Abstract: We have generalized our “unified” model of evolutionary ecology by taking into account the possible movements of the organisms from one “patch” to another within the same eco-system. We model the spatial extension of the eco-system (i.e., the geography) by a square lattice where each site corresponds to a distinct “patch”. A self-organizing hierarchical food web describes the prey-predator relations in the eco-system. The same species at different patches have identical food habits but differ from each other in their reproductive characteristic features. By carrying out computer simulations up to $10^9$ time steps, we found that, depending on the values of the set of parameters, the distribution of the lifetimes of the species can be either exponential or a combination of power laws. Some of the other features of our “unified” model turn out to be robust against migration of the organisms.

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1 Introduction

Direct experimental evidence in recent years [1, 2, 3, 4, 5, 6, 7] has established that significant evolutionary changes can occur in an ecosystem over ecologically relevant time scales. In other words, the dynamics of ecology and evolution are inseparable. Significant progress has been made over the last two years in developing detailed models that describe not only ecological phenomena on short periods of time but also evolutionary processes on longer time scales [8, 9, 10, 11, 13, 14, 15, 16, 17]. Some of these models describe the population dynamics of each species in terms of only a single dynamical variable, whereas some other more detailed models monitor the birth, ageing and death of individual organisms. A thorough comparison of these recent models will be given elsewhere [18].

In all the versions of our “unified” model [8, 9, 10, 11] so far we have assumed that the population of the prey as well as that of predators are uniformly distributed in space. The absence of the spatial degrees of freedom in such models of spatially-extended systems should be interpreted, using the language of statistical physics [19], as a mean-field-like approximation. This situation is similar to a well-stirred chemical reaction where the spatial fluctuations in the concentrations of the reactants and the products is negligibly small. On the other hand, spatial inhomogeneities in the eco-systems and migration of organisms from one eco-system to another are known to play crucial roles in evolutionary ecology [20, 21, 22].

In recent years, the spatial inhomogeneity of the populations observed in real ecosystems have been captured by extending the Lotka-Volterra systems on discrete lattices where each of the lattice sites represents different spatial “patches” or “habitats” of the ecosystem [23, 24, 25, 26, 27, 28, 29, 30, 31]. However, almost all these investigations of “geographical” effects were restricted to only a single pair of species one of which is the predator while the other is the prey.

For modelling the population dynamics of more than two species, one needs to know the food web which is a graphical way of describing the prey-predator relations, i.e., which species eats which one and which compete among themselves for the same food resources [32, 33, 34, 35]. More precisely, a food web is a directed graph where each node is labelled by a species’ name and each directed link indicates the direction of flow of nutrient (i.e., from a prey to one of its predators).

A static (time-independent) food web may be a good approximation over a short period of time. But, a more realistic description, valid over longer periods of time, must take into account not only the adaptations of the species and their changing food habits, but also their extinction and creation of new species through speciation [36]. These processes make the food web a slowly evolving graph. Such slow time evolution of the food webs were naturally incorporated in our earlier mean-field descriptions [8, 9, 10, 11].

In this paper we extend the latest version of our “unified” model [11] of evolutionary ecology incorporating spatial inhomogeneities of the eco-system, i.e., spatial variations from one patch to another. Biologically motivated simulations on lattices, to take into account the geographical extent of an ecosystem, have a long tradition, e.g. for prey-predator relations [37], ageing [38], speciation [39]; their results sometimes [40] differ drastically compared with those of the homogeneous models that ignore the spatial extension. Such type of simulations are part of the widespread efforts to apply statistical physics methods to biology [41] or other fields outside physics [42].
Our model[8, 9, 10], in its latest and most realistic form[11], allows each individual organism to give birth to $M$ offspring at each time step, provided the age of the adult organism is above some minimum reproduction age $X_{\text{rep}}$ (which varies from one species to another), with a probability that depends on the current age as well as $X_{\text{rep}}$. Similarly, each organism can die, for genetic reasons, with a probability (mortality rate) increasing exponentially with age, up to some species-dependent maximum age $X_{\text{max}}$. Moreover, mutations happen at each time step, with the probability $p_{\text{mut}}$, which change $X_{\text{rep}}$ and $M$ randomly by $\pm 1$.

