EVOLUTION OF SPATIALLY INHOMOGENEOUS ECO-SYSTEMS: 
AN UNIFIED MODEL BASED APPROACH

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Abstract

Recently we have extended our the "unified" model of evolutionary ecology to incorporate the spatial inhomogeneities of the eco-system and the migration of individual organisms from one patch to another within the same eco-system. In this paper an extension of our recent model is investigated so as to describe the migration and speciation in a more realistic way.

Keywords: Evolution and Extinction; Foodweb; Migration; Power-law; Self-organized critical

1 INTRODUCTION

The evolution of life has been simulated often. Our unified model [1] describes both "micro"-evolution over ecological time scales (i.e. birth, aging and natural death of individual organisms) and "macro"-evolution over geological time scales (i.e., the origination, evolution and extinction of species). Recently we have extended our unified model to incorporate the spatial inhomogeneities of the eco-system and the migration of individual organisms from one patch to another [2]. In this paper an extension of our recently developed model is investigated to describe the migration and speciation in a more realistic manner. The paper is organized as follows. Section 2 gives details of the model. Section 3 describes the main results and conclusions are drawn in section 4.

2 THE ECOSYSTEM

2.1 The Architecture

We model ecosystems on a square lattice where each lattice site represents a distinct patch, the total number of lattice sites being \( T_{\text{max}} \). A self-organising hierarchical foodweb [3, 4] describes the prey-predator relation at each lattice site. We assume that species are organised in different trophic levels of this hierarchical foodweb at each patch. The hierarchical structure of the foodweb captures the well-known fact that fewer species exist in higher trophic levels for normal ecosystems. The allowed range of levels, \( \ell \) at any patch is \( 1 \leq \ell \leq \ell_{\text{max}} \). We assume that only one species occupies the highest level \( \ell = 1 \). Each node at level \( \ell \) leads to \( m \) branches at the level \( \ell + 1 \); therefore the maximum allowed
number of nodes in any level $\ell$ is $m^{\ell-1}$. Each node represents a niche that can be occupied by at most one species at a time. If a species occupies the $\nu$-th node in the $\ell$-th trophic level of the food web at lattice site $T$ then we denote its position by the set $T, \ell, \nu$.

At any arbitrary instant of time $t$ the total number of species $N(t)$ at any site $T$ cannot exceed $N_{\text{max}} = (m^{\ell_{\text{max}}}-1)/(m-1)$, the total number of nodes. Our model allows $N(t)$ to fluctuate with time over the range $1 \leq N(t) \leq N_{\text{max}}$, where $\ell$ itself can fluctuate over the range $1 \leq \ell \leq \ell_{\text{max}}$. The population of $i$-th species at any arbitrary instant of time $t$ is given by $n_i(t)$. Competition among the individuals of the same species for limited availability of resources, other than food, imposes an upper limit $n_{i,\text{max}}$ on the allowed population of each species. Thus, the total number of individuals $n(t)$ at any arbitrary site $T$ at time $t$ is given by $n(t) = \sum_{i=1}^{N(t)} n_i(t)$ where $N(t)$ is the number of species at that site. $T_{\text{max}}, \ell_{\text{max}}, N_{\text{max}}$ and $n_{i,\text{max}}$ are time-independent parameters in the model.

2.2 Prey-predator interactions

The prey-predator interaction between any two species $i$ and $k$ that occupy two adjacent trophic levels is denoted by $J_{ik}$. In this model $J_{ik}$ can take three values +1, −1 or 0. The sign of $J_{ik}$ gives the direction of nutrient flow, i.e. it is +1 if $i$ is predator of $k$, it is −1 if $i$ is prey of $k$. Thus, $J_{ik} = 0$ means that there is no prey-predator relation between the two species $i$ and $k$.

The elements of matrix $J$ account for the inter-species as well as intra-species interactions. Let $S_{i}^+$ be the number of all prey individuals for species $i$ on the lower trophic level, and $S_{i}^-$ be $m$ times the number of all predator individuals on the higher trophic level. Since we assume that a predator eats $m$ prey per time interval (because of larger body size of predators [5]), $S_{i}^+$ gives total available food for species $i$, and $S_{i}^-$ is the contribution of species $i$ to all predators on the higher level. If $n_i - S_{i}^+$ is larger than $S_{i}^-$ then food shortage will be the dominant cause of premature death of some individuals of species $i$, even if none of them is killed by any predator. In this way our model accounts not only for the inter-species prey-predator interactions but also for the intra-species interactions arising from the competition of individuals of species during shortage of food. On the other hand, if $S_{i}^- > n_i - S_{i}^+$, then some organisms will be eliminated from the existing population due to killing by predators. To capture the starvation deaths and killing by the predators, in addition to the natural death due to ageing, a reduction of the population by

$$C \max(S_{i}^-, n_i - S_{i}^+) \quad (1)$$

is implemented at every time step, where $n_i$ is the population of the species $i$ that survives after the natural death. $C$ is a constant of proportionality. If the reduction of population leads to $n_i \leq 0$, species $i$ becomes extinct.

