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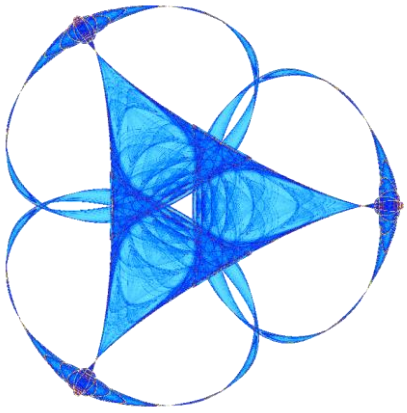

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Cristina Di Pasquale *) and Ezio Marchi **)

ABSTRACT:

The theory of niche space for different species under a situation of competition among them is considered. In other words as a general situation where all possibilities and degree of interactions might be present.

This descriptive situation is given analytically by means of a strategy game in normal form where the players involved in it are the respective species as separate entities. The total competition is given by means of the payoff functions and the strategy sets.

A modern concept of solution for cooperative games due to Schmeidler D. (1969) but modified for competitive normal games is used: the nucleolar solution. Its existence is proved.

Other interesting results proved in this paper are that the nucleolar solution, this is convex and has extremal solutions, from which all the other solutions can be derived.

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1- INTRODUCTION

Among several introductions to the study of competitive situations using game theory in biology, one is faced with important contributions, as for example Lewontin R.C. (1961) and recently Maynard Smith J. (1974). These are concerned with different aspects of the competitive questions in this field.

However much more has to be done in this appealing, important and intricate area.

In this paper we are concerned with the theory of niche space for different species in a situation of competition among them. Here the term competition as to be understood as interaction with the possibility of head on conflict or even the same interest among some of the species. In other words as a general situation where all possibilities and degrees of interactions might be present.

This descriptive situation is given analytically by means of a strategy game in normal form where players involved in it are the respective species as separate entities. The total competition is given by means of the payoff functions and the strategy sets. The first ones take into account the general interaction situation among the species.

In this first paper on the subject the food webs of the ecological interaction as considered by Cohen J. (1978) are implicitly assumed in the payoff functions of the different species. We hope to describe this in more details in the future.

As a general tool the theory we now wish to present, we use a modern concept of solution for cooperative games due to Schmeidler, D. (1969) but modified to handle the competitive normal games needed in order to present the new theory for the niche space. The concept of solution for cooperative games used is that of nucleolus, which is appealing from many points of view, in particular for its conceptual solution which in a sense involves the minimax concept.

Indeed, we use such a concept in a modified way for normal games, involving now the maximin concept. All this will be explained in detail in the paper.

2- MODEL DESCRIPTION

In this paragraph we are going to describe the model of the interactive situation among an arbitrary number of species.

Thus, consider the set of species described by a set $N = \{1, \dots, n\}$ which is technically called the set of players. An $i \in N$ described a unique species.

For the special distributions of the agents of each species in the geographical configuration we assume that field where the study is done is described as a grid in a two

dimensional space. Consider K_j with $j = 1, 2$ as a finite interval of natural numbers, then the grid n given by:

$$K = K_1 x K_2$$

that is to say the set of all positions $k = (k_1, k_2)$ with $k_1 \in K_1$ and $k_2 \in K_2$. This indeed describes in a discrete way the ecological positions of the geographical space. Only for simplicity we assume it rectangular and in two dimensions. However more general shapes of the ecological space in higher dimensions can be described without any problem.

From an ecological point of view $k = (k_1, k_2)$ describes a unit cell where individuals of the different species may live together.

The concept of the niche space is therefore introduced in a functional way by means of those points $k \in K$ with a distribution given by the number $x_{ik} \geq 0$ of individuals of species $i \in N$ lives is:

$$N_i(x) = \{k: x_{ik} > 0\}$$

In each cell of $N_i(x)$ we find individuals of the species $i \in N$. Thus, in static terms the $N_i(x)$ gives us the geographical part of the niche space.