In our model, we assumed a simple hierarchical food web where the species are arranged in trophic levels $\ell$ ($1 \leq \ell \leq \ell_{\text{max}}$), with no more than $m^{\ell-1}$ species in each level. $\ell = 1$ thus represents one species at the top of all food chains; typically, $m = 2$. Species in level $\ell$ can prey on (or ignore) species on the immediately lower level $\ell + 1$. Moreover, the prey-predator relations are dynamic; because of random mutation, the food habits of the species change. Thus, an individual organism may fall victim to one of its predators. However, scarcity of food may also lead to starvation deaths among the predators.

A species becomes extinct when all the corresponding population vanishes. We re-fill each ecological niche left empty by an extinct species, separately with probability $p_{\text{sp}}$, by another species on the same (or a lower) level; independent random mutation of the parent and daughter species leads, eventually, to two different species.

If the total biomass of the surviving individuals in the whole ecosystem is below the pre-assigned maximum possible value, a new trophic level is created, with probability $p_{\text{lev}}$, i.e. $\ell_{\text{max}}$ is increased by one. The actual number of occupied levels can fluctuate with time depending on extinction and speciation.

The maximum possible age of individual organisms, $X_{\text{max}}$, for each species is assumed to depend only on the trophic level and fixed at $100/2^{(\ell-1)/2}$. The minimum reproduction age $X_{\text{rep}}$ is initially distributed randomly between one and this maximum age. 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.

The paper is organized as follows. In section 2 we study a simplified version of our “unified” model that provides a coarse-grained description of evolutionary ecology where the birth, ageing and death of the individual organisms do not appear explicitly. After studying the homogeneous version of this model we also investigate the effects of inhomogeneities arising from population migration. A few variants of this model are considered. In section 3 we extend the model formulating it in terms of the detailed “micro-dynamics” of individual organisms which can also migrate from one “patch” of the eco-system to another. The main results are summarized and conclusions are drawn in section 4.

2 A coarse-grained description of evolutionary ecology

In this section we do not monitor the “microscopic” dynamics of birth, ageing and death of the individuals explicitly. Instead, we describe the population dynamics of each species, in a coarse-grained manner, in terms of a single dynamical variable. In the first subsection below we ignore the spatial fluctuations while in the second subsection we take into account the fluctuations from one “patch” to another by modelling the eco-system as a lattice where each site represents a “patch”.

3
2.1 Homogeneous approximation

Figure 1: Histogram for the lifetimes (part a) and minimum reproduction times (part b) of species, without lattice, with observation time \( t = 10^3, 10^4, 10^5, 10^6, 10^7 \) from right to left, summing over \( 10^4, 10^3, 10^2, 10, 1 \) samples, respectively.

Figure 2: Histogram for the lifetimes (part a) and minimum reproduction times (part b) of species, with diffusion on a \( 31 \times 31 \) square lattice, with observation time \( t = 10^3, 10^4, 10^5 \) from right to left, using one sample only.

When we deal with species and no longer with individuals, we have to omit the individual births and genetic deaths and replace them by a fitness of the whole species; normalized to unity this fitness gives the survival probability of the species as a whole. Our fitness has two components, both taken from the birth and death probabilities of our previous model [11]:

a) High birth rates \( M \) decrease the life expectancy of the parent; thus a species is assumed to survive a time step with probability \( \exp(-rM) \), where \( r \) is taken as 0.05 as in [11].

b) Having survived step a, a species is the fitter, the higher the number \( M \) of offspring per time step is and the lower the minimum age of reproduction \( X_{rep} \) is. Thus each species survives
with probability $\left(\frac{X_{\text{max}} - X_{\text{rep}}}{(X_{\text{max}} - X_{\text{min}}) M_{\text{max}}}\right)$ where $M_{\text{max}}$ is the current maximum litter size $M$ in the entire ecosystem, and $X_{\text{min}}$ the current minimum value of the $X_{\text{rep}}$ in the whole ecosystem. In this way, the fittest species, and only this species, survives for sure, all others survive with the above probability only.

[Another modification is required in the prey-predator deaths. The Verhulst deaths are now omitted, and instead of a reduction of the population by the amount given in eq(1) of \cite{11}, the population goes extinct with a probability given by this amount.]

We took $p_{\text{sp}} = 0.1$, $p_{\text{mut}} = 0.001$, $p_{\text{lev}} = 0.0001$, $r = 0.05$, $C = 0.2$ as in \cite{11}, and allowed the creation of a new level only if at most four species were alive above the lowest level. We averaged over $t$ consecutive time steps, after making $t/5$ time steps to establish a reasonable equilibrium.

