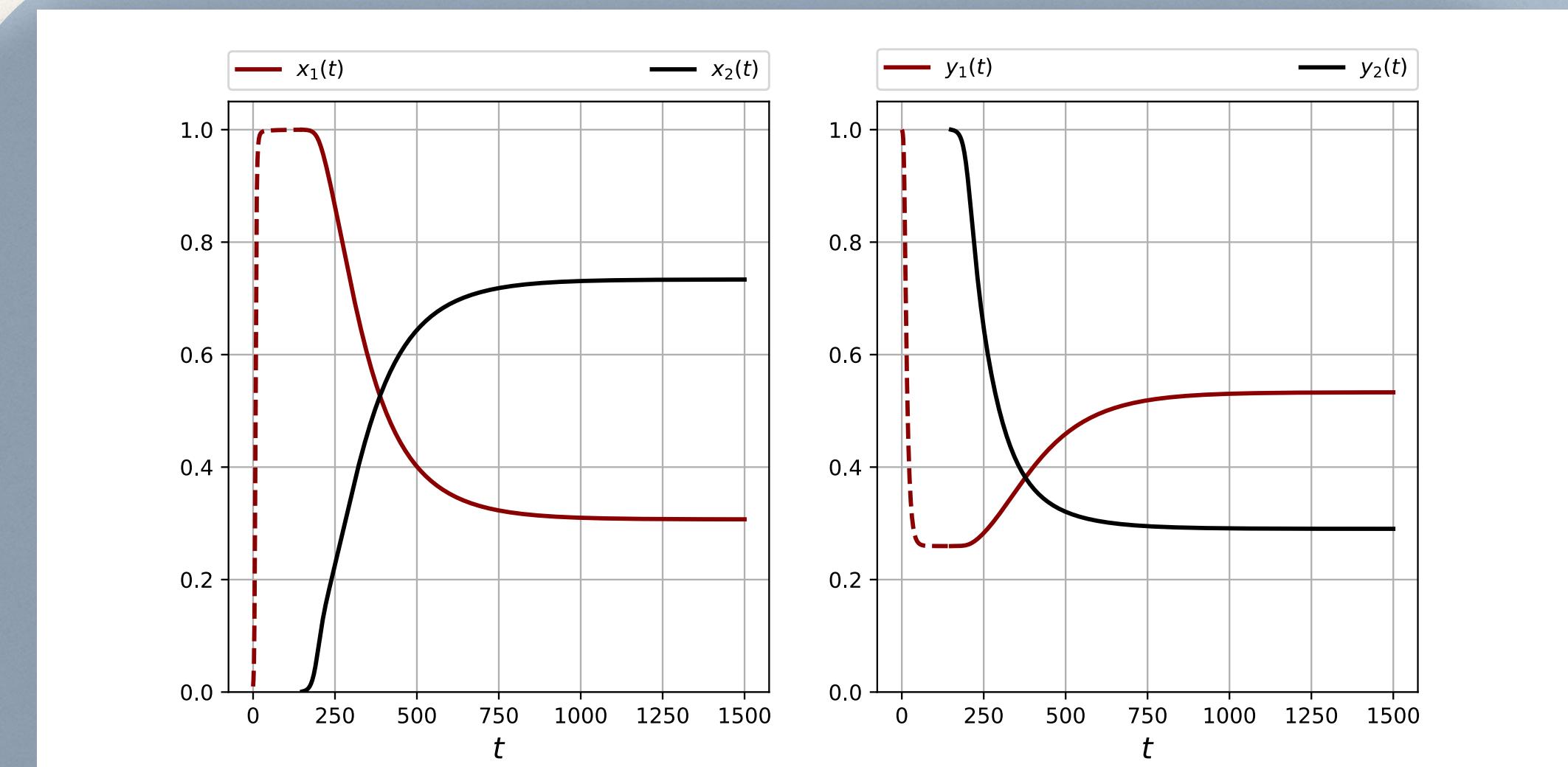


¿Divergence > 0?

