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SOME THRESHOLD THEOREMS OF A TWO-SPECIES COMPETING ECOLOGICAL MODEL

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ABSTRACT

In the present investigation the stability analysis of a two-species competing ecological model is highlighted in view of principle of competitive exclusion due to Gause (1934). The model is charecterised by a pair of non-linear system of ordinary differential equations. The four equilibrium states are identified and a threshold theorem is derived to establish the stability of the co-existent equilibrium state.

KEY WORDS: Competitive exclusion, Threshold results, Stability,Equilibrium states
AMS CLASSIFICATION: 92 D 25, 92 D 40

1. Basic Equations

The model equations for a two species(S_1 & S_2) competing system is given by the system of following couple of non-linear ordinary differential equations employing the following notations.

$$\frac{dN_1}{dt} = a_1N_1 - a_{11}N_1^2 - a_{12}N_1N_2 \qquad (1.1)$$

$$\frac{dN_2}{dt} = a_2 N_2 - a_{22} N_2^2 - a_{21} N_1 N_2 \qquad (1.2)$$

N_1, N_2 : Population sizes of species S_1 & S_2 respectively at time 't'

a_1, a_2 : Natural growth rates

a_{11}, a_{22} : Rates of decrease of species due to limitation of natural resources

a_{12}, a_{21} : Inhibition coefficients (Rates of decrease of each because of inhibition of other)

All these coefficients $a_1, a_2, a_{11}, a_{22}, a_{12}, a_{21} > 0$

2. Equilibrium States

Under the conditions , $\frac{dN_1}{dt} = 0$, $\frac{dN_2}{dt} = 0$ (2.1)

The competing system under investigation has four equilibrium states. They are

I. $\overline{N_1} = 0$, $\overline{N_2} = 0$ (Fully washed out state) (2.2)

II. $\overline{N_1} = 0$, $\overline{N_2} = \frac{a_2}{a_{22}}$ (S_1 washed out state) (2.3)

III. $\overline{N_1} = \frac{a_1}{a_{11}}$, $\overline{N_2} = 0$ (S_2 washed out state) (2.4)

IV. $\overline{N_1} = \frac{a_1 a_{22} - a_2 a_{12}}{a_{11} a_{22} - a_{12} a_{21}}$; $\overline{N_2} = \frac{a_2 a_{11} - a_1 a_{21}}{a_{11} a_{22} - a_{12} a_{21}}$ (Co-existent state) (2.5)

This is possible when $\frac{a_{12}}{a_{22}} < \frac{a_1}{a_2} < \frac{a_{11}}{a_{21}}$ (2.6)

The co-existent state where both species would exist is also known as "Normal steady state''.

3. Threshold Theorems

Principle of competitive exclusion (Gauss (1934)).

"Two species cannot indefinitely co-exist in the same locality if they have identical ecological requirements"

In consonance with the above principle we derive a Threshold Theorem for the co-existent equilibrium state. We write the basic equations as

$$\frac{dN_1}{dt} = \frac{a_1 N_1}{k_1}\{k_1 - N_1 - \beta_1 N_2\} \;, \quad \frac{dN_2}{dt} = \frac{a_2 N_2}{k_2}\{k_2 - N_2 - \beta_2 N_1\} \qquad (3.1)$$

where

$$k_1 = \frac{a_1}{a_{11}}; \qquad k_2 = \frac{a_2}{a_{22}}; \qquad ;\ \beta_1 = \frac{a_{12}}{a_{11}} \qquad .\ \beta_2 = \frac{a_{21}}{a_{22}}$$

Theorem 1: Principle of Competitive Exclusion for Equilibrium State IV:

$$\overline{N_1} = \frac{a_1 a_{22} - a_2 a_{12}}{a_{11} a_{22} - a_{12} a_{21}}; \overline{N_2} = \frac{a_2 a_{11} - a_1 a_{21}}{a_{11} a_{22} - a_{12} a_{21}}$$

When $\frac{k_1}{\beta_1} > k_2$ and $\frac{k_2}{\beta_2} > k_1$ then every solution ($N_1(t)$,$N_2(t)$) of (3.1) approaches the equilibrium solution $N_1(t) = \overline{N_1}(\neq 0)$ and $N_2(t) = \overline{N_2}(\neq 0)$ as t approaches infinity. In other words if species 1 and 2 are nearly identical and the microcosm can support both the members of species 1 and 2 depending up on the initial conditions.

