

## NETWORK COMPETITION AND ECOLOGICALLY BASED MODELS

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### INTRODUCTION

Spatial dynamics is often the result of competitive forces in a network. It is increasingly recognized that dynamic interactions and (re)locations can hardly be described by conventional equilibrium models. In this paper the attention will be focused on the relevance of ecologically-based theories which have proven to be valid in dynamic ecosystems. Especially niche theory will be dealt with here. It will be shown that transportation dynamics can be meaningfully represented by means of ecologically-based frameworks. Based on a simple transport model, the relevance of niche theory will be illustrated by means of some simulation experiments.

### 1. CONNECTIONS BETWEEN ECOLOGY AND ECONOMICS

Social sciences seem to orient themselves increasingly towards the methodology of natural sciences. The analysis of the evolution of dynamic systems is, for instance, more and more based on concepts from ecology. In this context the potential of using the formalism of mathematical ecology in economics is advocated by an increasing number of researchers. We may refer here to Samuelson (1971) who attempted more than 20 years ago to construct a unified economic-ecological theory. But it is noteworthy that already in 1932 Lotka claimed that "economic competition is only a special form of the more general phenomenon of biological competition". However, the real initiator of this dialogue between economics and ecology was essentially Malthus (1798) with his principle (and model) of population dynamics and saturation, including his scientific influence on the co-discoverers of the theory of natural selection in organic evolution, viz., Darwin and Wallace (1858) (see Rosser, 1991). An interesting review of the historical evolution of the connection between economy and ecology can be found in Rosser (1991) where also the 'dialectical' difficulties between these disciplines are pointed out. We may also refer here to Marshall (1920) as the greatest admirer of Darwin among economists by accepting the proposition that the 'struggle for existence' explains the evolution of market structure and that human society gradually and continuously evolves (gradualism in evolution).

It is interesting to note that economics preceded ecology in developing the concept of static equilibrium (see again Rosser, 1991). However, the reverse is the case for the development of cyclical models. Lotka developed the non-linear predator-prey model in 1920, more than one decade before the first formal business cycle model was designed by Kalecky (1935). In particular Lotka (1920) and later on Volterra (1931) explained the occurrence of coupled oscillations in nature by means of a system of two differential equations (the so-called 'Lotka-Volterra model'). One equation expresses the fact that the evolution of a species (the so-called prey) is limited in its growth by the presence of a predator which feeds on it. The second one (the so-called predator equation) implies that the growth of the predator is positively related to the prey population. Surprisingly, the work of Lotka was recognized by economists only 47 years later (see e.g. Goodwin, 1967 who analyzed a Lotka-Volterra system for describing both the motion of the employment rate and that of the workers' income share).

In Lotka's analysis also the possibility of different dynamic trajectories, including saddle points, limit cycles and bifurcations is present. On this basis, May (1976) developed various models of chaotic dynamics of population, which are more recently also used by several economists (see, for example, Day, 1982, and Benhabib and Day, 1980). It should be added that the role of instabilities in economics was previously already recognized by the 'saltationalist' approach (see Schumpeter, 1934), on the basis of

population leading to chaos. May's model is a simple form of the S-shaped logistic equation (first developed by Verhulst, 1938) in which a time lag of one generation exists (in other words, the logistic function assumes a discrete form). May discovered in his simple growth model the possibility of oscillations and chaotic dynamics for certain values of the growth parameter (in particular for a range of values between 3 and 4). His study focused on single species of insect populations. However, it is interesting that May claimed the possibility of extending his model to commodity quantity and price analysis, to learning processes, to propagation of rumours, etc.

In the seventies there has also been an increasing amount of literature on mathematical ecology applied to urban and regional economics. We recall here, for example, the work by Allen et al. (1978) and Wilson (1981) on modelling urban dynamics and primarily based on the logistic law for growth processes. The use of models based on the Lotka-Volterra formalism was later on advocated, among others, by Dendrinos and Mullally (1985), in their study of inter-urban and intra-urban (in)stability, by Curry (1981) and Nijkamp and Reggiani (1990) in their analyses of labour market evolution, by Camagni (1985), Nelson and Winter (1982), and Sonis (1986) in their models of innovation-diffusion processes.

