

The economics of ecology

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Abstract

We construct a simple economic model for a biological system using Markov chains with variable coefficients, in order to investigate how a biological system organizes itself and whether any measure of progress can be defined. We show that if exchange of resources between creatures is based on relative scarcity, we get a similar outcome to a market economy even though such exchanges are not reciprocal. An implicit price system may be defined for biological systems, and the biological economy promotes the development of specialization and interdependence - an ecology. Within the framework of this simple model, the number of creatures increases over time which may be construed as a form of progress.

Keywords: progress, non-market mechanism, biological model, genetic algorithm, Markov chain

JEL classification: C62, D21, D24, D49, D51

1. Introduction

The naive economist might imagine that the point of the 'theory of evolution' in biology is to explain biological progress, but apparently this is not so. The noted biologist Stephen Gould famously stated at the 1987 Spring Systematics Symposium at the Chicago Field Museum that "progress is a noxious, culturally embedded, untestable, nonoperational, intractable idea that must be replaced if we wish to understand the patterns of history", Gould (1988). This statement was made in the context of a wider debate on the nature of progress occurring at the time and still proceeding today. It is not possible or necessary to summarize that debate here, but biology as a discipline has gone from taking progress for granted to investigating the definition and reality of progress far more critically. Nowadays biologists prefer to

speak in terms of 'large scale trends'. McShea (1998) identifies eight trends which might be identified in evolution:

- entropy
- energy intensiveness
- evolutionary versatility
- developmental depth
- structural depth
- adaptedness
- size of creature
- complexity

Gould (1997) took the position that there are no trends which last for the entire history of evolution on earth, because things which are advantageous in one context will not be so in another. He took the apparent increase in biological complexity to reflect a simple dispersion of this characteristic from a starting point of zero, which has no broader significance.

What is interesting about McShea's list is the omission of two dimensions which to an economist would seem most obvious:

- efficiency
- total amount

We build a model of an ecology which differs from the biological models and resembles economic models in looking explicitly at resources and their processing.

The model is based on Markov chains with coefficients which are not constant but can vary over time. We investigate the development of interrelationships and complexity in the system. The conclusions are that efficiency in resource processing will increase over time, and the number (or biomass) of individuals will increase as a result. The

model is biological in a broad conceptual sense but it is a question whether enough biological detail has been incorporated to make our conclusions compelling to a practicing biologist.

2 The model

We assume an economy of atomistic creatures which may occupy various states.

Π_{M^*1} measures the quantity of these creatures in each of M states. It is convenient to break this up as per:

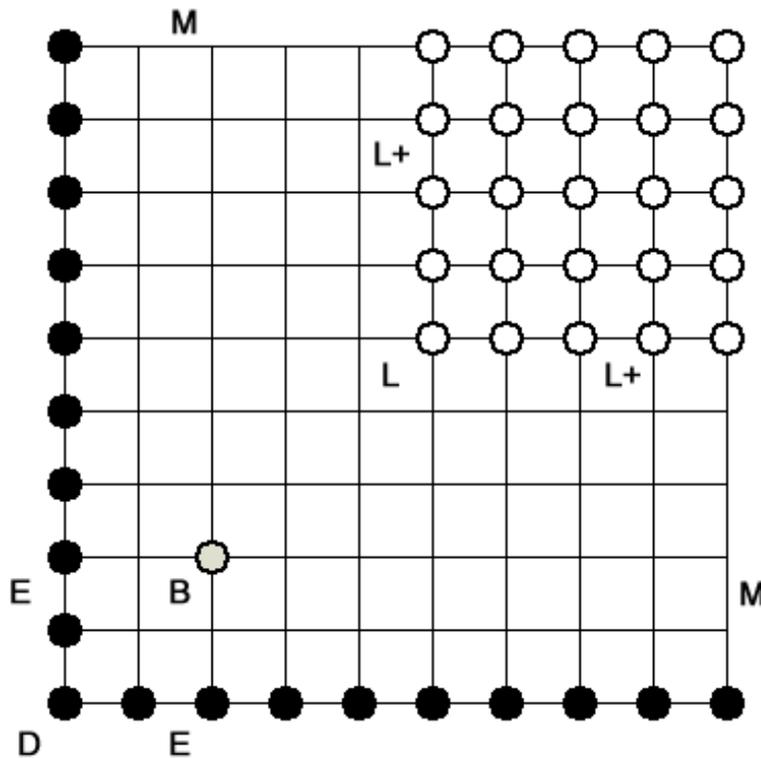
$$\Pi_{M^*1} = N_{scalar} \boldsymbol{\pi}_{M^*1} \quad (1)$$

$$\text{where } \boldsymbol{\iota}_{1^*M} \boldsymbol{\pi}_{M^*1} = 1 \quad (2)$$

i.e. the elements of $\boldsymbol{\pi}$ sum to unity, and N is a scalar which measures the number of units of creature.

There are two resources which a creature needs to sustain itself and that the creature can both produce and consume these resources. The resources are essential for survival and if the creature runs out of either one of them it dies. One of the resources is rationed: there is a finite amount of r_1 made available in the environment in each period which must be shared amongst all extant creatures. Creatures produce Resource 2, hereafter r_2 , from r_1 . Creatures are born with an initial endowment of both resources (X^{1B}, X^{2B}) , where superscript B denotes the born state B. When a creature has increased both resources to the life state L (X^{1L}, X^{2L}) it reproduces, creating S new creatures which commence their lives back at the B state. The maximum amount of resource which can be gained is (X^{1MAX}, X^{2MAX}) , but these levels are set sufficiently high that there is negligible chance, taken to be zero, of their being reached. We refer to states with a maximum level of either resource as M (maximum) states. States other than D, E or M are referred to as active states A.

There are three processes which can occur in any given period: production, consumption including reproduction and death, and trade. These occur with probabilities which may be constant, or may depend in various ways on the parameters of the system. The creature can also do nothing in the period. The situation is depicted as follows:



Processes.

- Production. In the case of r_1 , production means that the amount of resource increases by 1. There is a fixed amount of resource **in each period**, L , available to be allocated amongst N creatures, so

$$N p^{p_1} = L \quad (3)$$

where p^{p_1} is the probability of a creature producing r_1 in the period.

In the case of r_2 , production means that the amount of r_2 increases by 1 and the amount of r_1 decreases by 1.

- Consumption. For both types of resource, consumption means that the amount of resource decreases by 1, plus possible wastage. There are three subcategories:

- Metabolic
- Reproduction. When a creature has the resources required for production (X^{1L}, X^{2L}) or more and the reproduction transition is chosen, S new creatures are created at the birth state B . This does not cost any resources, i.e.

Reproduction criterion:

$$\begin{bmatrix} X^{1L} \\ X^{2L} \end{bmatrix} = S \cdot \begin{bmatrix} X^{1B} \\ X^{2B} \end{bmatrix} \quad (4)$$

If the creature reproduces from a higher state than L , there will be a reduction of net resources. This is a type of wastage referred to as L (life) wastage.

- Death. If consumption or production causes a creature to run out of a resource then it dies and is transferred to the death state D . There is no transition from the death state. The resource which has been consumed will decrease by 1 as usual, but some amount of the other resource will be lost also - this type of wastage is referred to as D (death) wastage.
- Trade. We assume that creatures move around their environment and they meet randomly. Where one creature has a resource and meets another creature, there is some chance that a unit of resource will be transferred to the other creature. The resource flow can go either way, but there is no reciprocity in a given transaction. Nor of course is there any expectation of

reciprocity in the future, although it may work out that way. Such trade is symbiotic, each creature produces resources which the other creature can use. In practice most symbiotic relationships in biology occur at the cellular level, where different kinds of bacteria have various chemical roles to play; bacteria are the chemical processing plants of the living world. Symbiotic relationships can be distinguished from parasitic relationships, where the flow of resources can only go one way. The chains of predation which we tend to associate with biology fit into this class.

We assume trading relationships which reflect relative abundance (and scarcity), and this is what gives rise to the economic character of the trading.

Trade is divided into:

- Trade in. Resources are received by the creature
- Trade out. Resources are lost by the creature
- Sitting. This means that the creature stays in its current state and nothing changes. It has residual probability remaining after other processes have been accounted for.

The transition matrix: We represent state transitions by a transition matrix $\mathbf{M}_{M \times M}$.