Proof: The first step in our proof is to show that $N_1(t)$ and $N_2(t)$ can never become negative. To this end, observe that

$$N_1(t) = \overline{N_1} = \frac{a_1 a_{22} - a_2 a_{12}}{a_{11} a_{22} - a_{12} a_{21}}; \qquad N_2(t) = \overline{N_2} = \frac{a_2 a_{11} - a_1 a_{21}}{a_{11} a_{22} - a_{12} a_{21}}$$

Is a solution of (3.1) for any Choice of N1(t).The orbit of this solution in the N_1-N_2 plane is the point (0,0) for $N_1(t)=0$, $N_2=0$: the line $0<N_1<k_1.N_2=0$ for $0<N_1(t)<k_1$; the point $(k_1,0)$ for $N_1(t)=k_1$;

And the line $k_1<N_1<\infty$, $N_2=0$ for $N_1(t)>k$. thus the N_1 axis , for $N_1\geq 0$ is the union of four distinct orbits of (3.1) .Similarly the N_2 axis ,for $N_2\geq 0$ is the union of four distinct orbits of (3.1). thus implies that all solutions $(N_1(t),N_2(t))$ of (3.1) which start in the first quadrant $(N_1(t)>0,N_2(t)>0)$ of the N_1-N_2 plane must remain there for all future time.

The second step in our proof is to split the first quadrant into regions in which both $\frac{dN_1}{dt} and \frac{dN_2}{dt}$ have fixed signs. This is accomplished in the following manner.

Let l_1 and l_2 be the lines $k_1-N_1-\beta_1 N_2=0$ and $k_2-N_2-\beta_2 N_1=0$ respectively and the point of their intersection is $(\overline{N}_1,\overline{N}_2)$. Observe that $\frac{dN_1}{dt}$ is negative if (N_1,N_2) lies above the line l_1 and positive if (N_1,N_2) lies below l_2. Similarly $\frac{dN_2}{dt}$ is negative if (N_1,N_2) lies above l_2 and positive if (N_1,N_2) lies below l_2 thus the two lines $l_1$and l_2 split the first quadrant of the N_1-N_2 plane into four regions in which both $\frac{dN_1}{dt} and \frac{dN_2}{dt}$ have fixed signs.

$N_1(t)$,$N_2(t)$ both increase with time (along any solution of (3.1) in region I;

$N_1(t)$ increases and $N_2(t)$ decreases with time inregion II;

$N_1(t)$ decreases and $N_2(t)$ increases with time inregion III;

And both $N_1(t)$ and $N_2(t)$ decreases with time in region IV . in this region both the S_1 and S_2 complete with each other but do not flourish and at the same time do not get exitinct as shown in Fig 1.1

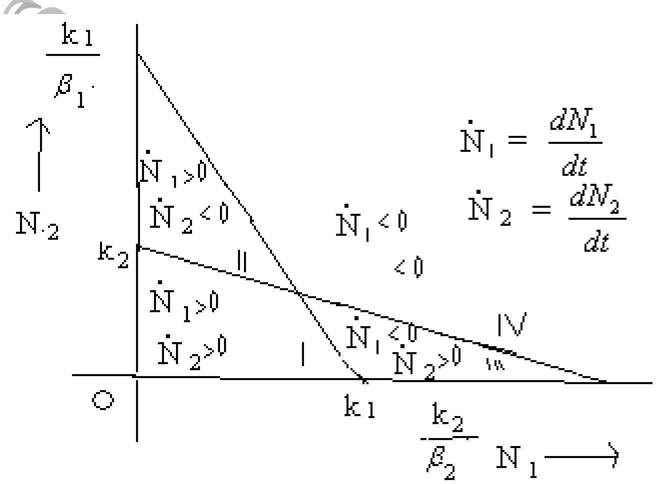

Fig.1.1

Finally we require the following four lemmas.

Lemma 1: Any Solution (N_1(t), N_2(t)) of (3.1) which starts in region I at time t=t_0 will remain in this region for all future $t \geq t_0$, and ultimately approach the equilibrium solution N_1(t)= $\overline{N_1}$, N_2(t)= $\overline{N_2}$ (Fig.1.2).