We assume that the simplest species (bacterium) occupies the lowest trophic level and always gets enough resources that neither natural death nor predators can affect their population. We do not monitor the ageing and death of the the “bacteria” occupying the lowest level of the food web; instead, we assume a constant population of the “bacteria” throughout the evolution.

2.3 Collective characteristic of species

An arbitrary species $i$, occupying the $\nu$-th node at the $\ell$-th level of any patch $T$ is collectively characterized by $\Pi$:

(i) the minimum reproduction age $X_{\text{rep}}(i)$,

(ii) the birth rate $M(i)$,

(iii) the maximum survival age $X_{\text{max}}(i)$.

An individual of the species $i$ can give birth to offsprings only after attaining the age $X_{\text{rep}}(i)$.
For simplicity, we assume the reproduction to be *asexual*. Whenever an organism of this species gives birth to offsprings, $M(i)$ of these are born simultaneously. The maximum survival age $X_{\text{max}}(i) = 100 \times 2^{(1-\ell)/2}$ of a species depends only on the trophic level occupied by it. None of the individuals of this species can live longer than $X_{\text{max}}(i)$, even if an individual somehow manages to escape its predators.

### 2.4 Birth and natural death

At each time step, each individual organism $\alpha$ of the species $i$ gives birth *asexually* to $M(i)$ offsprings with a probability $p_b(i, \alpha)$. The time-dependent birth probability $p_b(i, \alpha)$ is a product of two factors. One of these two factors, $(X_{\text{max}} - X)/(X_{\text{max}} - X_{\text{rep}})$, decreases linearly with age, from unity, attainable at the minimum reproduction age, to zero at the maximum age. The other factor is a standard Verhulst factor $1 - n_i/n_{\text{max}}$ which takes into account the fact that the ecosystem can support only a maximum of $n_{\text{max}}$ individual organisms of each species.

Each individual organism, irrespective of its age, can meet its natural death. However, the probability $p_d$ of this natural death depends on the age of the individual. In order to mimic age-independent constant mortality rate in childhood, we assume the probability $p_d$ of natural death (due to ageing) to be a constant $p_d = \exp[-r(X_{\text{max}} - X_{\text{rep}})/M]$, (where $r$ is a small fraction), so long as $X < X_{\text{rep}}$. However, for $X > X_{\text{rep}}$, the probability of natural death is assumed to increase following the Gompertz’s law $p_d = \exp[-r(X_{\text{max}} - X)/M]$.

### 2.5 Mutations

#### 2.5.1 Effect of mutation on species

$X_{\text{rep}}$ and $M$ of each of the species of the ecosystem randomly increases or decreases, with equal probability, by unity with probability $p_{\text{mut}}$ per unit time due to mutation. $X_{\text{rep}}$ is restricted to remain in the interval from 1 to $X_{\text{max}}$, and $M > 0$.

#### 2.5.2 Effect of mutation on foodweb

In order to reduce the computational requirements it has been assumed that food habits of all species occupying similar niche on different patch (i.e., all nodes with identical set of index $\ell$ and $\nu$ irrespective of $T$) changes simultaneously due to mutation. To capture this; with the same probability $p_{\text{mut}}$ per unit time, one of the links $J$ from prey and one of the links $J$ to predators is re-adjusted. If the link $J_{ij}$ to the species $i$ from a higher level species $j$ is non-zero, it is assigned a new value of $J_{ij} = J_{ji} = 0$. On the other hand, if the link $J_{ik}$ to a species $i$ from a lower species $k$ is zero, the new values assigned are $J_{ik} = 1, J_{ki} = -1$. These readjustment of the prey-predator interactions is motivated by the fact that each species tries to minimize its predators but, at the same time, looks for new prey (food).

### 2.6 Speciation

The niches (nodes) left empty because of extinction are re-filled by new species, with probability $p_{sp}$ per unit time. All the simultaneously re-filled nodes in a trophic level of foodweb originate from one common ancestor which is picked up randomly from among the non-extinct species at the same trophic level. The characteristic parameters $X_{\text{rep}}, M$ of each of the new species are identical to their ancestor unlike earlier models but can mutate later. However, occasionally, all the niches at a level
may lie vacant. Under such circumstances, all these vacant nodes are to be filled by a non-extinct species occupying the closest lower populated level.