Each element m_{ij} of \mathbf{M} gives the probabilities of transition from state j in this period to state i in the next period, i.e. we read down the columns to see what happens to state j . The creature may remain in the same state between one period and the next, this is represented by a probability at the diagonal element m_{jj} . Each possible combination of resource amounts (X^1, X^2) corresponds to a state, so the dimension M of the matrix \mathbf{M} is equal to the number of distinct resource states, i.e.

$$M = (X^{1MAX} + 1) \cdot (X^{2MAX} + 1) \quad (5)$$

Resource states like $(X^1, 0)$ and $(0, X^2)$ which contain 0 of one resource are included to allow resource tracking but they are never occupied and their columns contain only zeros. They are referred to as empty states E. The D state also contains only zeros. It will be observed that within the columns of the matrix \mathbf{M} representing the life L and death D states, the elements do not sum to unity as probabilities are expected to, so the matrix \mathbf{M} is not exactly a Markov chain matrix. Matrices which represent reproduction such as \mathbf{M} have this characteristic - within biology they are referred to as Lesley matrices after Patrick Lesley who introduced them in the 1940s (Lesley 1945). In the biological literature the states in Lesley matrices represent different ages or developmental stages, whereas here states represent resource states.

The steady state. The distribution of the population of the creature is denoted by π_{M^*1} . The Perron-Frobenius theorem states that for an irreducible non-negative real matrix there is a unique positive real and maximal eigenvalue, and a corresponding unique real positive eigenvector. As it is possible within transition matrix \mathbf{M} to move from any states other than the D and E states to adjacent resource states (i.e. neighbouring states on the resource grid) and subsequently to any other state, \mathbf{M} is irreducible save for the D and E states. We ignore the D and E state and their corresponding rows and columns in matrix \mathbf{M} , and apply the Perron-Frobenius theorem to the remainder of \mathbf{M} . We then apply the results to \mathbf{M} by adding a zero to the eigenvectors for the D and E states.

$$\text{So } \mathbf{M}\pi = \lambda \pi \quad (6)$$

where π_{M^*1} represents the steady state distribution of population (elements sum to unity by (2)). Elements π^D , π^E are zero.

λ_{1^*1} is the rate of increase of the population per period

Also $\mathbf{vM} = \lambda \mathbf{v}$ (7)

where $\mathbf{v}_{1 \times M}$ represents the fitness coefficients (within the biological literature, the reproduction coefficients) of a population. Each element of fitness vector \mathbf{v} represents the expected number of descendants that creatures in that state will have, measured relative to other states. Here we scale eigenvector \mathbf{v} so that

$$\mathbf{v} \boldsymbol{\pi} = 1 \quad (8)$$

Elements v^D, v^E are zero.

Resources. We now introduce the resource vector $\mathbf{X}_{K \times M}$, which presents the amount of each of K resources for each state in \mathbf{M} . Here $K = 2$. The expected amount of resource held per creature $R_{K \times 1}$ is given by:

$$\mathbf{R} = \mathbf{X}\boldsymbol{\pi} \quad (9)$$

Resource matrix \mathbf{R} must be non-negative. The change in resource per creature per period is denoted $\Delta \mathbf{R}_{K \times 1}$.

RESULT 1: RESOURCE THEOREM. A population is stable (expanding, decreasing) if and only if the expected amount of resource per creature is stable (expanding, decreasing). Specifically if the population is stable then:

$$\mathbf{X}(\mathbf{M} - \mathbf{I})\boldsymbol{\pi} = \mathbf{0}_{K \times 1} \quad (10)$$

PROOF: *Expected change in resource per creature by state* = $\mathbf{X}^{final} - \mathbf{X}^{initial}$ (11)

$$= \mathbf{X}\mathbf{M} - \mathbf{X} = \mathbf{X}(\mathbf{M} - \mathbf{I}) \quad (12)$$

so $\Delta \mathbf{R} = \mathbf{X}(\mathbf{M} - \mathbf{I})\boldsymbol{\pi} = (\lambda - 1)\mathbf{X}\boldsymbol{\pi} = (\lambda - 1)\mathbf{R} \quad \#$ (13)

Creatures: We introduce different types of creature, denoted $c1$ and $c2$ and indicated by subscripts on the variables. We assume that the creatures share same set of resource requirements and states although their transition matrices might differ in certain respects. This may appear to fly in the face of the obvious differences

between different creatures, but the biochemical differences between creatures are surprisingly small on a cellular level, with similar or identical chemical processes being employed. What we observe are largely differences in scale and adaptation. Here we are interested in speciation - development of different species from one original - and the branching species will be identical in the first instance.

Stability methodology: We assume that changes in evolutionary time are relatively slow compared to the flow of generations, so only the steady state eigenvectors need to be considered and not transitory population dynamics.

3 Modelling evolution

By representing creatures and their processes with a Markov chain we have a natural entry point for imposing mutation on the production function, namely changing the elements in the transition matrix. Two distinct types of mutation can be implemented in this model:

- incremental shifts, where a transition matrix parameter is perturbed incrementally.
- Deletions, where the creature loses the ability to do something. Deletions are not incremental but involve setting parameters to zero. It is relatively easy for a creature to lose the ability to do something, since doing it requires everything to be functioning correctly. Different groups of Mexican cavefish have repeatedly and independently lost their sight over the past ten thousand to one hundred thousand years (Jeffery Strickler Yamamoto 2003).

The following result applies to incremental shifts:

RESULT 2: FITNESS THEOREM. The impact on the growth rate $d\lambda$ of a mutation in the transition matrix \mathbf{M} is given by:

$$d\lambda = \mathbf{v} d\mathbf{M} \boldsymbol{\pi} \tag{14}$$

PROOF: Differentiate (14) to get

$$d\mathbf{M}\boldsymbol{\pi} + \mathbf{M}d\boldsymbol{\pi} = d\lambda \boldsymbol{\pi} + \lambda d\boldsymbol{\pi} \quad (15)$$

$$\mathbf{v} d\mathbf{M}\boldsymbol{\pi} + \mathbf{v} \mathbf{M}d\boldsymbol{\pi} = \mathbf{v} d\lambda \boldsymbol{\pi} + \mathbf{v} \lambda d\boldsymbol{\pi} \quad \text{times } \mathbf{v} \text{ on LHS} \quad (16)$$

$$\mathbf{v} d\mathbf{M}\boldsymbol{\pi} + \lambda \mathbf{v} d\boldsymbol{\pi} = d\lambda \cdot 1 + \mathbf{v} \lambda d\boldsymbol{\pi} \quad \text{by (7), (8)} \quad \# \quad (17)$$

This result (which curiously I have not found within the biological literature) gives a very simple test of the fitness of a mutation representable by the elements of the transition matrix \mathbf{M} . We do not have to consider the change in the transition matrix $d\mathbf{M}$ in the context of changes to the population vector $d\boldsymbol{\pi}$ or the fitness vector $d\mathbf{v}$ - which may not be known - but can evaluate $d\mathbf{M}$ using the existing population and fitness vectors $\boldsymbol{\pi}$ and \mathbf{v} . It needs to be remembered that if there is no explicit formula characterizing the eigenvectors, determining the properties of the product $\mathbf{v} d\mathbf{M}\boldsymbol{\pi}$ may not be possible. Our main tool is that \mathbf{v} , $\boldsymbol{\pi}$ are strictly positive for active states A, i.e. states other than D, E and M.

As we will show, deletion mutations may have considerable evolutionary importance as they cause the creature to specialize. We now prove a variant form of the Fitness Theorem which applies to these discrete jumps in matrix coefficients.