The interest in the use of ecological models for (spatial) economic analysis is mainly methodological, since the two principal ecological models (i.e., the May model and the Lotka-Volterra model) have the possibility of showing complex dynamics starting from very simple mathematical equations which may be similar in both economics and ecology. Next also by means of more recent mathematical tools such as catastrophe and bifurcation theory, chaos theory or fractal theory, it is possible to study and to interpret a multiplicity of phenomena, such as cycles, fluctuations, dramatic changes, which appear to prevail some times in the empirical world.

Now the question is whether models from natural sciences have a high degree of validity in spatial sciences. In order to avoid a purely mechanistic and non behavioural 'transfer' of ecological formalism to spatial-economic analysis, it is necessary to anchor the above mentioned ecological models strongly in theoretical hypotheses or propositions rooted in economics (see Camagni, 1990). In this context, Nijkamp and Reggiani (1992a) have imposed five conditions for a valid application of so-called 'social physics' (the use of models and concepts from natural sciences in social sciences):

- (1) The model should satisfy normal logical conditions for the social system at hand.
- (2) There should be a high degree of plausible correspondence between the phenomenon described in the physical (or biological) world and that from a socio-spatial system.
- (3) The physical (or ecological) basis of the approach should be interpreted in terms of social aspects of the system at hand.
- (4) The mathematical specification of the various relationships should correspond to reasonable hypotheses about the behaviour of spatial (inter)actors.
- (5) The empirical results of a physically - or ecologically - based spatial-economic interaction approach should be confirmed by data from social reality.

Such conditions were for instance also used to test the methodological validity of gravity theory and entropy theory in regional science and geography, and they seem to have also a relevance for ecology-based models. This does not only hold true for May type and Lotka-Volterra type of models, but also for a more recent and increasingly popular approach to competition analysis, viz. niche theory. This will be dealt with in the next section.

## 2. SOME CONCEPTS FROM 'NICHE THEORY'

### 2.1. Definitions of 'niche' in ecology

The term 'niche' has become a popular concept in ecology and biology. Grinnell (1917) was the first scientist using the term 'niche' in order to describe the 'functional role and position of an organism in its community.' His work was followed by other ecologists such as Elton (1927) who claimed: 'the niche of an animal can be defined to a large extent by its size and food habits' and Clarke (1954) who distinguished between the 'functional niche' and the 'place niche'. Clarke also observed that the same functional niche may be filled by quite different species in different geographical regions. This concept was subsequently more specified by Odum (1959) who considered the habitat as the organism's 'address'

functional niche may be filled by quite different species in different geographical regions. This concept was subsequently more specified by Odum (1959) who considered the habitat as the organism's 'address' and the niche as its 'profession'.

Later, a modern approach was offered by Hutchinson (1957) who defined a niche as 'the total range of conditions under which the individual (or population) lives and replaces itself'. He also made a distinction between the 'fundamental' and the 'realized' niche (see Section 2.2).

It is thus clear that the term 'niche' has been used in a wide variety of different contexts, while it has also met some criticism by a few ecologists (see Pianka, 1976). Following Pianka (1978, p. 238), we will now define here a niche as "the total sum of the adaptations of an organismic unit or as all of the various ways in which a given organismic unit conforms to its particular environment". This definition emphasizes in particular dynamic feedback patterns, which are the subject matter of our paper.

Recently, the niche concept has also been linked to the phenomenon of inter-species competition and to dynamic patterns of resource utilization.

## 2.2. Formalization of the niche concept

The niche concept deals with optimal adjustment (or survival) processes in dynamic systems with scarce resources. Usually niche relationships among potentially competing species are often visualized by means of bell-shaped resource utilization curves, starting from Hutchinson's works (1957) on the law of tolerance (or curves of performance - or tolerance curves - analyzed by Shelford, 1913) (see Figure 1).

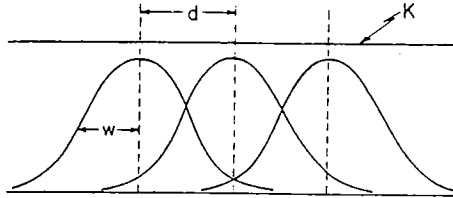


FIGURE 1. A bell-shaped tolerance curve. The curve labeled K represents some resource continuum, say amount of food as a function of food size, which sustains various species whose utilization functions (characterized by a standard deviation  $w$  and a separation  $d$ ) are as shown). (Source: May, 1973, pp. 140)

Tolerance curves are typically bell-shaped and unimodal, with their peaks representing optimal conditions for a particular process and their tails the limits of tolerance. Performance or tolerance curves are often sensitive to environmental variables. Such external conditions may be multidimensional in nature and governed by synergistic linkages. In order to identify optimal adjustment (or survival) patterns of species (i.e., the best fitness), a non-linear programming model would have to be specified, which - in case of multiple objectives for the organisms concerned - might even take the form of a non-linear multi-objective programming model.