### 2.7 Emergence of a new trophic level

If the total biomass of the surviving individuals in the whole ecosystem is below the preassigned maximum possible value, a new trophic level is created, with probability $p_{\text{lev}}$, i.e. $\ell$ is increased by one. To prevent the number of levels to increase towards $\ell_{\text{max}}$, a new level could be created only if the total population on that lattice site was at most $2n_{\text{max}} = 200$. The actual number of occupied levels can fluctuate with time depending on extinction and speciation. The total number of levels, which determines the lengths of the food chains, depends on several factors, including the available bio-mass [12].

### 2.8 Migration

The individuals of a species can migrate to a neighboring lattice site with probability $p_{\text{mig}}$ per unit time, if the population at the corresponding niche (i.e. at the same level and at the same node) of the neighboring site is zero for the same species on the same level. The population at the old site diminishes by a random fraction and exactly the same number shows up at the neighboring site. The age of these immigrants do not change on migration but at their new habitat they continue to age as usual (unlike our recent model [2]).

### 2.9 Initial conditions and update rules

The requirements of computational resources increase rapidly with increasing $T_{\text{max}}$, $\ell_{\text{max}}$, $m$, $n_{\text{max}}$. Therefore, in almost all simulations values of these parameters were $T_{\text{max}} = 169$, $\ell_{\text{max}} = 10$, $m = 2$, $n_{\text{max}} = 100$. Simulations always began with a random initial condition where $M = 1$ for all species, with only three levels in the foodweb. Since larger species occupy the higher tropic levels and are expected to live longer than those at lower levels, we assigned $X_{\text{max}} = 100, 71, 50, 35, 25, 18, 12, 9, 6, 4$ to the species at level $\ell = 1, 2, 3, 4, 5, 6, 7, 8, 9, 10$, respectively. Initially, $X_{\text{rep}}$ was assigned randomly between 1 and $X_{\text{max}}$, the population randomly between 1 and $n_{\text{max}}/2$. The ages of the individuals were chosen randomly between 1 and the $X_{\text{max}}$ of the corresponding species. We allowed the eco-system to evolve for $t_{\text{warm}}$ time steps before we started collecting data from it and the data were collected for subsequent $t = 5t_{\text{warm}}$ time steps. The state of the system is updated in discrete time steps where each step consists of a sequence of seven stages:

- **I- Birth**
- **II- Natural death**
- **III- Mutation**
- **IV- Starvation death and killing by prey**
- **V- Speciation**
- **VI- Emergence of new trophic level**
- **VII- Migration**

### 3 RESULTS
Figure 1: Histogram for the lifetimes of species, with migration on a $13 \times 13$ square lattice, with observation time $t = 10^4(+)$, $10^5(\times)$, $10^6(*)$ summing over $10^2, 10, 1$ sample respectively. One run with $13 \times 13$ lattice for observation time $t = 10^7$ is shown with dots. The line with slope -2 corresponds to a power-law distribution predicted by several models. The common parameters for all the plots are $m = 2$, $n_{max} = 100$, $p_{sp} = 0.1, p_{mut} = 0.01, p_{lev} = 0.001, p_{mig} = 0.5, C = 0.05, r = 0.05$.

### 3.1 Lifetime distribution

The distributions of lifetimes of species are plotted in Fig.1 for different sets of values of the parameters. The Power-law with an exponent of -2, claimed by several simple models based on macro-evolution [13, 14], holds approximately only over the shorter lifetime regime; for longer lifetimes a strong deviation from power-law is observed. Since available fossil data have various known difficulties, it is questionable whether real extinctions follow power laws and, if so, over how many orders of magnitude.

Figure 2: Histogram for the minimum reproductive age of species, with migration on a $13 \times 13$ square lattice, with observation time $t = 10^4(+)$, $10^5(\times)$, $10^6(*)$ summing over $10^2, 10, 1$ sample respectively. The values of the common parameters for all the plots are identical to those used in Fig. 1.
3.2 Distribution of minimum reproductive ages

The distributions of minimum reproductive age $X_{rep}$ of the species for different set of values of parameters have been show in Fig. 2. The distribution of minimum reproductive age broadens in the early stages of macro-evolution but it shrinks in the late stages where it appears to take a stationary form where largest value of minimum reproduction age is around 35.