RESULT 3: DISCRETE FITNESS THEOREM. Suppose a population is stable ($\lambda = 1$) and a coefficient in the transition matrix \mathbf{M} is set to zero and the diagonal element altered

to compensate (i.e. $m_{ij}^{new} = 0$ and $m_{jj}^{new} = m_{jj}^0 + m_{ij}^0$). Use the notation $\Delta\mathbf{M} = \begin{bmatrix} \Delta m_{ij} \\ \Delta m_{jj} \end{bmatrix}$ to

show the changes to the m_{ij} and m_{jj} elements of matrix \mathbf{M} .

$$\text{If } \mathbf{v}\Delta\mathbf{M}\boldsymbol{\pi} > 0 \quad (18)$$

$$\text{then } \mathbf{v}^{new}\mathbf{M}^{new}\boldsymbol{\pi}^{new} > 1 \quad (19)$$

where $\Delta \mathbf{M} = \begin{bmatrix} -m_{ij} \\ +m_{ij} \end{bmatrix}$, $\Delta \mathbf{M}$ is not infinitesimal,

and $\mathbf{M}^{new} = \mathbf{M}^0 + \Delta \mathbf{M}$

$$\text{PROOF: } \mathbf{v} \Delta \mathbf{M} \boldsymbol{\pi} = (-\mathbf{v}_i m_{ij} + \mathbf{v}_j m_{ij}) \boldsymbol{\pi}_j > 0 \quad (20)$$

$$\text{Construct } \mathbf{M}^1 \text{ from } \mathbf{M} \text{ by adding } \Delta \mathbf{M}^1 = \begin{bmatrix} -m_{ij} \\ m_{ij} + \frac{\mathbf{v}_i m_{ij} - \mathbf{v}_j m_{ij}}{\mathbf{v}_j} \end{bmatrix} \quad (21)$$

where $\frac{\mathbf{v}_i m_{ij} - \mathbf{v}_j m_{ij}}{\mathbf{v}_j}$ which by (20) is negative is added to the diagonal element.

$$\text{Then } \mathbf{v} \Delta \mathbf{M} \boldsymbol{\pi} = \mathbf{v}_i \cdot -m_{ij} + \mathbf{v}_j \left(m_{ij} + \frac{\mathbf{v}_i m_{ij} - \mathbf{v}_j m_{ij}}{\mathbf{v}_j} \right) = 0 \quad (22)$$

$$\text{so } \mathbf{v} \mathbf{M}^1 = \mathbf{v} (\mathbf{M} + \Delta \mathbf{M}^1) = \mathbf{v} \mathbf{M} + 0 = \mathbf{v} \quad (23)$$

So the maximal eigenvalue of \mathbf{M} remains at unity. Consider a small increase dm_{jj} in the diagonal element m_{jj} .

$$d\lambda^2 = \mathbf{v}^1 d\mathbf{M} \boldsymbol{\pi}^1 \text{ by the Fitness Theorem} \quad (24)$$

$$= \mathbf{v} \begin{bmatrix} 0 \\ dm_{jj} \end{bmatrix} \boldsymbol{\pi}_j^1 \quad (25)$$

$$> 0 \quad \text{given } \mathbf{v} > 0, dm_{jj} > 0, m_j^1 > 0 \quad (26)$$

$$\text{and so } \lambda^2 = \mathbf{v}^2 \mathbf{M}^2 \boldsymbol{\pi}^2 > \lambda^1 = 1 \quad (27)$$

We can add further infinitesimal increments dm_{jj} to m_{jj} and at each stage the eigenvalue will be greater than the step before (recall the positivity of $\mathbf{v}, \boldsymbol{\pi}$ is guaranteed by the Perron Frobenius Theorem). Proceed until the initial negative

increment $\frac{\mathbf{v}_i m_{ij} - \mathbf{v}_j m_{ij}}{\mathbf{v}_j}$ has been negated and $\mathbf{M}^n = \mathbf{M}^{new}$. Then

$$\lambda^{new} = \lambda^n > 1 \quad \# \quad (28)$$

If this criterion is satisfied by every column of the transition matrix \mathbf{M} then the deletion of the capability will enhance fitness.

4 Modelling the processes

γ_{M^*M} : the gamma matrix for a process consists of the coefficients for the process in transition matrix \mathbf{M} together with an offsetting entry in the diagonal element. There is a gamma matrix for each different process and resource. For the reproduction process (one of the consumption processes), the offset entry in the diagonal element is $-p^{REPROD}$ not $-S \cdot p^{REPROD}$. In this way we can break up the \mathbf{M} matrix into components:

$$\mathbf{M} = \mathbf{I} + \sum_{K=1,2} \gamma^{KP} + \gamma^{KC} + \gamma^{KT} + \gamma^{KD} + \gamma^{KL} \quad (29)$$

i.e.
$$\mathbf{M} - \mathbf{I} = \sum_{K=1,2} \gamma^{KP} + \gamma^{KC} + \gamma^{KT} + \gamma^{KD} + \gamma^{KL} \quad (30)$$

Γ_{M^*M} : Signature matrix. Some processes (production, consumption and trade) use signature matrices, which factor out the probability of the event and leave the elements which define the process, i.e.

$$\gamma_{M^*M} = p_{1^*1} \Gamma_{M^*M} \quad (31)$$

Usually the signature matrix Γ consists of unity elements and p , a scalar, is the probability of the process, which can vary. For the trading out signature matrix the signature matrix takes a different form given below.

$a_{1^*1}^{TYPE}$: This is the expected amount of resource generated per creature per period for the given process shown by the superscript.

$$a_{1^*1}^{TYPE} = \mathbf{X} \gamma^{TYPE} \boldsymbol{\pi} = p \mathbf{X} \Gamma^{TYPE} \boldsymbol{\pi} \quad \text{using (31)} \quad (32)$$

Now for a process at equilibrium:

$$\mathbf{X}(\mathbf{M} - \mathbf{I}) \boldsymbol{\pi} = \mathbf{0}_{K^*1} \quad \text{by (10)} \quad (33)$$

$$= p^{2P} \begin{bmatrix} -1 & -1 & -1 & \\ 1 & 1 & 1 & \end{bmatrix} \boldsymbol{\pi} \quad (40)$$

$$= p^{2P} \begin{bmatrix} -1 \\ 1 \end{bmatrix} \quad (41)$$

i.e. expression $\mathbf{X} \boldsymbol{\Gamma} \boldsymbol{\pi}$ reduces to a production vector. This can be used to apply this model to linear production theory; this is not pursued in this paper.

Consumption: Gamma γ^{KC} subtracts one from the resource. In the case of reproduction there is no resource cost as per (4). So

$$\boldsymbol{\gamma}^{KC} = \begin{bmatrix} 0 & p^{KC} & & & \\ & -p^{KC} & p^{KC} & & \\ & & -p^{KC} & p^{KC} & \\ & & & p^{KC} & \\ & & & & -p^{KC} \end{bmatrix} = p^{KC} \begin{bmatrix} 0 & 1 & & & \\ & -1 & 1 & & \\ & & -1 & 1 & \\ & & & -1 & 1 \\ & & & & -1 \end{bmatrix} = p^{KC} \boldsymbol{\Gamma}^{KC} \quad (42)$$

In the D and E states there are zeros, but there is no probability of being in these states.

$$a^{1C} = p^{1C} \begin{bmatrix} 0 & 1 & 2 & 3 \\ 2 & 2 & 2 & 2 \end{bmatrix} \begin{bmatrix} 0 & 1 & & \\ & -1 & 1 & \\ & & -1 & 1 \\ & & & -1 \end{bmatrix} \boldsymbol{\pi} = -p^{1C} \begin{bmatrix} \mathbf{1} \\ 0_{K^*1} \end{bmatrix} \boldsymbol{\pi} = - \begin{bmatrix} p^{1C} \\ 0 \end{bmatrix} \quad (43)$$

D wastage: This matrix $\boldsymbol{\gamma}^{KD}$ transfers from an E state to the D state. It is used to account for resource stocks lost when the creature dies after running out of another resource.

$$\boldsymbol{\gamma}^{KD} = \begin{bmatrix} m^D : & p^{KC} \\ m^E : & -p^{KC} \\ m^A : & \end{bmatrix} \quad (44)$$

Matrix $\boldsymbol{\gamma}^{KD}$ is added to gammas $\boldsymbol{\gamma}^{KC}$ or $\boldsymbol{\gamma}^{2P}$ to get the complete result for the transition:

$$\gamma^{KC} + \gamma^{KD} = \begin{bmatrix} m^D : \\ m^E : & p^{KC} \\ m^A : & -p^{KC} \end{bmatrix} + \begin{bmatrix} p^{KC} \\ -p^{KC} \end{bmatrix} = \begin{bmatrix} p^{KC} \\ -p^{KC} \end{bmatrix} \quad (45)$$

We see that probabilities involving the E state net out. In this way consumption can continue to conform to the rule of costing one unit of resource, which means quantity equals $-p^{KC}$. Amount of D wastage will vary for different D+ states, for instance:

$$a^{KD} = \mathbf{X} \gamma^{KD} \boldsymbol{\pi} \quad (46)$$

$$\text{e.g. } a^{KD} \text{ for state } 0,2 = \begin{bmatrix} 0 & 1 & 2 & 3 \\ 2 & 2 & 2 & 2 \end{bmatrix} \begin{bmatrix} p^{KC} \\ 0 \\ -p^{KC} \\ 0 \end{bmatrix} \boldsymbol{\pi}^{2,0} = p^{KL} \begin{bmatrix} -2 \\ 0 \end{bmatrix} \boldsymbol{\pi}^{2,0} \quad (47)$$

Consider the effect of D wastage. New creatures are created to replace the ones which have died. One creature with x^K (the average) dies and one with X^{KL} reproduces to generate two creatures with X^{KB} of resource. The average amount of resource in the population falls and the species diminishes as average levels of the resource K move closer to the lower boundary - unless the losses are made good by compensating production. D wastage is similar to consumption - a cost - but it is not constant under all conditions, nor is it the same for all species as it depends on the mortality risk imposed by the other resource processes of the creature.