Consequently, when tolerance is plotted against a single variable we get the following shape for a chain of niches (see Figure 2).

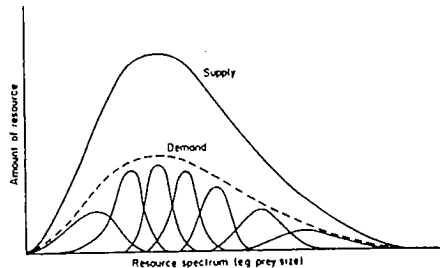


FIGURE 2. Chain of niches (Source: Pianka, 1976, p. 117)

In Figure 2 the vertical axis measures the amount of resource available in some time interval. The upper curve represents the supply of resources along a single resource continuum (e.g., prey size or height above ground). The seven lower curves represent seven (hypothetical) species; in particular those with longer tails have broader utilization curves (i.e., broader niches) because their resources are less abundant. Their total sum indicates more or less the envelope curve of their demand.

By adding next new variables to the horizontal axis we get the tolerance curves in a 'more-dimensional' space (see, e.g., Figure 3 for two dimensions).

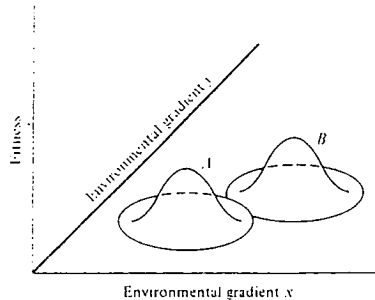


FIGURE 3. A three-dimensional plot with a fitness axis (Source: Pianka, 1978, p. 240).

Besides these concepts of tolerance and fitness, also other concepts are useful in this context such as the concept of niche 'breadth' (or 'width' or 'size') which is simply the total sum of the variety of different resources exploited by an organismic unit (or individual or species).

It is clear that any real organismic unit does not exploit its fundamental niche (or virtual niche, i.e., the idealized niche in which the individual can live and replace itself in the absence of any competitors or other enemies), since its activities are curtailed by its competitors (or its predators). Thus the realized niche (or actual niche) is a subset of the fundamental niche, since the difference between the fundamental and realized niche reflects the effects of interspecific competition.

Another central aspect of niche theory concerns the amount of resource sharing, or niche overlap. Many ecological models (see Pianka, 1976) suggest that the maximum tolerable niche overlap should decrease as the number of competing species increases, where such a decrease in overlap would by approximation be a decaying exponential function. From a mathematical viewpoint measures of niche overlap are often divided by the estimates of the competition coefficients in the usually Lotka-Volterra competition equations (see also the next Section 3). However, it should be noticed that relationships between niche overlap and competition are dubious. For example, "although niche overlap is nearly a prerequisite to exploitative competition overlap need not necessarily lead to competition unless resources are in short supply" (cf. Pianka, 1976, p. 122).

Thus niche overlap is only a necessary but not a sufficient condition for exploitation competition. For instance, in case of complementarity (i.e., joint positive use of a resource) there may often be an inverse relationship between competition and niche overlap, so that extensive overlap might be correlated with reduced competition (see again, Pianka, 1976).

In order to clarify the above concepts but to offer at the same time a framework for confronting ecological concepts with those from the social sciences, we will in the next sections present some formal models on niches and niche chains.

### 3. EVOLUTION OF A SYSTEM BY MEANS OF 'NICHE' CHAINS

#### 3.1. Introduction

Starting from an analysis carried out by May (1973) we will show here how niche theory can be embedded in standard competition models whose potential has recently been advocated for geography

and economics (see Nijkamp and Reggiani, 1992b, as well as Section 1).