We found that the number of food levels actually occupied at any one moment (between 1 and 9) is normally distributed (“Gaussian” parabola on a semi-logarithmic plot; not shown). Thus for extremely long times $t$ the maximum number of food levels should increase with the square-root of log($t$). This extremely slow increase is compatible with one simulation (Figs.3 and 7) for $t = 10^8$. Biologically, longer times do not make much sense; 100 million years ago we did not have the genus homo on earth.

The histograms for the lifetimes of species, and for the minimum reproduction times $X_{\text{rep}}$, Fig.1, both show that $t = 10^3$ and $10^4$ are too short, $t = 10^5$ is intermediate between short- and long-time behaviour, and $t = 10^6$ and $10^7$ give barely distinguishable long-time behaviour. For this comparison we summed up $10^7/t$ samples so that the total number of measurements

Figure 3: Variation with time for the average of the maximal number of levels, with (x) and without (line) lattice (same simulations as in Figs.1 to 4.). The + symbols show one run without lattice to much longer times. These data show the need to iterate up to $10^6$ time steps for equilibration.
is the same in all five cases.

Fig.1a also shows an exponential lifetime histogram for long $t$, as opposed to the more complicated histogram in [8, 9, 10, 11] and the simple power law often claimed for reality [11, 12]. Thus the treatment of individuals, not the other complications, seems to be responsible for the complex lifetime distributions in these earlier models. Fig.1b, on the other hand, is not much different from Fig.3 in [11]. The average litter size $M$ fluctuates strongly, increasing overall perhaps logarithmically with the number of time steps (not shown).

### 2.2 Spatial inhomogeneity

With a whole ecosystem of several food layers on every site of a lattice, computational requirements increase drastically. To reduce memory requirements we thus assume that the prey-predator relations are the same on each lattice site; only the other species-dependent properties like $X_{rep}$ and $M$, and the number $\ell_{max}$ of food levels, can change from site to site. Mutations thus act on the latter quantities differently for different sites, while mutations on prey-predator relations act simultaneously on the whole lattice, for the given niche (= possible species in ecosystem). If the expansion of one species to another site, where it later undergoes different mutations, is called speciation (i.e. parapatric speciation), then the previously discussed speciation events which also change the prey-predator relations, are changes of a higher taxonomical level, like changes of genus. Alternatively, if we call the changes of the preceding section a speciation, the changes due to expansion onto two lattice sites allows the formation of sub-species (“races”) of the same species, sharing the same predator-prey relations.

If we only allow for different ecosystems on different lattice sites, the results are roughly equivalent to averaging over many separate runs of a single site, as we did in the previous section. Only the fluctuations are reduced due to the agreement for prey-predator relations. More interesting and realistic is motion of species across the lattice. Thus at every time step each non-extinct species with probability 1/2 stays where it is, and otherwise selects randomly one of its four neighbour sites on the square lattice (using periodic boundary conditions). If that site is occupied at the corresponding niche (i.e. at the same level and on the same node) then again nothing happens; if the selected neighbour site is not already occupied for that niche, then the old species occupies this place but also stays at its old site. Thus we have an expansion, not a mere displacement, of the species. From then on, both sites undergo the usual mutations and thus slowly the two populations drift apart genetically to become different (sub-)species.

Apart from somewhat shorter lifetimes, our results in Fig.2 look similar to Figs. 1: Simple exponential decay for the distributions of lifetimes and minimum reproduction ages, for long enough times. More interesting is Fig.3 with the maximal number of levels, $\ell_{max}$, averaged over all lattice sites. As a function of time, this quantity at first increases roughly linearly in time from its initial value 3. After about $10^5$ time steps, a much slower increase is observed, leading to a plateau near 8. Diffusion barely changes the lattice results without diffusion, and even without a lattice the results are about the same except that the single run without a lattice shows stepwise increase of $\ell_{max}(t)$. 
Figure 4: As Fig.1, but with fitness tested every tenth time step, and \( r \) ten times smaller. The two longest times are shown by small dots in the left part. The straight line has the slope \(-2\) sometimes claimed for real extinctions.

Figure 5: With diffusion on a \( 31 \times 31 \) square lattice, \( f = 0.01, \ r = 0.5 \).