Heuristically speaking, we have that the more overlapping among the $N_i(x)$ the more conflict among the species appears.

Now the competitive situation among the species is therefore given by payoff functions:

$$A_i(k)\ (x_{1k}, x_{2k}, \dots, x_{nk})$$

which take into consideration all the interactions among the species in the context of game theory in the geographical unit cell $k = (k_1, k_2)$, if the species are distributed by x_{ik} individuals in such a cell. Thus, x_{ik} plays the role of a strategy of species $i \in N$ in the geographic cell k.

Moreover, since here we wish to study only a static theory of the special niche, that is to say, we do not take into consideration the variation in time of the individuals of the species, we have that the total number of individuals of each species:

$$\sum_k x_{ik} = m_i > 0 \qquad \textbf{(1)}$$

is already specified and constant.

We recall that the food webs are not considered explicitly as in Cohen J. (1978) but are implicitly assumed in the payoff functions of all the species. The payoff functions biologically describe the utility for each species of having a determined number of individuals in the geographic cell k under a strategic distribution of x_{ik} by all the species.

For simplicity since the real number of individuals of the species $i \in N$ in general might be considered to be large, x_{ik} is considered to be a real non negative number. However such a restriction is not essential and can be withdrawn.

Thus, the ecological competition among the species is described in a series of generalized game with strategy x_{ik} for the species $i \in N$. This involves all the competitive situations in all the k geographical cells, constrained with the condition (1). Now any concept of solution for the ecological game gives rise to functional niches given by the family:

$$\{N_i(x), x_{ik}, i \in N, k \in K\}.$$

3- CONCEPT OF SOLUTION

Therefore it is important to introduce a somewhat strong concept of solution for our set of games. We are going to introduce a type of nucleolus already studied by Schmeidler (1969). Here the results are in the spirit of the nucleolar concepts.

First, given an element x satisfying:

$$x \in X = \underset{i \in N}{X} \quad X_i = \underset{i \in N}{X} \left\{ x_i : \sum_k x_{ik} = m_i > 0 \right\},$$

that is to say a joint strategy for all the species, we order the numbers:

$$A_i(k)(x_{1k}, \dots, x_{ik}, \dots, x_{nk})$$

varying k and i in a non- decreasing way. Thus, we have obtained a vector $\theta(x)$.

Now we say that x dominates y for $x, y \in X$, if the first component of $\theta(x)$ different from the corresponding component of $\theta(y)$ is greater. We write it as $x \geq y$ or equivalently:

$$\theta(x) \geq \theta(y)$$

We say that a distribution $x \in X$ is a nucleolar solution if $x \geq y$ for each $y \in X$.

Such a point x is one of the best in the intuitive sense that the utility of the species in the worse situation for the geographical cells is maximized. We recall that this is a type of nucleolar concept as already mentioned but is different in the context and in concept technically speaking.

Our next task is the determination of the existence of such a nucleolar solution.

Assuming that all the payoff functions $A_i(k)$ for the different geographical cells are continuous, then we have the result that the nucleolar solution $N(x)$ is non- empty.

Indeed, the set of all joint strategies X for all the species is convex, bounded, closed and non- empty.

Define now the following number, which corresponds to the first component of $\theta(x)$:

$$\theta_1(x) = \min_{J:\,|J|=1} \ \max_{(i,k)\epsilon J} \ A_i(k)\ (x_{1k}, \dots, x_{ik}, \dots, x_{nk})$$

where $|J|$ is the cardinality of the set J. Analogously the $e-th$ component of $\theta(x)$ may be seen to be given by:

$$\theta_e(x) = \min_{J:\,|J|=e} \ \max_{(i,k)\epsilon J} \ A_i(k)\ (x_{1k}, \dots, x_{ik}, \dots, x_{nk})$$

With these functions let us define the sets:

$$x^1 = \{x \in X \,/\, \theta^1(x) \geq \theta^1(y)\ \forall\, y \in X\}$$
$$x^2 = \{x \in X \,/\, \theta^2(x) \geq \theta^2(y)\ \forall\, y \in X^1\}$$
$$x^e = \{x \in X \,/\, \theta^e(x) \geq \theta^e(y)\ \forall\, y \in X^{e-1}\}$$

By the continuity of the function, the first set X^1 is non- empty, bounded and closed.