As a starting point we will analyze here the prototype model of several competing populations studied by Lotka (1925) and Volterra (1926) and interpreted on the basis of niche theory by May (1973):

$$\dot{x}_i = x_i \left( k_i - \sum_{j=1}^m \alpha_{ij} x_j \right) \quad (3.1)$$

where  $x_i$  is the population of a species  $i$  ( $i = 1, 2, \dots, m$ ), the constant  $k_i$  represents the suitability of the environment for the  $i$ th species (e.g., carrying capacity) and the competition coefficients  $\alpha_{ij}$  measure the overlap in the utilization functions depending via the ratio of  $d$  to  $w$  (see Fig. 1) on the  $i$ th and  $j$ th species. Thus model (3.1) is tied now to the underlying 'microscopic' model illustrated by Fig. 1. While first the 'macroscopic' parameters  $k_i$  and  $\alpha_{ij}$  were phenomenological constants, we have now an explicit interpretation for  $k_i$  and  $\alpha_{ij}$  in terms of direct biological assumptions (see again May, 1973). This implies also an eventual feedback between the macroscopic structure of the evolutionary process described by (3.1) and the related microscopic mechanisms displayed in Fig. 1, so that the macroscopic structures emerging from microscopic events would in turn lead to a modification of the microscopic mechanisms (i.e., niche overlapping).

Model (3.1) is not only a standard model in ecology, but has also been applied elsewhere, even without an explicit reference to niche theory. For example, system (3.1), simply interpreted as a competition system, was used by Johansson and Nijkamp (1987) in their study on urban and regional development with competing regions.

It is well-known (see Smith, 1974) that for the system of type (3.1) (for both the continuous and discrete time specification) the equilibrium - if it exists - is either stable or unstable, but in either case non-oscillatory. However, in a recent analysis (see Nijkamp and Reggiani, 1992b) the possibility of irregular behaviour emerging in case of the presence of a 'chaotic' evolution in the system has been shown. An interesting step from this latter analysis is consequently the introduction of the niche concept in such a competition system. For this purpose we will analyze in the following subsection the evolution of a competition system on the basis of equation (3.1), where we will analyze the self-organizing potential of a dynamic system with two species.

### 3.2. Evolution of self-organizing systems

Biological evolution takes normally for granted three determining factors:

a) reproduction, b) selection through competition and c) variation through "mutation" (see Nicolis and Prigogine, 1977). All these factors can be represented by a generalized equation of the type (3.1) (see Nicolis and Prigogine, 1977):

$$\dot{x}_i = N_i x_i \left[ k_i - \sum_j \beta_{ij} x_j \right] - d_i x_i + F_e(x_j) + F_r(x_i) + F_m \{ (x_j, x_i^*) \} \quad (3.2)$$

where:

$N_i$  = growth rate of species  $i$

$k_i$  = carrying capacity of species  $i$

$F_e, F_r, F_m$  = non-linear functions describing, respectively, the rate of competition other than implied by equation (3.1), the rate of regulation and the rate of migration (or movement), the latter one depending also on external values of  $x_i$ .

It is clear that from equation (3.1) many particular cases can arise, for example, the well-known prey-predator system. It is noteworthy that from equation (3.2) also the concept of 'ecological evolution' emerges as described by Allen (1988, p. 19) "The important point is that 'evolution' implies some changes of form, character or behavioural strategy, which affects the manner in which individuals perform in capturing prey, reproducing and avoiding death".

In this framework equation (3.2) may be applied to socio-cultural and economic evolution (where the population dynamics can be extended to urban and regional development, economic activities, diffusion of ideas, transport systems, etc.) in which learning mechanisms, innovations, or technological changes exist. In other words, we are facing a choice situation with different strategies which can be adopted or rejected by surrounding 'populations'.

Equations based on formulation (3.2) have been applied, for example, to urban dynamics (see Allen and Sanglier, 1981 and Camagni et al, 1985) where each center's growth path is subject to successive bifurcations which are linked to the appearance of new economic functions as well as to the pace of general technical progress. In particular, an evolutionary model of type (3.2) can be interpreted in the framework of the self-organization of systems (i.e., the inner dynamics which drive them to reconstitute themselves in new structures) (see Prigogine, 1976), where the new 'competitors', or new 'species', may be considered in terms of ecological fluctuations. These fluctuations continue and replace the old population when the new species have a better capability of exploiting the same resources, or the 'ecological' niche (see Figure 4).

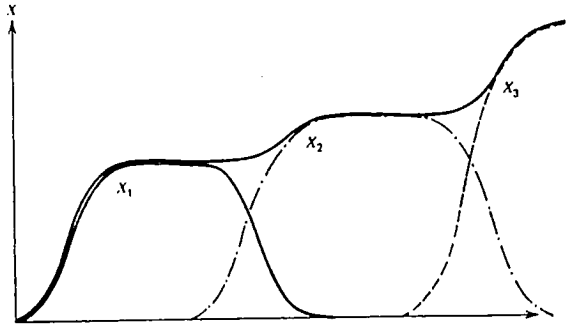


FIGURE 4. Niches occupied successively by species of increasing effectiveness.