Proof: Suppose that a solution (N_1(t),N_2(t)) of (3.1) leaves region at time t=t^*. Then either $\frac{dN_1(t^*)}{dt}$ or $\frac{dN_2(t^*)}{dt}$ is zero, since the only way a solution of (3.1) can leave region is by crossing I_1 or I_2. Assume that $\frac{dN_1(t^*)}{dt}$=0. Differentiating both sides of the first equation of (3.1) with respect to t and setting t=t^* gives

$$\frac{d^2N_1(t^*)}{dt^2} = \frac{-a_1\beta_1N_1(t^*)}{k_1}\frac{dN_2(t^*)}{dt} < 0 \qquad (3.2)$$

Hence N_1(t) is monotonic increasing and it has maximum whenever a solution of N_1(t), N_2(t) of (3.1) is in region I.

Similarly, if $\frac{dN_2(t^*)}{dt}$=0

Then

$$\frac{d^2N_2(t^*)}{dt^2} = \frac{-a_2\beta_2N_2(t^*)}{k_2}\frac{dN_1(t^*)}{dt} < 0 \qquad (3.3)$$

implies that N_2(t) is monotonic increasing and it has maximum whenever a solution N_1(t), N_2(t) of (3.1) is in region I.

If a solution (N_1(t), N_2(t)) of (3.1) remains in region I for $t \geq t_0$, then both N_1(t) and N_2(t) are monotonic increasing functions of time for $t \geq t_0$, with and N_1(t)< k_1 an N_2(t)<k_2, consequently, both N_1(t) an N_2(t) have limits ξ, η respectively, as t approaches infinity. This, in turn implies that (ξ, η) is an equilibrium point of (3.1). Now, (ξ, η) obviously cannot equal (0, 0) (k_1,0) or (0, k_2) consequently (ξ, η)= $(\overline{N_1}, \overline{N_2})$.

Lemma 2: Any solution of (N_1(t), N_2(t)) of (31) which starts in region II at time t=t_0 will remain in this region for all future time $t \geq t_0$ and ultimately approach the equilibrium solution $N_1(t) = \overline{N_1}$, $N_2(t) = \overline{N_2}$ (Fig.1.2).

Proof: Suppose that a solution (N_1(t), N_2(t)) of (3.1) leaves region II at time t=t^*. Then either $\frac{dN_1(t^*)}{dt}$ or $\frac{dN_2(t^*)}{dt}$ is zero, since the only way a solution of (3.1) can leave region II is by crossing I_1 or I_2. Assume that $\frac{dN_1(t^*)}{dt}=0$. Differentiating both sides of the first equation of (3.1) with respect to t and setting t=t^* gives

$$\frac{d^2N_1(t^*)}{dt^2} = \frac{-a_1\beta_1 N_1(t^*)}{k_1}\frac{dN_2(t^*)}{dt} \tag{3.4}$$

This quantity is positive. Hence N_1(t) has a minimum at t=t^*. However this is impossible, since N_1(t) is increasing whenever a solution of (N_1(t), N_2(t)) of (3.1) is in region II.

Similarly, if $\frac{dN_2(t^*)}{dt}=0$,

Then

$$\frac{d^2N_2(t^*)}{dt^2} = \frac{-a_2\beta_2 N_2(t^*)}{k_2}\frac{dN_1(t^*)}{dt} \tag{3.5}$$

This quantity is negative. Hence N_1(t) has a maximum at t=t^*. However this is impossible, since N_2(t) is decreasing whenever a solution of (N_1(t), N_2(t)) of (3.1) is in region II.

The previous argument shows that any solution (N_1(t), N_2(t)) of (3.1) which starts in region II at time t=t_0 will remain in region II for all future time $t \geq t_0$. This implies that N_1(t) is monotonic increasing and N_2(t) is monotonic decreasing for $t \geq t_0$ with $N_1(t)<k_1$ an $N_2(t) >k_2$. Consequently both N_1(t) and N_2(t) have limits ξ, η respectively as t approaches infinity. This in turn implies that (ξ, η) is an equilibrium point of (3.1).Now obviously cannot equal (0, 0) (k_1, 0) or (0, k_2). Consequently (ξ, η)= $(\overline{N_1}, \overline{N_2})$ and this proves Lemma 2.

Lemma 3: Any solution (N_1(t), N_2(t)) of (3.1) which starts in region III at time t=t_0 will remain in this region for all future time $t \geq t_0$, and ultimately approach the equilibrium solution N_1(t) = $\overline{N_1}$, N_2(t) = $\overline{N_2}$ (Fig.1.2).