Following the same reasoning the last set $X^{|N||K|}$ results to be non- empty, bounded and closed.

It is clear that $X^{|N||K|}$ is just the set of nucleolar solutions. Thus we have the existence of the nucleolar solution. Any point in $X^{|N||K|}$ gives rise to a functional distribution x_{ik} with $i \in N$ and $k \in K$ which in terms provides a functional niche for the ecological geographical problem x_{ik}, N_i. We point out that here we use the adjective functional since the concept that we introduce is more general than a strict geographical region. This involves N_i with the corresponding distribution of species $i \in N$.

As a second relevant result we have that if all the payoff functions $A_i(k)$ for all the species and geographical cells are linear, then the nucleolar solution $N(x)$ is convex.

Indeed consider two nucleolar solutions $x, y \in N(x)$, then we have that:

$$\theta(x) = \theta(y)$$

with

$$\theta(x) = \left\{A_{i_1}(k_1)\left(x_{1k_1}, \dots, x_{ik_1}, \dots, x_{nk_1}\right), \quad A_{i_2}(k_2)\left(x_{1k_2}, \dots, x_{ik_2}, \dots, x_{nk_2}\right), \dots\right\}$$

and

$$\theta(y) = \left\{A_{\bar{i}_1}(\bar{k}_1)\left(y_{1\bar{k}_1}, \dots, y_{i\bar{k}_1}, \dots, y_{n\bar{k}_1}\right), \quad A_{\bar{i}_2}(\bar{k}_2)\left(y_{1\bar{k}_2}, \dots, y_{i\bar{k}_2}, \dots, y_{n\bar{k}_2}\right), \dots\right\}$$

We define the formation vectors:

$$a_1, a_2, \dots\dots\dots\dots, a_r$$

for both vectors as those (i,k) such that the corresponding components are all the same, therefore:

$$\begin{aligned}
&(i,k) \in a_1(x) && A_i(k)\,(x_{1k}, \dots, x_{nk}) = K_1\\
&(i,k) \in a_2(x) && A_i(k)\,(x_{1k}, \dots, x_{nk}) = K_2\\
&\dots\\
&(i,k) \in a_r(x) && A_i(k)\,(x_{1k}, \dots, x_{nk}) = K_r
\end{aligned}$$

where:

$$K_1 < K_2 < \dots\dots\dots\dots < K_r$$

We would now like to show that:

$$a_1(x) = a_1(y), \dots\dots\dots\dots, a_r(x) = a_r(y)$$

Indeed suppose the contrary, then there is a first number $1 \leq s \leq r$ such that:

$$a_s(x) \neq a_s(y),$$

which says that for an $(i,k) \in a_s(x)$ and $(i,k) \notin a_s(y)$ or viceversa. In such an instance

$$(i,k) \in a_{\bar{s}}(y)$$

for an $\bar{s} > s$, and then $A_i(k)\,(x_{1k}, \dots, x_{nk}) < A_i(k)\,(y_{1k}, \dots, y_{nk})$. The functional distribution:

$$\lambda\, x + (1-\lambda) y$$

obtained as a convex combination of x and y with $0 \leq \lambda \leq 1$ would hold:

$$\begin{aligned} & A_i(k)(\lambda\,(x_{1k}, \dots, x_{nk}) + (1-\lambda)(y_{1k}, \dots, y_{nk})) \\ &= \lambda\, A_i(k)\,(x_{1k}, \dots, x_{nk}) + (1-\lambda)\, A_i(k)(y_{1k}, \dots, y_{nk}) \\ &> \lambda\, A_i(k)\,(x_{1k}, \dots, x_{nk}) + (1-\lambda)\, A_i(k)(x_{1k}, \dots, x_{nk}) \\ &= A_i(k)\,\big(\lambda(x_{1k}, \dots, x_{nk}) + (1-\lambda)\,(x_{1k}, \dots, x_{nk})\big) = A_i(k)\,(x_{1k}, \dots, x_{nk}) \end{aligned}$$

which says that x would not be in $N(x)$. Therefore:

$$a_1(x) = a_1(y), \dots\dots\dots\dots, a_r(x) = a_r(y)\,.$$

Now having the equalities among the as we have for the convex combination:

$$\begin{aligned} & A_i(k)\big(\,(x_{1k}, \dots, x_{nk}) + (1-\lambda)(y_{1k}, \dots, y_{nk})\big) \\ &= \lambda\, A_i(k)\,(x_{1k}, \dots, x_{nk}) + (1-\lambda)\, A_i(k)(y_{1k}, \dots, y_{nk}) = A_i(k)\,(x_{1k}, \dots, x_{nk}) \\ &= A_i(k)(y_{1k}, \dots, y_{nk}) \end{aligned}$$

which implies that:

$$a_1(\lambda\, x + (1-\lambda\,)y) = a_1(x), \dots, a_r(\lambda\, x + (1-\lambda\,)y) = a_r(x)$$

Therefore the distribution $\lambda\, x + (1-\lambda\,)y$ belong to the nucleolar solution $N\,(x)$. Thus, the set of solutions $N\,(x)$ is convex.

We notice that if x and y are two different distributions in the nucleolar solution $N\,(x)$, with the corresponding $N_i\,(x)$ and $N_i\,(y)$, therefore the:

$$N_i\,(\lambda x + (1-\lambda\,)y)$$

with $0 < \lambda < 1$ is given just by:

$$N_i\,(x) \cup N_i\,(y).$$

This fact leads us to think that the nucleolar solution has extremal solutions. Indeed, we now will prove that $N\,(x)$ is a polyhedron. Consider am element $x \in N\,(x)$, then from what we have already seen, it holds true that:

$$(i,k) \in a_1(x) \qquad A_i(k)(x_{1k}, \dots, x_{nk}) = K_1$$
$$(i,k) \in a_2(x) \qquad A_i(k)(x_{1k}, \dots, x_{nk}) = K_2$$
$$\dots\dots\dots$$
$$(i,k) \in a_r(x) \qquad A_i(k)(x_{1k}, \dots, x_{nk}) = K_r$$

with:

$$K_1 < K_2 < \ \dots \ < K_r.$$

Any other point y is an element of $N\ (x)$ if and only if it satisfies:

$$(i,k) \in a_1(x) \qquad A_i(k)(y_{1k}, \dots, y_{nk}) = K_1$$
$$(i,k) \in a_2(x) \qquad A_i(k)(y_{1k}, \dots, y_{nk}) = K_2$$
$$\dots\dots\dots\dots\dots$$
$$(i,k) \in a_r(x) \qquad A_i(k)(y_{1k}, \dots, y_{nk}) = K_r$$

That together with the equalities defining the strategy sets x_i and $y_{ik} \ \geq 0$ determines geometrically a polyhedron.

This shows us that there are extremal distributions can be derived.

As a final remark we would like to point out that other concept for the nucleolar solution might be introduced when families of species are in special competition situations, as for example the double nucleolus recently studied in Cesco, J.C. and Marchi, E. (1980). Moreover various results of Kohlberg, E. (1971) with the nucleolus and others, Cesco, J.C. and Marchi, E. (1980) related with the double nucleolus might be interpreted from an ecological point of view. In particular with the functional niche. We expect to present such result together with a further analysis introducing the food webs elsewhere.

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