(Source: Nicolis and Prigogine, 1977, p. 457)

A further example of the process described in Figure 4 is provided by the evolution of technological innovation, where the new series are represented by new technological products (or in general 'new technological paradigms'). But just like in ecology, each technology which replaces an old one is not capable of doing the same, but generally also generates new opportunities (see Jantsch, 1980). An empirical example of the above process can also be found in the substitution of transport infrastructures (see e.g. Figure 5 related to the U.S. context).

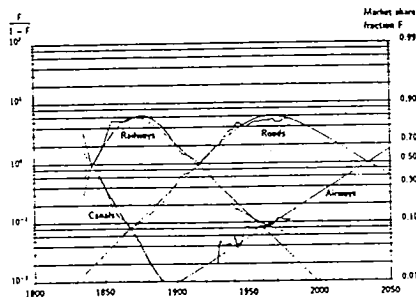


FIGURE 5. Substitution of transport infrastructures in the USA; shares in length, logit transformation.

(Source: Grübler and Nakicénovic, 1991, p. 10)

It is noteworthy that system (3.2) - which represents a hierarchy of levels of self-organisation - is also an autopoietic system, i.e. a system whose function is primarily geared to self-renewal (or self-

production) (see, for the concept of autopoiesis Maturana, 1970, and Maturana and Varela, 1975).

It is thus clear now that, from a modelling point of view, the competition coefficient  $\beta_j$  in (3.2) which represents the measure of niche overlap, plays a fundamental role in the evolution of a 'self-organizing' system, since its value generates the possibility of extinction or co-existence of species. In the next section we will consider the indigenous dynamics of such a system by examining the particular case of the evolution of two species, focusing the attention on the role played by the competition coefficient  $\beta_j$ .

#### 4. ANALYSIS OF A TWO-DIMENSIONAL NICHE SYSTEM

##### 4.1. Introduction

In this subsection we will analyze the case of two competing niches, i.e., niches occupied successively by species of increasing effectiveness, starting from the analysis carried out by Nicolis and Prigogine (1977). We will use here a particular case of system (3.2) where, for the sake of simplicity, the terms  $F_{\sigma}F_{\sigma}$  and  $F_{\sigma}$  are considered to be equal to zero. Furthermore we will examine the evolution of these two competing species in both continuous and discrete time.

Our interest is mainly oriented towards the application of the above methodology to a transport network where the competing species can be arcs or nodes to be chosen in a network, or the modes to be chosen in a segment with one origin and one destination, or - given a certain mode - different infrastructural opportunities to be selected (for example, the introduction of high speed trains).

In all these cases the analysis of time in a discrete form seems well suitable since these types of data are often discrete in nature. Moreover it is well known that results emerging from an analysis of differential equations do not always straightforwardly apply to the corresponding difference equations.

##### 4.2. A model in continuous form

For the case of two competing species, system (3.2) in continuous form can be reduced to (for  $x_1 = x$  and  $x_2 = y$ ) :

$$\begin{aligned} \dot{x} &= N_1 x (k_1 - x - \beta_1 y) - d_1 x \\ \dot{y} &= N_2 y (k_2 - y - \beta_2 x) - d_2 y \end{aligned} \quad (4.3)$$

where the meaning of the parameters is the same as in system (3.2). In a 'niche' interpretation, the competition coefficients represents a niche overlap over time, so that  $\beta_1 = \beta_2 = \beta$ . In particular for  $\beta = 0$  we have no competition (or no common resources), while for  $\beta = 1$ ,  $x$  and  $y$  completely overlap, meaning the use of the same resources. Partial overlap is consequently expressed by the condition  $0 < \beta < 1$ .