Proof: Suppose that a solution (N_1(t), N_2(t)) of (3..1) leaves region III at time t=t^*, then either $\frac{dN_1(t^*)}{dt}$ or $\frac{dN_2(t^*)}{dt}$ is zero .Since the only way a solution of (3.1) can leave region III is by crossing I_1 or I_2 . Assume that $\frac{dN_1(t^*)}{dt}$=0. Differentiating both sides of the first equation of (3.1) with respect to t and setting t=t^* gives

$$\frac{d^2N_1(t^*)}{dt^2} = \frac{-a_1\beta_1 N_1(t^*)}{k_1}\frac{dN_2(t^*)}{dt} \qquad (3.6)$$

This quantity is negative. Hence N_1(t) has a maximum at t=t^*. However this is impossible since N_1(t) is decreasing whenever a solution of (N_1(t), N_2(t)) of (3.1) is in region III.

Similarly, if $\frac{dN_2(t^*)}{dt}$=0,

Then

$$\frac{d^2N_2(t^*)}{dt^2} = \frac{-a_2\beta_2 N_2(t^*)}{k_2}\frac{dN_1(t^*)}{dt} \qquad (3.7)$$

This quantity is positive. Hence N_2(t) has a minimum at t=t^*. However this is impossible since N_2(t) is increasing whenever a solution of (N_1(t), N_2(t)) of (3.1) is in region III.
The previous argument shows that any solution N_1(t), N_2(t) of (3.1) which starts in region at time t=t_0 will remain in region III for all future time $t \geq t_0$. This implies that N_1(t) is monotonic increasing N_2 (t) is monotonic decreasing for $t \geq t_0$ with $N_1(t)>k_1$ and $N_2(t)<k_2$. Consequently both N_1(t) and N_2(t) have limits ξ, η respectively as t approaches infinity . This in turn implies that (ξ, η) is an equilibrium point of (3.1). Now (ξ, η) obviously cannot equal (0, 0) (k_1, 0) or (0, k_2). Consequently (ξ, η) = $(\overline{N_1}, \overline{N_2})$ and this proves Lemma 3.

Lemma 4: Any solution of (N_1(t), N_2(t)) of (3.1) which starts in region IV at time t will remain in this region for all future time $t \geq t_0$ and ultimately approach the equilibrium solution $N_1(t) = \overline{N_1}$, $N_2(t) = \overline{N_2}$ (Fg.1.2)

Proof: Suppose that a solution (N_1(t) ,N_2(t)) of (3.1) leaves region IV at time t=t^* .Then either $\frac{dN_1(t^*)}{dt}$ or $\frac{dN_2(t^*)}{dt}$ is zero. Since the only way a solution of (3.1) and leave region IV is by crossing I $_1$or I_2. Assume that $\frac{dN_1(t^*)}{dt}$=0. . Differentiating both sides of the first equation of (3.1) with respect to t and setting t= t^* gives

$$\frac{d^2N_1(t^*)}{dt^2} = \frac{-a_1\beta_1 N_1(t^*)}{k_1}\frac{dN_2(t^*)}{dt} \qquad (3.8)$$

This quantity is positive. Hence N_1(t) is monotonically decreasing and it has minimum whenever a solution (N_1(t), N_2(t)) of (3.1) is in region IV.

Similarly, if $\frac{dN_2(t^*)}{dt}$=0,

Then

$$\frac{d^2N_2(t^*)}{dt^2} = \frac{-a_2\beta_2 N_2(t^*)}{k_2}\frac{dN_1(t^*)}{dt} \qquad (3.9)$$

This quantity is positive, implying that N_1(t) is monotonically decreasing and it has minimum whenever a solution (N_1(t) ,N_2(t)) of (3.1) is in region IV.