L wastage: This matrix γ^{KL} is used to account for resources lost when the creature reproduces at a higher state than the L state, by transferring from a state having more resources than required for reproduction, L+, to the L state.

$$\gamma^D = \begin{bmatrix} m^B : \\ m^L : & p^{REPROD} \\ m^{L+} : & -p^{REPROD} \end{bmatrix} \quad (48)$$

Matrix γ^D , which can affect both resources, is added to gamma γ^C to get the complete result for the transition.

$$\gamma^C + \gamma^L = \begin{bmatrix} m^B : & S p^{REPROD} \\ m^L : & -p^{REPROD} \\ m^{L+} : & \end{bmatrix} + \begin{bmatrix} p^{REPROD} \\ -p^{REPROD} \end{bmatrix} = \begin{bmatrix} S p^{REPROD} \\ -p^{REPROD} \end{bmatrix} \quad (49)$$

Probabilities involving the L state net out to zero, and the rule of reproduction costing no resources is preserved. Amount of wastage will vary, for instance:

$$a^L = \mathbf{X} \gamma^L \boldsymbol{\pi} \quad (50)$$

$$a^L \text{ for state } 12,13 = \begin{bmatrix} 10 & 12 \\ 10 & 13 \end{bmatrix} \begin{bmatrix} m^{L:10,10} : & p^{REPROD} \\ m^{12,13} : & -p^{REPROD} \end{bmatrix} \boldsymbol{\pi}^{12,13} \quad (51)$$

$$= p^{REPROD} \begin{bmatrix} -2 \\ -3 \end{bmatrix} \boldsymbol{\pi}^{12,13} \quad (52)$$

Trade: The signature matrix for trading in contains unity elements, so

$$\mathbf{X}^K \boldsymbol{\Gamma}^{KTI} = \mathbf{1}_{1^*M}^K \quad (53)$$

The product $\mathbf{X}^K \boldsymbol{\Gamma}^{KTI} \boldsymbol{\pi}$ measures the creature's average level of resource requirement.

$$\mathbf{X}^K \boldsymbol{\Gamma}^{KTI} \boldsymbol{\pi} = \mathbf{1} \boldsymbol{\pi} = 1 \quad (54)$$

The signature matrix for trading out reflects relative abundance.

$$\mathbf{X}_{1^*M}^K \boldsymbol{\Gamma}_{M^*M}^{KTO} = -\mathbf{X}^K \quad (55)$$

$$\text{e.g. } \begin{bmatrix} 0 & -1 \\ & 1 & -2 \\ & & 2 & -3 \\ & & & 3 \end{bmatrix} = \begin{bmatrix} 0 & -1 & -2 & -3 \end{bmatrix} \quad (56)$$

Recall $\gamma_1^{KTO} = p_1^{KTO} \boldsymbol{\Gamma}^{KTO}$ so the elements in the gamma matrix will be smaller than these integers. At higher levels of resource X^K the elements in gamma γ_1^{KTO} are

interpreted as expected values - the probability is kept at a reasonable level and more than one unit of resource is transferred.

The product $-\mathbf{X}^K \Gamma^{KTO} \boldsymbol{\pi}$, adjusted to be positive, measures the creature's level of resource availability.

$$-\mathbf{X}^K \Gamma^{KTO} \boldsymbol{\pi} = \mathbf{X}^K \boldsymbol{\pi} = x^K \quad \text{by (55)} \quad (57)$$

where scalar x^K is the average amount of resource K held by the creature.

Trading in: The probability of c1 trading in resource K from c2 is assumed to be some proportion, c^K , of the resource availability of c2, multiplied by the number of c2 denoted N_2 .

$$p_1^{KTI} = c^K x_2^K N_2 \quad \text{by (57)} \quad (58)$$

so the trading in gamma matrix (used within the transition matrix \mathbf{M}_1 as per (30)) is:

$$\boldsymbol{\gamma}_1^{KTI} = p_1^{KTI} \Gamma^{KTI} = c^K x_2^K N_2 \Gamma^{KTI} \quad (59)$$

The expected amount of trading into c1 from c2 is given by

$$a_1^{KTI} = \mathbf{X}^K \boldsymbol{\gamma}_1^{KTI} \boldsymbol{\pi}_1 \quad \text{by (32)} \quad (60)$$

$$= \mathbf{X}^K \cdot c^K x_2^K N_2 \Gamma^{KTI} \cdot \boldsymbol{\pi}_1 \quad \text{substituting (59)} \quad (61)$$

$$= c^K x_2^K N_2 \quad \text{using (54)} \quad (62)$$

Trading out: The probability of c1 trading out to c2 is the same proportion c^K of the resource requirements of c2.

$$p_1^{KTO} = c^K \cdot 1 \cdot N_2 \quad \text{by (54)} \quad (63)$$

so the trading out gamma matrix used within \mathbf{M}_1 is:

$$\boldsymbol{\gamma}_1^{KTO} = p_1^{KTO} \Gamma^{KTO} = c^K N_2 \Gamma^{KTO} \quad (64)$$

The expected amount of trading out from c1 to c2 is given by:

$$a^{KTO} = \mathbf{X}^K \boldsymbol{\gamma}^{KTO} \boldsymbol{\pi} \quad \text{by (32)} \quad (65)$$

$$= \mathbf{X}^K \cdot c^K N_2 \Gamma^{KTO} \cdot \boldsymbol{\pi}_1 \quad \text{substituting (64)} \quad (66)$$

$$= c^K N_2 \cdot -\mathbf{X}^K \cdot \boldsymbol{\pi}_1 = -c^K x_1^K N_2 \quad \text{using (57)} \quad (67)$$

Net trade: The expected amount of net trade is given by:

$$a_1^{KT} = a_1^{KTI} + a_1^{KTO} \quad (68)$$

$$= c^K x_2^K N_2 - c^K x_1^K N_2 = N_2 c^K (x_2^K - x_1^K) \quad (69)$$

We see trade is proportional to the difference in means between the populations. Note that intra-species trade will net out to zero as there is no difference in means. The reader may ask why we didn't just assume this in the first place and leave out the tedious development, but it needs to be remembered that gamma matrices $\boldsymbol{\gamma}$ must be available for the transition matrices \mathbf{M} , so the structure given is required.

5 Price

A concept of price is implicit in the fitness coefficient \mathbf{v} - specifically we can find a price vector $\boldsymbol{\rho}$ such that

$$\boldsymbol{\rho}_{1*K} \Delta \mathbf{R}_{K*1} = \Delta \mathbf{v}_{1*1} \quad (70)$$

where $\boldsymbol{\rho}_{1*K}$ is a vector which puts a price on each of the K resources in terms of their contribution to the fitness coefficient \mathbf{v} .

$\Delta \mathbf{R}_{K*1} = \mathbf{X}_i - \mathbf{X}_j$ is the change of resources for a transition from state j to state i .

$\Delta \mathbf{v} = \mathbf{v}_i - \mathbf{v}_j$ is the change in the fitness coefficient \mathbf{v} for transition j to i .

Any given price vector $\boldsymbol{\rho}$ can hold exactly at one point, but only approximately across the resource domain.