It is easy to find the conditions for the evolution of the species  $y$  by writing system (4.1) as follows:

$$\begin{aligned} \dot{x} &= x (a - bx - cy) \\ \dot{y} &= y (e - fy - gx) \end{aligned} \quad (4.2)$$

where:

$$\begin{aligned} a &= N_1 k_1 - d_1 \\ e &= N_2 k_2 - d_2 \\ b &= N_1 \\ f &= N_2 \\ c &= \beta N_1 \\ g &= \beta N_2 \end{aligned} \quad (4.3)$$

It is well known from the literature (see Smith, 1974 and Nijkamp and Reggiani, 1992b) that

a stable equilibrium exists for:

$$e/g > a/b \text{ and } a/c > e/f \tag{4.4}$$

or, by considering (4.3):

$$(k_2 - d_2 / N_2) > B (k_1 - d_1 / N_2) \tag{4.5}$$

and

$$(k_1 - d_1 / N_1) > B (k_2 - d_2 / N_2) \tag{4.6}$$

From (4.5) and (4.6) it is clear that, if the two species are limited by different resources ( $k_1$  and  $k_2$ ), the above inequalities are likely to hold, but if they have identical requirements, one of the species (the most efficient one) will eliminate its competitor. It should be noted that this latter result is also the so-called 'Gause's Principle' or 'the principle of competitive exclusion (see Smith, 1974).

By considering now condition' (4.5) we see that it represents the growth of species  $y$  up to a finite limit value, by occupying a 'niche' in the system. Then, if  $B = 1$ , condition (4.5) shows that  $y$  completely replaces  $x$ ; on the other hand, if  $B = 0$ ,  $y$  grows towards a steady population  $y^* = k_2 - (d_2 / N_2)$  and will coexist with the steady population  $x^* = k_1 - (d_1 / N_1)$ .

Consequently, conditions (4.5) and (4.6), in the interpretation of niche theory, represent the intermediate case of niche overlapping, by indicating the coexistence of  $x$  with  $y$ .

### 4.3. A model in discrete form

The specification of the discrete system related to the above competition functions (4.2) is the following:

$$x_{t+1} = x_t (n - bx_t - cy_t) \tag{4.7}$$

$$y_{t+1} = y_t (m - fy_t - gx_t)$$

where  $m = e+1$  and  $n = a+1$

It can be demonstrated that also in the case of a discrete system of type (4.7), competitive interactions do not produce oscillations (see Smith, 1974). However it is interesting to report here a recent result on competition models (see Nijkamp and Reggiani, 1992b). If the evolution of one species is chaotic (more precisely, if it follows on equation of a May-type) the whole system may exhibit the possibility of oscillating behaviour based on a Hopf bifurcation, when the carrying capacity of species  $y$  exceeds a critical threshold value.

Let us, for the sake of illustration, consider the following system:

$$x_{t+1} = x_t (n - nx_t) \tag{4.8}$$

$$y_{t+1} = y_t (m - fy_t - gx_t) < 1$$

This is a simple dominance representation of system (4.7) by supposing that species  $y$  has no impact on the evolution of species  $x$  (clearly, the evolution of  $y$  is influenced by  $x$ ).

Hypothesis (4.8) is plausible from a spatial economic viewpoint, as this may reflect hierarchy in spatial systems. This may imply, in the context of a central place situation, that high-order places (or regions) have a decisive influence on spatial interaction connections with lower-order places (or regions), without being influenced by means of feed-back effects by lower-order places.

An equilibrium analysis regarding system (4.8) shows then the existence of two fixed points: a trivial one,  $P_1 (0,0)$ , and a non-trivial one,  $P_2 [(n-1)/n; (mn - gn + g-n) / nf]$  (see also Annex B in Nijkamp



and Reggiani, 1992b). Next, a stability analysis shows for  $P_1$  unstable behaviour when  $n > 1$  and  $m > 1$ . In particular when  $m = 1/n$  we get a Hopf bifurcation.

For the second fixed point  $P_2$ , we can easily find the critical value of the carrying capacity related to region  $y$ ,  $m^*$ , at which a Hopf bifurcation (i.e., a bifurcation of a fixed point into a closed orbit) occurs, viz:

$$m^* = (gn^2 + 2n^2 - 3n - 3ng + 2g) / (n^2 - 2n) \quad (4.9)$$

This implies that when the carrying capacity of region  $y$  exceeds the critical value  $m^*$ , the fixed point  $P_2$  becomes unstable with the possibility of oscillations. An interesting remark concerns also the form of equation (4.9). It appears that  $m^*$  depends only on the competition coefficient  $g$  as well as on the growth rate of  $x$ . Thus the intrinsic growth rate of  $y$  does not influence the onset of instability of the system at hand!