If a solution (N_1(t), N_2(t)) of (3.1) remains in region IV for $t \geq t_0$, the both N_1(t) and N_2(t) are monotonic decreasing functions of time for $t \geq t_0$, with $N_1(t)>k_1$ an $N_2(t)>k_2$, consequently, both N_1(t) and N_2(t) have limits ξ, η respectively ,as t approaches infinity. This, in turn implies that (ξ, η) is an equilibrium point of (3.1). Now, obviously (ξ, η) cannot equal (0, 0) (k_1, 0) or (0, k_2). Consequently. (ξ, η) = $(\overline{N_1}, \overline{N_2})$

Proof of Theorem 1: Lemmas 1,2,3 and 4 state that every solution (N_1(t) ,N_2(t)) of (3.1) which starts in region I, II, III or IV at time t=t_0 and remains there for future time must also approach equilibrium solution N_1(t)= $\overline{N_1}$, N_2(t)=$\overline{N_2}$ as t approaches infinity. Next, observe that any solution ($N_1(t)$, $N_2(t)$) of (3.1) which starts on I_1 and I_2 must immediately afterwards enter regions I, II, III or IV. Finally the solution approaches the equilibrium solution $N_1(t)= \overline{N_1}$, $N_2(t)= \overline{N_2}$. This is illustrated in Fig.1.2

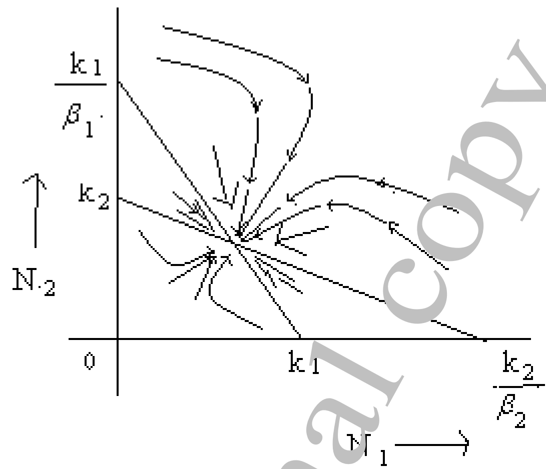

Fig.1.2

In the similar lines as above two more threshold theorems ,one for each of the non-washedout equiolibrium states are deduced below.

Theorem 2: Principle of Competitive Exclusion for Equilibrium State III

$$\overline{N_1}=\frac{a_1}{a_{11}} \; : \; \overline{N_2}=0$$

When $k_1>k_2$, then every solution ($N_1(t)$, $N_2(t)$) of (3.1) approaches the equilibrium solution $N_1 = k_1$, $N_2 = 0$ as t approaches infinity . In other words, if species 1 and 2 are nearly identical and the microcosm can support more members of species 1 than species 2, then species 2 will ultimately becomes extinct.

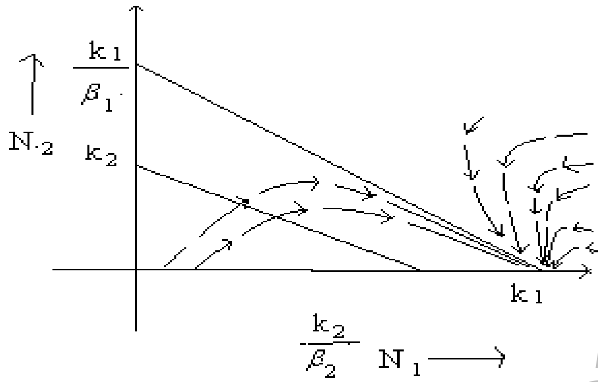

Fig1.3

Theorem 3: Principle of Competitive Exclusion for Equilibrium State II:

$$\overline{N_1} = 0 : \overline{N_2} = \frac{a_2}{a_{22}}$$

When $k_1 < k_2$, then every solution $(N_1(t), N_2(t))$ of (2.8.1) approaches the equilibrium solution $N_1=0$, $N_2=k_2$ as t approaches infinity. In other words, if species 1 and 2 are nearly identical and the microcosm can support more members of species 2 than species 1, then species 1 will ultimately becomes extinct.

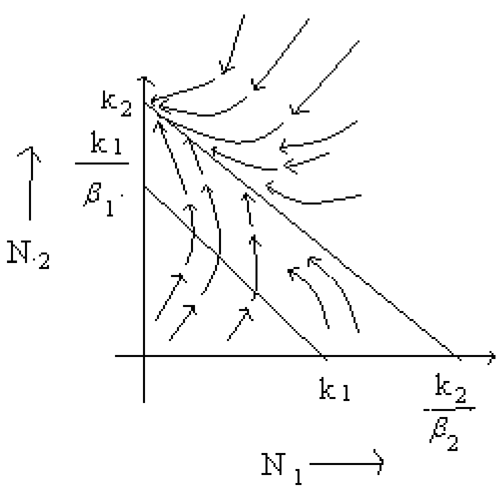

Fig.1.4

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