RESULT 4: RESOURCE DOMINANCE THEOREM. Assume that the available transitions are the same at all points except boundary points, and that no transition can increase two resources at once (no Land of Cockaigne) or decrease both at once. If one point

has more of one (or more) resource than another, then its fitness coefficient is strictly greater.

$$\text{i.e. } \mathbf{X}^1 > \mathbf{X}^2 \Rightarrow \mathbf{v}^1 > \mathbf{v}^2 \quad (71)$$

PROOF. We use Markov matrix \mathbf{M}' defined earlier. Consider sequences starting at the states 1,2 corresponding to $\mathbf{X}^1, \mathbf{X}^2$. Let $\mathbf{S}_1^0, \mathbf{S}_2^0$ be $M \times 1$ vectors with unity at the element corresponding to the state. If we start at \mathbf{S}_1^0 , the subsequent distribution of outcomes \mathbf{S}_1^n in period n is given by:

$$\mathbf{S}_1^n = (\mathbf{M}')^n \mathbf{S}_1 \quad (72)$$

Break up Markov matrix \mathbf{M}' into the probability of each possible step and a matrix $\mathbf{D}_{M \times M}$ which consists of unity elements which show the change in state of the step. So

$$\mathbf{M}'\mathbf{S}_1^1 = \sum_{\text{all possible transitions } D1} p^1 \mathbf{D}^1 \mathbf{S}_1^0 \quad (73)$$

Continue likewise with the next step.

$$(\mathbf{M}')^2 \mathbf{S}_1^1 = \sum_{\text{all possible transitions } D1, D2} p^1 p^2 \mathbf{D}^1 \mathbf{D}^2 \mathbf{S}_1^0 \quad (74)$$

and so forth. Refer to each matrix $\mathbf{D}^n \dots \mathbf{D}^2 \mathbf{D}^1$ of relative state transitions as a path.

We can apply the same path to states 1 and 2 because the same transitions are available at each non boundary point, the associated probabilities $p^n \dots p^2 p^1$ will differ for state 2. Where the path meets a boundary in resource space then the same transitions may not be available to both states but because the resource domain is rectangular the following situations apply:

- The path reaches an E state for state 2 but not for state 1. In this case the path terminates for state 2 and increases $P(D)$, but it goes on for state 1.

- The path reaches an L or L+ state and consequently the LA state, for state 1 but not for state 2. In this case the path terminates for state 1 and increases $P(L)$, but continues for state 2.
- The path reaches a maximum resource state when applied to state 1 but not for state 2. In this case the next move must be available to state 1, and consequently to state 2.

Thus for all n greater than some initial threshold, there are paths reaching L and D in each period:

$$P(D)_1^n < P(D)_2^n, \quad P(L)_1^n > P(L)_2^n \quad (75)$$

and the discrepancy increases as n increases.

$$\text{Now } \lim_{n \rightarrow \infty} P(L)^n + P(D)^n = 1 \quad (76)$$

$$\text{So } P(L)_1 > P(L)_2 \quad (77)$$

The LHS eigenvalue \mathbf{v} is equivalent to the probability of success (reaching state L) up to a proportionality constant. Thus (77) can be restated as $\mathbf{v}^1 > \mathbf{v}^2$ #

RESULT 5: POSITIVE PRICE. The price of a resource \mathbf{p}^K is always strictly positive.

$$\text{PROOF: } \mathbf{p} \Delta \mathbf{R} = \Delta \mathbf{v} \text{ definition (70)} \quad (78)$$

$$\mathbf{p}^K \cdot 1 = \mathbf{v}^{K N+1} - \mathbf{v}^{KN} > 0 \text{ by previous result } \# \quad (79)$$

Constant price: Finally we can show that if a particular matrix transition gave the same change in fitness coefficient across the entire resource domain, then a constant price vector would apply across the resource domain. This assumption is never realized for the model as defined, so the result could be taken as suggesting that a constant price vector cannot apply across the domain. Nonetheless it will be approximately correct if both resources are acquired in a fair game (chance of gaining

a unit of resource is equal to the chance of losing it) because in such a situation, the fitness coefficient vector \mathbf{v} is close to linear in the resources as per (110).

RESULT 6: PRICE THEOREM. If transitions producing the same change in resources $\Delta\mathbf{R}$ result in the same change in fitness coefficient $\Delta\mathbf{v}$ at every state in resource space, then there is a constant vector $\boldsymbol{\rho}$ satisfying

$$\boldsymbol{\rho} \Delta\mathbf{R} = \Delta\mathbf{v} \quad (80)$$

PROOF: Assemble independent vectors $\Delta\mathbf{R}_{K \times K} = [\Delta\mathbf{R}_1 \quad \Delta\mathbf{R}_2 \quad \Delta\mathbf{R}_K]$, there must be K to ensure any transition is possible. Assemble corresponding $\Delta\mathbf{v}_{1 \times K} = [\Delta\mathbf{v}_1 \quad \Delta\mathbf{v}_2 \quad \Delta\mathbf{v}_J]$ which are constant by assumption. As $\Delta\mathbf{R}$ has full rank, solution $\boldsymbol{\rho}$ is available to:

$$\boldsymbol{\rho} \cdot [\Delta\mathbf{R}_1 \quad \Delta\mathbf{R}_2 \quad \Delta\mathbf{R}_J] = [\Delta\mathbf{v}_1 \quad \Delta\mathbf{v}_2 \quad \Delta\mathbf{v}_J] \quad (81)$$

Now consider any other transition vector $\Delta\mathbf{R}_A$. It must be expressible as:

$$[\Delta\mathbf{R} \quad \Delta\mathbf{R}_A] \begin{bmatrix} \mathbf{y}_{\text{basis}} \\ y_A \end{bmatrix} = 0 \quad \text{where} \quad \begin{bmatrix} \mathbf{y}_{\text{basis}} \\ y_A \end{bmatrix} \neq \mathbf{0} \text{ and integral} \quad (82)$$

Corresponding $\Delta\mathbf{v}$ must also satisfy

$$[\Delta\mathbf{v} \quad \Delta\mathbf{v}_A] \begin{bmatrix} \mathbf{y}_{\text{basis}} \\ y_A \end{bmatrix} = 0 \quad \text{as round trip has } \Delta\mathbf{v} = 0, \Delta\mathbf{v} \text{ same everywhere} \quad (83)$$

$$(\boldsymbol{\rho}\Delta\mathbf{R} - \Delta\mathbf{v}) \mathbf{y}_{\text{basis}} + (\boldsymbol{\rho}\Delta\mathbf{R}_A - \Delta\mathbf{v}_A) y_A = 0 \quad \boldsymbol{\rho} \text{ times (82) minus (83)} \quad (84)$$

$$\text{so} \quad (\boldsymbol{\rho}\Delta\mathbf{R}_A - \Delta\mathbf{v}_A) y_A = 0 \quad \text{using (81).} \quad y_A \neq 0 \text{ so result follows \#} \quad (85)$$

6. Existence results

Although the existence of an eigenvalues and eigenvectors for a transition matrix \mathbf{M} is guaranteed by the Perron Frobenius theorem, it does not follow from this that a stable equilibrium with eigenvalue $\lambda = 1$ exists. We start here by proving existence for the simple case without trade. For the purposes of this section the given reproduction

ratio is denoted S^* not S . It is important to realize that other reproduction ratios S'' do not satisfy the Reproduction Criterion (4), but this does not affect the other properties of matrices constructed with a given reproduction ratio S'' .

Definition:

p^{MAX} : the highest probability which can be assigned to production probability p^{P1} .

Associated Markov chain matrix. It is useful to define a Markov chain matrix \mathbf{M}' associated with the transition matrix \mathbf{M} . Markov matrix \mathbf{M}' has been modified so

- instead of transferring to B, each L and L+ state transfers to an absorbing state LA with probability p^{REPROD} . LA has 1 at its diagonal element, and will have fitness coefficient:

$$v^{LA} = Sv^B \quad (86)$$

- The E states transfer to D state with probability 1.
- D state has 1 at its diagonal element and becomes an absorbing element.

Such a matrix will satisfy eigenvector \mathbf{v} of \mathbf{M} and avoids any complications associated with the transit from the L state to the B state.

RESULT 7: PROBABILITY OF SUCCESS. If the population is stable, the probability at birth B of a creature reaching state LA (i.e. the win state) is given by:

$$P^{LA} = \frac{1}{S} \quad (87)$$

PROOF: The LHS eigenvector \mathbf{v} gives the expected number of descendants in every state. From \mathbf{v} take the entries for state B and the absorbing states D, LA.

$$v^B = P^D v^D + P^{LA} (v^{LA}) \quad (88)$$

$$v^B = P^D \cdot 0 + P^{LA} \cdot v^B S \quad \text{by (86) Rearrange for result \#} \quad (89)$$

RESULT 8: EXISTENCE OF STABLE REPRODUCTION RATIO. For every positive production probability p^{1P} up to p^{MAX} , there exists reproduction ratio $S''(p^{1P})$ such that transition matrix \mathbf{M}'' constructed using S'' is stable, i.e. has unity eigenvalue.