2.3 Variants

In the above simulations, the lowest level is by construction always fully occupied, but only a few species exist in the higher levels. We avoided the extinction of so many species by reducing the "birth punishment" factor \( r \) from 0.05 to 0.005, and by making the fitness test only with a probability of \( f \), that means, on average only at every \((1/f)\)-th time step the less fit species may go extinct. Now figure 4 for \( f = 0.1 \) shows for the lifetime distribution a more complicated behaviour, similar to [8, 9, 10, 11], without a lattice. For diffusion on a lattice, the lifetimes may become log-normally distributed for these parameters. Fig.5 shows a more interesting distribution for \( f = 0.01, \ r = 0.5 \). Simulations with different system size give similar results, Fig. 6. In real palaeontology, of course, it would be difficult to measure lifetime distributions over ten decades with a single criterion, as is done here and in Fig. 2. Fig.7 suggests that the maximum number of layers increases very weakly; again times varying over nine decades are
3 Inhomogeneous eco-system: a individual-based description

In this section we report results of the most detailed description of the eco-system. We not only incorporate explicitly the birth, ageing and death of individual organisms, but also take into account the spatial inhomogeneities of the populations in terms of a lattice model that is very similar to the one considered in the preceding section.

Thus we assumed that each individual either ages by one time unit for each time step, or it dies. Besides the deaths as prey, unchanged from the previous section, the above selection according to fitness and litter size is replaced by a Gompertz-type death probability as a function of the age $a$ of the individual, and depending also on the maximum age $X_{\text{max}}$ and litter size $M$ of the whole species:

$$p_{\text{death}} = \exp[(a - X_{\text{max}})r/M]$$

where $r$ is the same free parameter, e.g. 0.05, as in the earlier sections. (For ages below the minimum reproduction age $X_{\text{rep}}$ the death probability is assumed to be age-independent, with $a$ replaced by $X_{\text{rep}}$ in the above equation.)

The survivors give birth to $M$ offspring at each time step with probability

$$p_{\text{birth}} = (X_{\text{max}} - a)/(X_{\text{max}} - X_{\text{rep}})$$

if their age $a$ is above the minimum reproduction age $X_{\text{rep}}$. The just-born babies die with a Verhulst probability $1 - n/n_{\text{max}}$ where $n$ is the actual current population of the given species on the given lattice site, and $n_{\text{max}}$, taken here as 100, is its maximum possible population.

A population may expand into a neighbouring lattice site, if the population there is zero for the same species on the same level. The population stays the same at the old site, whereas
Figure 7: Variation of $\ell_{\text{max}}$ with time up to nearly $10^9$ time steps for the parameters of Fig.4, showing the less than logarithmic increase at long times (big symbols). The small dots below the big symbols are the actual numbers of occupied levels in the same simulations. The higher dashed line gives $\ell_{\text{max}}$ for ten times higher probabilities of mutation and level formation.

at the new site, as in our standard sympatric speciation assumption, the population is taken randomly between one and the population at the old site; also the age of the emigrants starts at zero.

Fig. 8 shows lifetimes and minimum age of reproduction with the individuals on a $31 \times 31$ lattice; smaller lattices gave similar curves. To speed up equilibration, $p_{\text{mut}} = 0.01$, $p_{\text{lev}} = 0.001$ were taken ten times higher than before. To prevent the number of levels to increase towards 10, a new level could be created only if the total population on that lattice site was at most $2n_{\text{max}} = 200$. We see that roughly but not precisely the lifetimes follow an inverse-squared power law (straight line in Fig. 8a).

4 Discussion

We have extended our earlier “unified” models of evolutionary ecology \cite{8,9,10,11} by taking into account the spatial inhomogeneities arising from migration of populations from one patch to another. Besides, individuals and species, we also allowed evolution of genera (i.e., sets of species with the same food habits). By carrying out extensive computer simulations, we find that, depending on the details of the parameter set, the distribution of the lifetimes of the species may be simple exponential or, as before, a combination of power laws. Other aspects like, for example, the self-organization of the minimum reproduction ages, are less affected by this generalization.
Figure 8: Distribution of lifetimes and minimum reproduction ages with individuals on a 13 lattice at $t = 10^3$, $10^4$, $10^5$, $10^6$. The thin curves (or dots) refer to $t = 10^5$ for $5 \times 5$ (lower data) and $31 \times 31$ (higher data) for the lifetimes.

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