![Figure 3: Histogram for the litter size, with migration on a 13x13 square lattice, for observation time $t = 10^4(\cdot), 10^5(\times), 10^6(\ast)$ and $10^7(\square)$ for 1 sample only. The values of the common parameters for all the plots are identical to those used in Fig. 1](image)

3.3 Distribution of litter size

Fig. 3 shows the litter size distribution for different set of model parameter values. The litter size distribution is roughly exponential.

3.4 The number of populated levels

At some lattice sites all the species in a trophic level may become extinct occasionally due to randomness in the evolutionary process and all niches in that level may lie vacant (this may happen for all levels except the lowest one occupied by bacteria). Variation of average of minimum level (quantity $\sum_{i=1}^{T_{max}} l_i(t)/T_{max}$ where $l_i(t)$ is the maximum number of level at site $i$ at time $t$) and average of number of populated levels (quantity $\sum_{i=1}^{T_{max}} p_i(t)/T_{max}$ where $p_i(t)$ is the number of those trophic levels at site $i$ at time $t$ in which at least one niche is occupied by a non-extinct species) with time is shown for a single run in Fig. 4. Fig. 4 upper plot clearly shows a growing bio-diversity during early stages of the evolution. Lower plot shows that the actual number of occupied levels and hence the total number of species in the eco-system keep fluctuating at all stages of evolution due to extinction and speciation.

3.5 Age distribution and Mortality rate

Fig. 5 shows the age distribution of the individuals occupying the highest trophic level $\ell = 1$. The mortality rate defined by the relation $\frac{-d}{d(\text{age})} \ln[\text{Age distribution}]$ has been extracted from the age distribution of the individuals at the highest trophic level is shown in Fig. 6. The mortality curve is consistent with the usual census data where
Figure 4: Average of maximum level as function of time (upper plot). Average of number of populated levels as a function of time (lower plot). $T_{\text{max}} = 13 \times 13$ (with solid line) and $T_{\text{max}} = 5 \times 5$ (with dashed line), otherwise the common parameters for all the plots are as in Fig. 1.

Figure 5: Age distribution of the individuals occupying the highest level, with migration on a $13 \times 13$ square lattice, for 100 samples and $10^4$ time steps (+), 10 samples and $10^5$ time steps(×), 1 sample and $10^6$ time steps(∗). The values of the common parameters for all the plots are identical to those used in Fig. 1.
Figure 6: Mortality rate extracted from the age distribution shown in Fig. 5. Gompertz’s law corresponds to straight line.

mortality rate goes through a minimum in the childhood and increases exponentially with age in adults.

Figure 7: variation of mortality for different values of parameter $C$. $C = 0.02(+), C = 0.05(\times), C = 0.1(\ast), C = 0.2(\square)$. The values of the common parameters for all the plots are identical to those used in Fig. 1.

3.6 Natural death versus death due to predators (starvation)

Fig. 7 shows variation of mortality rate for different values of $C$. With increasing values of $C$, death due to predators/hunger starts dominating over the genetic(natural) death and mortality function becomes almost independent of age. However, when genetic death dominates the mortality function obeys Gompertz’s law. Branching ratio of 2 gave highest variation of mortality in simulations but the range over which mortality varied was identical for higher branching ratio 3 and 4 (not shown).
Figure 8: Lifetime distribution and Minimum reproductive age distribution for migration probabilities $p_{\text{mig}} = 0.0(+), 0.5(\times), 1.0(*)$ with 1 sample and $10^6$ time steps. The common parameters for all the plots are $T_{\text{max}} = 13 \times 13$, $m = 2$, $n_{\text{max}} = 100$, $p_{\text{sp}} = 0.1$, $p_{\text{mut}} = 0.01$, $p_{\text{tev}} = 0.001$, $C = 0.05$, $r = 0.05$. 
4 SUMMARY AND CONCLUSION

In this paper, the "unified" model of ecosystem, which incorporates the spatial inhomogeneities of the eco-system and the migration of individual from one patch to another within the same eco-system has been extended to describe the migration and speciation in a more realistic manner. In this model the age of immigrants do not change on migration and they continue to age as usual at their new habitat. Moreover, in this model all empty niches initially filled (occupied) by one common ancestor during speciation lead to different species (due to random mutations occurring independently for each filled niche) in due course of evolution. Qualitative features of lifetime distributions and minimum reproductive age distributions are barely affected by migration (see Fig.8).

We presented a systematic study of the dependence on input parameters. The model presented here is capable of self-organization; the total number of species, prey-predator interactions in the foodweb, number of trophic levels in the foodweb and the collective characteristics of the species are emergent properties of the self-organizing dynamics of the model.

5 Acknowledgements

AK thanks D. Stauffer and D. Chowdhury for useful discussions and DFG/Sta130 for partial support.

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