PROOF: Consider $\mathbf{M}(p^{1P})$ with reproduction ratio S^* . Construct associated Markov

matrix $\mathbf{M}'(p)$. $\mathbf{M}'(p)$ has RHS eigenvector $\begin{bmatrix} 0 \\ 0 \\ m^{LA} = 1 \end{bmatrix}$ with eigenvalue $\lambda = 1$.

Then $\mathbf{v}\mathbf{M}' = \mathbf{v}$ where \mathbf{v} is corresponding LHS eigenvector (90)

Eigenvector \mathbf{v} is unique and positive except for D and E state elements (apply Perron Frobenius theorem to an irreducible matrix close to \mathbf{M}' and use limiting argument).

Find $S'' = \frac{v^{LA}}{v^B}$ (91)

Create $\mathbf{M}''(p^{1P})$ as a transition matrix identical to $\mathbf{M}(p^{1P})$ except using S'' instead of S^* . Then

$$\mathbf{v}\mathbf{M}'' = \mathbf{v} \quad \text{i.e. } \lambda = 1 \quad \# \quad (92)$$

RESULT 9: CONTINUOUS MONOTONIC S FUNCTION. Reproduction ratio S'' is a monotonically decreasing function of production probability $p^{1P} \leq p^{MAX}$.

PROOF: Consider p^{MAX} and its reproduction ratio S^{MIN} . For a change in p^{1P} , the corresponding change in S'' which is necessary to maintain stability is given by

$$d\lambda = \mathbf{v} d\mathbf{M} \boldsymbol{\pi} = \mathbf{v} (d\boldsymbol{\gamma}^{1P} + d\boldsymbol{\gamma}^{RE}) \boldsymbol{\pi} \quad \text{by (14)} \quad (93)$$

$$\text{where } d\boldsymbol{\gamma}^{RE} = \frac{d}{\partial S} \begin{bmatrix} Sp^{RE} & Sp^{RE} \\ -p^{RE} & -p^{RE} \end{bmatrix} dS = \begin{bmatrix} p^{RE} & p^{RE} \\ & \end{bmatrix} dS = \boldsymbol{\Gamma}^{RE} dS \quad (94)$$

$$\text{so } d\lambda = \mathbf{v} (dp^{1P} \boldsymbol{\Gamma}^{1P} + dS \boldsymbol{\Gamma}^{RE}) \boldsymbol{\pi} \quad (95)$$

$$0 = v dp^{1P} \Gamma^{1P} \boldsymbol{\pi} + v dS \Gamma^{RE} \boldsymbol{\pi} \quad \text{setting } d\lambda = 0. \text{ This establishes continuity. (96)}$$

$$\frac{dS}{dp^{1P}} = -\frac{v \Gamma^{1P} \boldsymbol{\pi}}{v \Gamma^{RE} \boldsymbol{\pi}} < 0 \quad \text{as } v \Gamma^{1P} \boldsymbol{\pi} > 0 \text{ see (39),(79), } v \Gamma^{RE} \boldsymbol{\pi} > 0 \text{ see (94) \# (97)}$$

RESULT 10: UNBOUNDED S FUNCTION. Reproduction ratio $S(p^{P1})$ is upper unbounded.

$$P^{LA} = \sum_{\substack{\text{all paths} \\ \text{reaching} \\ LA}} P(\text{path}) = \sum_{\substack{\text{all paths} \\ \text{reaching} \\ LA}} p_1 p_2 \dots p_n \quad \text{where } p_i \text{ is probability of step } i. \quad (98)$$

Say the minimum number of steps to reach state LA from B is T.

$$P^{LA} = \sum_{\substack{\text{all paths} \\ \text{reaching} \\ LA}} (p^{1P})^T p_{T+1} \dots p_n \quad (99)$$

$$= (p^{1P})^T \sum_{\substack{\text{all paths} \\ \text{reaching} \\ LA}} p_{T+1} \dots p_n \quad (100)$$

$$< \varepsilon \quad \text{for } p^{1P} < \varepsilon^{1/T} \quad (101)$$

$$\text{so } S'' > \frac{1}{\varepsilon} \quad \text{for } p^{1P} < \varepsilon^{1/T} \quad \text{by (87) \# (102)}$$

RESULT 11: SIMPLE CASE EXISTENCE. For reproduction coefficient $S^* \geq S^{MIN}$, there exists unique $p^{1P^*}, N^*, \boldsymbol{\pi}^*$ to the system such that:

$$\mathbf{M}(p^{1P^*}) \boldsymbol{\pi}^* = \boldsymbol{\pi}^* \quad (103)$$

$$N^* p^{1P^*} = L \quad (104)$$

PROOF: By Results 9,10, for $S \geq S^{MIN}$ there exists continuous monotonic f such that

$$S'' = f(p^{1P}) \quad (105)$$

$$\text{So } p^{1P^*} = f^{-1}(S^*) \quad p^{1P^*} \text{ is unique} \quad (106)$$

$$\mathbf{M}^* = \mathbf{M}''(p^{1P^*}) \quad \text{i.e. } S^* = S''(p^{1P^*}) \quad (107)$$

$$\lambda(\mathbf{M}^*) = \lambda(\mathbf{M}^n) = 1 \text{ and } \boldsymbol{\pi}(\mathbf{M}^*) \text{ is unique by Perron Frobenius.} \quad (108)$$

$$N^* = \frac{L}{p^{1P^*}} \text{ is unique as } p^{1P^*} \text{ is unique.} \quad \# \quad (109)$$

Existence in the trade case: When trade is introduced the problem becomes more difficult. The matrix \mathbf{M} is itself a function of a number of variables, not just probability p^{1P} but average x and quantity N variables. The eigenvalues and eigenvectors $\mathbf{v}, \boldsymbol{\pi}$ of \mathbf{M} are used in generating values of average x and quantity N which are not necessarily the same as the initial values.

7. Some heuristic results for resources

Standard results from classical ruin theory: The situation in the two resources of a creature represent two interconnected random walk problems. Standard results on random walk assume the probability of increase p and decrease q sum to unity and are constant over the domain. These premises are not exactly satisfied here but the results are indicative. In the following, ruin occurs when a particle hits 0 and success occurs at T a positive integer, the particle starts at t , an integer between the two.

- P_t^L , probability of success starting from t :

$$P_t^L = \frac{t}{T} \quad p = q \quad (110)$$

$$= \frac{1 - \left(\frac{q}{p}\right)^t}{1 - \left(\frac{q}{p}\right)^T} \quad p \neq q \quad (111)$$

$$\approx 1 \quad p \gg q \quad (112)$$

- D_t , duration of game starting from t :

$$D_t = t(T - t) \quad p = q \quad (113)$$

$$= \frac{T \cdot P_t^L - t}{p - q} \quad p \neq q \quad (114)$$

$$\approx \frac{T - t}{p - q} = \frac{\text{Distance to travel}}{\text{Expected gain per period}} \quad p \gg q \quad (115)$$

We see that duration is a function of T for a reasonably favourable game, but for a fair game ($p = q$) duration is a function of T^2 , a higher order term. This determines the nature of trade.

Positive, neutral and negative production: We define gross production in resource K per creature per period, a^{KG} , as the net of production, consumption and D wastage. It does not include trade or L wastage.

$$a^{KG} = a^{KP} + a^{KC} + a^{KD} \quad (116)$$

We define net production in resource K per creature per period, a^{KN} , as gross production plus net trade. L wastage is still excluded.

$$a^{KN} = a^{KP} + a^{KC} + a^{KD} + a^{KT} \quad (117)$$

If production sums to zero we refer to the process as being neutral. If production is positive (negative) we say the process is positive (negative). This applies to both gross and net measures.

We make the following heuristic assumption:

ASSUMPTION: POSITIVE PROCESS. If a resource process is positive then the probability of that resource running out is zero.

RESULT 12: NO NEGATIVE PROCESS. A creature cannot be net negative in a resource.

PROOF: If a creature were net negative, i.e. $a^{KN} < 0$, then

$$a^{K\text{TOTAL}} = a^{KN} + a^{KL} < 0 + 0, \text{ contrary to (10). } \# \quad (118)$$

RESULT 13: AT LEAST ONE NEUTRAL PROCESS. The creature cannot have positive net production in every process at equilibrium; net production in at least one process must be neutral.