# Conditions on the energy market diversification from adaptive dynamics



**Substitution Scenario.** **Left:**  $x_1(t)$  solution before innovation and after innovation. **Right:**  $y_1(t)$  solution before innovation and after innovation. With  $u_1 = 160$  and  $u_2 = 1.05u_1 = 168$ : small innovation.



**Coexistence Scenario.** **Left:**  $x_1(t)$  solution before innovation and after innovation. **Right:**  $y_1(t)$  solution before innovation and after innovation. With  $u_1 = 160$  and  $u_2 = 250$ : large innovation.

# Results and Conclusions from the application

---

- A generalized model is formulated, called resident-innovative model, to describe competition in the market when the established TS equilibrium is disturbed by the entry of an innovative TS.
- From study of the fitness function for specific model coefficient expressions. It is possible to determine general conditions that must be met to guarantee or not the success of the innovation, **understanding a successful innovation, one that manages to penetrate and expand in the market.**
- For one TS, it is possible to obtain explicit conditions under which an equilibrium of partial adoption or one of total adoption can be achieved; according to this model, both cases are perfectly achievable without consuming all the available resources.

- ❖ The model makes possible to establish explicit conditions for the level of investment required in each case, information that may be useful in decision making.
- ❖ Coexistence after (large?) innovation is possible, but not the Divergence, this is an example of the situation reported by F. Dercole and S. Rinaldi, where the evolutionary equilibrium corresponds to a TP at which the established and innovative TSs can not coexist **in a neighborhood of the evolutionary equilibrium**; however, both systems evolve towards each other until one of them disappears.
- ❖ Coexistence and Divergence conditions, do not hold simultaneously, then evolutionary branching is not guaranteed by the analysis in this work.

# References

---

1. Lai, C. S., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F., & Monaco, A. P. (2001). A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature*, 413(6855), 519.
2. Dercole, F., & Rinaldi, S. (2008). Analysis of evolutionary processes: the adaptive dynamics approach and its applications. Princeton University Press.
3. Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of mathematical biology*, 34(5-6), 579-612.
4. Geritz, S. A., Mesze, G., & Metz, J. A. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary ecology*, 12(1), 35-57.
5. Geritz, S. A., Metz, J. A., Kisdi, É., & Meszéna, G. (1997). Dynamics of adaptation and evolutionary branching. *Physical Review Letters*, 78(10), 2024.
6. Dercole, F., & Rinaldi, S. (2010). Evolutionary dynamics can be chaotic: A first example. *International journal of bifurcation and chaos*, 20(11), 3473-3485.
7. Doebeli, M., & Dieckmann, U. (2000). Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *The american naturalist*, 156(S4), S77-S101.



PRINCETON SERIES IN THEORETICAL AND COMPUTATIONAL BIOLOGY

# Analysis of Evolutionary Processes

The Adaptive Dynamics Approach  
and Its Applications

FABIO DERCOLE AND SERGIO RINALDI

## The social diversification of fashion

Pietro Landi  <sup>a,b</sup> and Fabio Dercole<sup>c</sup>

<sup>a</sup>Department of Mathematical Sciences, Stellenbosch University, Stellenbosch, South Africa; <sup>b</sup>Evolution and Ecology Program, International Institute for Applied Systems Analysis, Laxenburg, Austria; <sup>c</sup>Department of Electronics, Information, and Bioengineering, Politecnico di Milano, Milan, Italy

J. Math. Biol. (1996) 34: 579–612

**Journal of  
Mathematical  
Biology**

© Springer-Verlag 1996

## The dynamical theory of coevolution: a derivation from stochastic ecological processes

Ulf Dieckmann<sup>1</sup>, Richard Law<sup>2</sup>

### Adaptive dynamics and technological change

Fabio Dercole<sup>a,\*</sup>, Ulf Dieckmann<sup>b</sup>, Michael Obersteiner<sup>b,c</sup>, Sergio Rinaldi<sup>a,b</sup>

<sup>a</sup>DEI, Department of Electronics and Information, Politecnico di Milano, Via Ponzio 34/5, 20133 Milano, Italy

<sup>b</sup>IIASA, International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria

<sup>c</sup>Department of Economics and Finance, IHS, Institute for Advanced Studies, A-1060 Vienna, Austria