Result (4.9) is indeed remarkable. It shows that, if the first competing species in system (4.7) is reduced to an equation of a May type (leading to chaos), we get in the whole system the possibility of oscillating behaviour based on Hopf bifurcations. In other words, result (4.9) underscores the relevance of the emergence of a 'chaotic' evolution, since in this case oscillations may arise in a system which in itself is not oscillatory. Some retrospective remarks on ecologically-based models will be offered in Subsection 4.4. Next, simulation experiments related to the case of a system of type (4.8) will be illustrated in Section 5, with particular reference to a simple transport model.

#### 4.4. A retrospective view

The use of ecologically-oriented paradigms in dynamic systems analysis seems to offer a new scope for analyzing evolutionary pathways in a dynamic spatial interaction system. Above we have specified a set of methodological conditions to be met in order to justify a transferability of such paradigms to the social sciences.

It turns out that the usual logical conditions (e.g., non-negativity, additivity) are easily fulfilled in such models, as this is a natural result of a common mathematical specification.

Next, there is quite a similarity between these phenomena from different worlds (or disciplines), as competitive behaviour in ecology bears a close resemblance to competition in a world of scarce resources, governed by the efficiency principle in using these resources. For instance, the functioning of cost-efficiency principles in spatial interaction models is in itself not fundamentally different from the functioning of ecosystems' efficiency goals.

Third, social science behaviour is - in the context of models presented above - based on an interweaving of spatial and socio-economic objectives of different actors whose behaviour may be either competitive or complementary.

Furthermore, the evolution of spatial interaction systems is dominated by various competition laws which may cause an extinction of some actors whose performance is sub-marginal.

And finally, the empirical validity of ecologically-based theories is difficult to validate, but simulation experiments can be used to come to grips with the empirical plausibility of such approaches. This issue will be further taken up in Section 5, where various simulation results will be presented.

## 5. SIMULATION RESULTS

### 5.1. A simple transportation model

Thus far the number of ecologically-based models in regional science is very low, while there are hardly any models in transportation science dealing with ecological niche analysis. It is clear that various examples of overlapping transportation systems in a dynamic environment can be imagined, such as mode competition, route choice, vehicle choice or systems' choice (see also Chapter 3). Here we will present - for the sake of illustration - a simple dynamic spatial interaction system based on hierarchically related transport flows.

For the sake of illustration - but without loss of generality in terms of basic thinking - we assume here a simple urban traffic system with two modes, viz. a bicycle and a car. Both modes are competing in the urban traffic system: too many bicycles slow down the speed of cars and hence discourage car use. On the other hand, too many cars are dangerous for cyclists and discourage bicycle use. Thus here we assume the logistic growth model with mutual competitive behaviour as specified in (4.7). Under normal weather conditions there might be an equilibrium configuration according to (4.7) where the mode choice is more or less stable for this type of competitive system. Moreover, as soon as the weather changes, the equilibrium solution will be affected. For instance, if it starts raining or snowing, then cyclists may be tempted to take a car, while the inverse will hardly happen. Thus depending on these initial conditions, a regime switch to system (4.8) will take place. Let us denote the dominant mode in case of rain by  $x$ , (i.e., car use), while we will denote the dependent mode (i.e., bicycle use) by  $y$ . Then it is evident that we find the hierarchical system specified in (4.8).

It is clear that many such examples in spatial systems can be found. Now the question is whether the originally non-oscillating behaviour of (4.7) may be affected by the above dominance regime to such an extent that unstable oscillating or even chaotic behaviour may emerge. This will be analyzed in Subsection 5.2 by means of simulation experiments.

5.2 Numerical experiments

As mentioned in the previous section, we will investigate here the behaviour of system (4.8) before and after reaching the critical value  $m^*$  leading to a Hopf bifurcation (see equation (4.9)).

Consequently, in the following simulations we will consider values of  $n$  which display in the conventional May equation both irregular behaviour (for example, for  $n = 3.6$ ) and chaotic behaviour (for example, for  $n = 3.9$ ).

We will therefore consider here two cases:

$$m < m^* \quad \text{and} \quad m > m^*$$

In particular, for the first simulation (Figure 6) we will assume:

$$m = 1.4 < m^* \quad n = 3.6 \quad f = 0.5 \quad g = 3$$

with the initial condition

$$x = y = 0.1$$

while for the second simulation (Figure 7) we will keep the same values, by only increasing the value of  $n$  toward the level  $n = 3.9$ .