PROOF: Suppose all resources have net positive processes. Expected time for a positive process to reach \mathbf{X}^{KL} in all resources K is:

$$D = \max_{K=1,2} \left(\frac{\mathbf{X}^{KL} - \mathbf{X}^{KB}}{a^{KN}} \right) \text{ restating (115) in our notation} \quad (119)$$

Suppose that K is the slowest resource. Then

$$a^{KL} \approx 0 \quad \text{the creature reproduces as soon as } K \text{ process reaches } \mathbf{X}^{KL} \quad (120)$$

$$a^{KP} + a^{KC} + a^{KD} + a^{KT} + a^{KL} = a^{KN} + 0 \quad (121)$$

$$> 0 \quad \text{by premise.} \quad \text{This contradicts (13)} \quad \# \quad (122)$$

RESULT 14 HABITAT THEOREM. If a creature is net neutral in resource K ,

$$x^K = \mathbf{X}^{KB} \quad (123)$$

PROOF: By Result 6, creature must be net neutral in at least one resource, J say.

$$D^J = k^J (\mathbf{X}^{JL})^2 \quad k^J \text{ is some constant, by (113)} \quad (124)$$

For a neutral resource,

$$x^J = \mathbf{X}^{JB} + \text{net gain} \cdot \text{average duration of process} \quad (125)$$

$$\approx \mathbf{X}^{JB} + 0 \cdot \frac{D^J}{2} = \mathbf{X}^{JB} \quad \# \quad (126)$$

A positive resource reaches its requirement \mathbf{X}^{KL} an order of magnitude sooner than neutral resource J but has to 'wait for it' there until the creature has a full quota of all resources and can reproduce.

RESULT 15: NET TRADE. If one creature $c1$ is net positive and another $c2$ is net neutral then trade is given by:

$$a_1^{KT} = N_2 c^K (\mathbf{X}^{KB} - x_1^K) \quad (127)$$

$$a_2^{KT} = N_1 c^K (x_1^K - \mathbf{X}^{KB}) \quad (128)$$

Result follows immediately from Result 7 Habitat theorem. The distinctive dynamic of trading is that c1 must remain in positive accumulation, and c2 in a random walk, to sustain it. If c2 does so well that it is positively accumulating then the average resource holding x_2^K will rise above \mathbf{X}^{KB} , and this will close off the flow of trade. Similarly if c1 loses so much resource that it can no longer positively accumulate, then average holding x_1^K will fall below \mathbf{X}^{KMAX} and again choke off the trade. At equilibrium c1 must maintain some margin of net production which allows it to maintain a level of average resource x^K higher than neutral level X^{KB} .

The following results work the other way around, inferring production strength from trading.

RESULT 16: POSITIVE FOR TRADE OUT. If a creature trades out resource K then it is net positive and gross positive in K .

PROOF: If c1 is neutral in a resource then

$$a_1^{KT} = N_2 c^K (x_2^K - \mathbf{X}^{KB}) \quad \text{by (123)} \quad (129)$$

$$\geq N_2 c^K (\mathbf{X}^{KB} - \mathbf{X}^{KB}) = 0 \text{ i.e. c1 is not trading out. Take contrapositive.} \quad (130)$$

$$\text{So } a^{KN} = a^{KG} + a^{KT} > 0 \quad \text{since c1 is net positive in } K \quad (131)$$

$$\text{so } a^{KG} > 0 \text{ as } a^{KT} < 0 \quad \text{by premise \#} \quad (132)$$

RESULT 17: COMPARATIVE PRODUCTION. If a creature's gross production exceeds another's in a resource, i.e.

$$a_1^{KG} > a_2^{KG} \quad (133)$$

then the creature is net positive in that resource.

PROOF: Assume not, then the creature c1 is net neutral.

$$\text{Then } a_1^{KT} = N_2 c^K (x_2^K - \mathbf{X}^{XB}) \geq 0 \quad \text{by (123)} \quad (134)$$

$$\text{so } a_2^{KT} \leq 0 \quad \text{i.e. trade is negative for c2} \quad (135)$$

$$\text{Now } a_1^{KN} = a_1^{KG} + a_1^{KT} \quad \text{i.e. } 0 = a_1^{KG} + a_1^{KT} \quad (136)$$

$$\text{so } a_1^{KG} \leq 0 \quad \text{by (134)} \quad (137)$$

$$\text{so } a_2^{KG} < 0 \quad \text{by (133)} \quad (138)$$

$$\text{Now } a_2^{K \text{ TOTAL}} = a_2^{KG} + a_2^{KT} + a_2^{KL} \quad \text{by definition} \quad (139)$$

$$< 0 + 0 + 0 \quad \text{by (138), (135), } a^{KL} \leq 0. \text{ Contra (10) \#} \quad (140)$$

RESULT 18: MAXIMUM TRADE OUT.

$$a^{KT} > a^{KL} \quad \text{in absence of trade} \quad (141)$$

$$\text{or } |a^{KT}| < |a^{KL} \quad \text{in absence of trade}| \quad \text{more intuitively given both are negative} \quad (142)$$

PROOF. For trade out, net production is must be positive by Result 10.

$$a^{KN} > 0 \quad (143)$$

$$\text{i.e. } a^{KP} + a^{KC} + a^{KD} + a^{KT} > 0 \quad \text{by (117)} \quad (144)$$

$$= a^{KP} + a^{KC} + a^{KD} + a^{KL} \quad \text{in absence of trade} \quad \text{by (10)} \quad (145)$$

$$\text{so } a^{KT} > a^{KL} \quad \text{in absence of trade} \quad \text{subtracting from both sides} \quad (146)$$

RESULT 19: TWO POSITIVE PROCESSES. If two different creatures are both gross positive in a resource, the creatures will be net positive in that resource as well.

PROOF: Suppose c1 trades out to c2 in resource K .

By Result 16, c1 must be net positive in K .

c2 is gross positive and receives more K from trade so is net positive in K . #

Death wastage: Death wastage in resource K occurs when a creature dies because it has run out of another resource. This must be a net neutral resource, because net

positive resources are assumed to have no chance of reaching zero. By Result 6 every creature must have at least one net neutral resource. It is possible for a creature to have more than one net neutral resource. In this case every process will have a death wastage component.

8. Evolution of ecologies

One creature: Assume the following:

- c1 produces r2 from r1 via the production process $\begin{bmatrix} -1 \\ 1 \end{bmatrix}$, i.e. one unit of r1 is used to produce a unit of r2.
- Production of r2 exceeds the need for it, so r2 is a gross positive process.

It follows by Result 13 that r1 is a neutral process, so $a^{1D} = 0, a^{1L} = 0$.

The system is (each row represents a resource, denoted by superscript 1,2) given

below. There are three equations in three unknowns N, x_2^1, a^{1P} . Processes

a^{2P}, a^{1C}, a^{2C} are constant with respect to amount N but production a^{1P} varies with amount N .

$$\begin{bmatrix} a^{1P} & -a^{2P} & a^{1C} & \\ & a^{2P} & a^{2C} & a^{2W} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \quad (147)$$

$$Na^{1P} = L \quad (148)$$

RESULT 20: SINGLE SPECIES EQUILIBRIUM. Total population is given by

$$N = -\frac{L}{a^{1C} + a^{2C} + a^{2W}} \quad (\text{note this is positive}) \quad (149)$$

PROOF: Add (147)A and (147)B to get:

$$a^{1P} + a^{1C} + a^{2C} + a^{2W} = 0 \quad (150)$$

$$\frac{L}{N} + a^{1C} + a^{2C} + a^{2W} = 0 \quad \text{sub } a^{1P} \text{ (148). Rearrange for result. \#} \quad (151)$$

Two creatures, incremental mutation case: Introduce a creature with an incremental mutation, so there are now two types of creature, one with the original transition matrix \mathbf{M} and the other with new transition matrix $\mathbf{M}_1 = \mathbf{M} + d\mathbf{M}$.

RESULT 21: INCREMENTAL MUTATION. If the mutation affects a neutral process, only one type of creature can survive in equilibrium.

PROOF: Denote original creature c_1 and suppose r_1 is its neutral process. Suppose firstly that the mutation is positive so new creature c_2 is more efficient in producing r_1 than c_1 . Process r_2 is unaffected so is gross positive for both creatures.

Assume c_1 and c_2 both survive in equilibrium.

By Result 17, c_2 is net positive in r_1 .

By Result 19, c_2 is net positive in r_2 .

By Result 13, c_2 is not net positive in both processes. CONTRA.

Similarly if the mutation is negative #

To see what happens in practice we employ a dynamic argument. Assess the fitness of the new creature c_2 using the Result 2 Incremental Fitness Theorem. If criterion $\mathbf{v}d\mathbf{M}\boldsymbol{\pi} < 0$, rate of increase $d\lambda < 0$ and c_2 will go extinct immediately. If $\mathbf{v}d\mathbf{M}\boldsymbol{\pi} > 0$ then $d\lambda > 0$ and c_2 will increase. As the total number of creatures N increases, the probability of production of r_1 , p^{r_1} , will decrease pursuant to resource constraint (148) and this impacts on both creatures. For c_2 , the decrease in p^{r_1} will reduce $\mathbf{v}d\mathbf{M}\boldsymbol{\pi}$ and rate of increase $d\lambda$ but c_2 will remain viable. For c_1 , decrease in p^{r_1} leads to $\mathbf{v}d\mathbf{M}\boldsymbol{\pi} < 0$ and $d\lambda < 0$. c_1 will reduce until it is extinct. The population size N will have been increased.

Two creatures, deletion mutation case: Given the excess of r_2 , Result 3 Discrete Fitness Theorem suggests that a mutation whereby the creature no longer produces r_2

will be viable. Assume such a creature, c2, arises. If c2 is going to be viable then the results in the previous section imply the following:

- By Result 12 No negative process, process c2r2 is gross negative so c2 must trade in and make the process net neutral.
- By Result 16 Positive for trade out, process c1r2 must remain net positive to sustain trade.
- By Result 13 At least one neutral process, process c1r1 must be a neutral process.
- By Result 17 Comparative production, process c2r1 must be a positive process as it is more productive than process c1r1, which has an additional subtraction of amount a^{P2} .

In writing the system, we omit creature subscripts where the process is the same for both creatures. There are five equations in five unknowns $N_1, N_2, x_1^2, x_2^1, a^{1P}$.

Processes a^{2P}, a^{1C}, a^{2C} are constant with respect to amounts N_1, N_2 and means x_1^2, x_2^1 .

We look at the change in resources which the introduction of c2 in amount N_2 creates.

$$\text{c1: } N_1 \begin{bmatrix} a^{1P} & -a^{2P} & +a^{1C} & & +N_2 a^{1T} \\ & a^{2P} & +a^{2C} & +a_1^{2W} & -N_2 a^{2T} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \quad (152)$$

$$\text{c2: } N_2 \begin{bmatrix} a^{1P} & & +a^{1C} & +a_2^{1W} & -N_1 a^{1T} \\ & & +a^{2C} & & +N_1 a^{2T} \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \quad (153)$$

$$N_1 a^{1P} + N_2 a^{1P} = L \quad a^{1P} = p^{1P} \text{ by (37) and ignoring 0 element} \quad (154)$$

The trade amounts are given by:

$$a^{1T} = c^1 (x_2^1 - X^{1B}) \quad (155)$$

$$a^{2T} = c^2 (x_1^2 - X^{2B}) \quad (156)$$

RESULT 22: SYSTEM EQUILIBRIUM. If c2 is viable, i.e. c2 is able to procure sufficient resources by trade to cover consumption of r2:

$$a^{2C} + N_1 a^{2T} > 0 \quad \text{evaluated at } N_1 = N^{ONE\ CREATURE}, N_2 = 0 \quad (157)$$

$$\text{then } N_2 > 0 \quad (158)$$

$$\text{and } \Delta N > 0 \quad \text{where } N = N_1 + N_2 \quad (159)$$

PROOF: Add equations (152)A, (152)B, (153)A, (153)B to get:

$$Na^{1P} + Na^{1C} + Na^{2C} + (N_1 a_1^{2W} + N_2 a_2^{1W}) = 0 \quad (160)$$

We want to compare waste with one creature case. Restate that case and subtract:

$$Na^{1P\ ORIG} + Na^{1C} + Na^{2C} + Na^{2W\ ORIG} = 0 \quad (150)*N, \quad a^{1C}, a^{2C} \text{ constant} \quad (161)$$

$$(Na^{1P} - Na^{1P\ ORIG}) + (N_1 a_1^{2W} + N_2 a_2^{1W}) - Na^{2W\ ORIG} = 0 \quad (160) \text{ less } (161) \quad (162)$$

Find the $(Na^{1P} - Na^{1P\ ORIG})$ term using the c1r1 process equations and eliminate:

$$(Na^{1P} - Na^{1P\ ORIG}) + N \cdot N_2 a^{1T} = 0 \quad (152)*N \text{ less } (147)*N \quad (163)$$

$$(N_1 a_1^{2W} + N_2 a_2^{1W}) - (Na^{2W\ ORIG} + N \cdot N_2 a^{1T}) = 0 \quad (162) \text{ less } (163) \quad (164)$$

Derive expression for N here and compare with the one creature case:

$$L + Na^{1C} + Na^{2C} + (Na_1^{2W\ ORIG} + N \cdot N_2 a^{1T}) = 0 \quad (160) \text{ with } (154), (164) \quad (165)$$

$$N = -\frac{L}{a^{1C} + a^{2C} + a_1^{2W\ ORIG} + N_2 a^{1T}} \quad \text{rearranging} \quad (166)$$

$$N^{ONE\ CREATURE} = -\frac{L}{a^{1C} + a^{2C} + a_1^{2W\ ORIG}} \quad \text{restating } (149) \quad (167)$$

$$N > N^{ONE\ CREATURE} \quad \text{i.e. } dN > 0 \quad \text{if } N_2 a^{1T} > 0, \text{ i.e. if } N_2 > 0 \quad (168)$$

We now evaluate N_2 using differentials. The initial position for evaluating

differential expressions is:

$$N_2 = 0 \quad (169)$$

$$da^{1P} = \frac{-a^{1P}dN}{N} \quad \text{differentiating (154)} \quad (170)$$

$$da^{1P} + dN_2a^{1T} + N_2da^{1T} = 0 \quad \text{differentiating (152)A} \quad (171)$$

$$\frac{-a^{1P}dN}{N} + dN_2a^{1T} = 0 \quad \text{by (170), (171) and (169)} \quad (172)$$

$$\text{so } dN_2 = \frac{dN}{N} \cdot \frac{a^{1P}}{a^{1T}} > 0 \quad \text{if } dN > 0 \quad (173)$$

We see by (168), (173) that a consistent positive solution exists for both variables. #

The amount of wastage of resource 1 in the one creature case is reduced here by the amount of resource 1 which creature 1 gains by trade, N_2a^{1T} , and this is what drives the increase in amount N . We see that the expansion of the ecosystem to two creatures leads to a more efficient utilization of the available resources, and consequently an expansion in the total number of creatures. We also see that a deletion mutation is compatible with the existence of both creatures, unlike incremental mutations. We might conclude deletion mutations are the cause of the specialization we see in nature, and indeed in human economies.

Two creatures, two deletion mutations (parasite) case: Could a new creature trade in both resources and survive? In this model, one of the original creature's processes would be a neutral process (Result 13 At least one neutral process) and not make resources available for trade (Result 16 Positive for trade out), so the answer is no. To model parasitism requires that a creature can trade in resources more aggressively than in the normal case.

9. Conclusion

We have shown that speciation will lead to an increase in the number of creatures which a given amount of resource L will support, because it allows a resource to be produced in proportion to its requirements even if the naturally available production function for the resource results in an oversupply. This conclusion holds within a system where the two creatures are identical in other respects. We can imagine that as the creatures begin to pursue different types of production, they will acquire further characteristics which fit them more nearly to their chosen role - in other words, they adapt and become more efficient. We have also shown that a concept of price can be defined in terms of the fitness coefficient, in other words the expected number of offspring of a creature. The effect of trade between different species is to alleviate their separate resource scarcities and bring their implicit price systems more closely together, just as in economic markets.

We suggest that an economic treatment of resource processing within biology may offer significant insights to biologists; whether this is true or not, the analysis presented here can be applied equally to economic situations. The Markov chain production function linked to resources (the 'XM' model) is particularly suited to examining questions of learning, adaptation and historical contingency because the parameters of the transition matrix can be perturbed. We have shown that a non-commercial economy can display efficiency in resource allocation in the same way as a market economy. There are other game-theory approaches which support this conclusion, for instance Piccione and Rubinstein (2006).

Finally, this approach can account for the evolution of money, as some situations (*viz.* intermediate goods) cannot be dealt with effectively by the free access model described here, but require a definite exchange.

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