Figures 6 and 7 show in general an unstable movement for variable  $x$  (clearly more 'chaotic' in Figure 7). Variable  $y$  reaches stability in the long run, being eliminated by  $x$  (however with some irregularity in the case of the 'chaotic' value  $n = 3.9$ ).

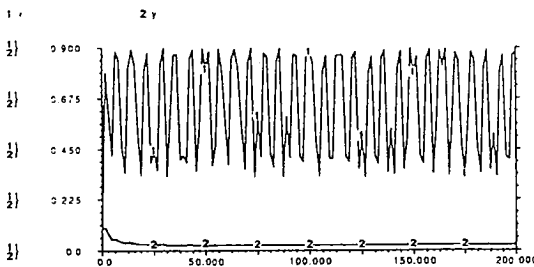


FIGURE 6. Oscillatory behaviour for car use ( $x$ ) and stable behaviour for bicycle use ( $y$ ) in case of bad weather conditions, for  $m < m^*$  and  $n = 3.6$

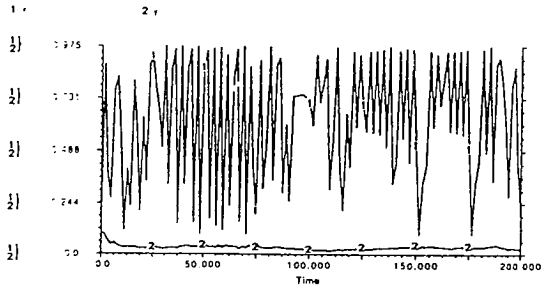


FIGURE 7. Again oscillatory behaviour for  $x$  and stable behaviour for  $y$ , for  $m < m^*$  and  $n = 3.9$ .

Let us consider now a value of the carrying capacity  $m$  beyond the critical value  $m^*$  (by keeping the same values of the other parameters utilized in the previous simulations).

Then Figure 8 shows an irregular behaviour in the evolution of variable  $y$  for the following parameter values:

$$m = 3.4 > m^* \quad n = 3.6 \quad f = 0.5 \quad g = 3$$

while Figure 9 displays an even more irregular pattern in the whole system, due to the increased value of  $n = 3.9$  (i.e., a 'chaotic' value).

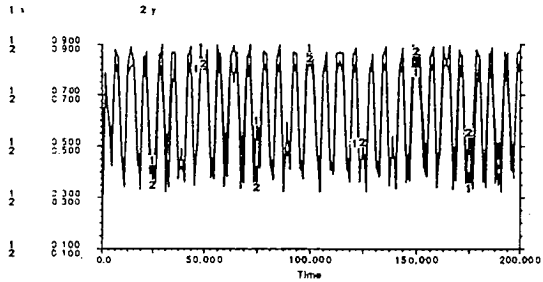


FIGURE 8. Irregular behaviour for both the variables  $x$  and  $y$  for  $m > m^*$  and  $n = 3.6$ .

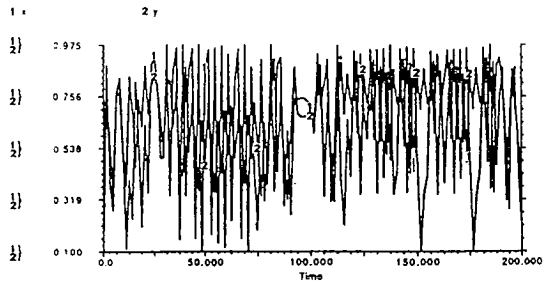


FIGURE 9. Again irregular behaviour for both the variables  $x$  and  $y$  for  $m > m^*$  and  $n = 3.9$ .

## 6. CONCLUDING REMARKS

In this paper we have shown how niche theory, derived from ecology, may offer more insight into the use of logistic functions, usually adopted by economists, for describing the evolution (introduction, adoption, etc.) of dynamic spatial-economic phenomena.

In particular a chain of niches can also be used to illustrate and interpret the evolution of a self-organizing system, in which ecological fluctuations are considered in terms of new competitors or new species.

This concept, in the framework of a transport network, with e.g. competing modes or routes, has in this paper led to the analysis of a particular case of a two-dimensional niche system. It appeared that the evolution of two competing modes may become irregular or even chaotic, as soon as - under given external initial conditions - the trajectory of one mode interacting with the other one (e.g., in a dominant choice regime) becomes turbulent.

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