Ecology and Extinction – Macroevolutionary Extinction Dynamics in a Simulated Ecosystem

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Abstract

A number of models of macroevolutionary extinction dynamics have been proposed during the past decade or so. Many of these models produce results that are in good accord with empirical data, as drawn from the fossil record. However, they all still suffer from significant shortcomings. A new simulation based model is presented here that attempts to address some of the weaknesses and limitations of these existing models. The simulation is driven by ecology level interactions amongst dynamically changing populations of species in a theoretical food web, coupled with the effects of external environmental stresses. The results of a number of extended runs of the simulation are presented and discussed. It is observed that it is the interactions between intrinsic ecological factors, and external environmental factors, that determine the specific extinction dynamics generated. Ecological factors appear key in defining the large-scale statistical trends of the system. Environmental factors appear to act as a sort of 'tempo keeper', determining the precise timing of extinction events within the large-scale framework. Overall, the results from the simulation suggest that macroevolutionary patterns of extinctions are primarily generated intrinsically by an ecosystem. Environmental factors are not so much a direct cause of extinction events, as a determinant of the precise timing of events that will, in any case, inevitably ensue.

Introduction

Over the past twenty years or so the dynamics, patterns, and underlying causes of extinction events throughout the history of life on this planet have been the focus of considerable scientific attention. The aim of this paper is to present a simulation of the dynamics of a set of interacting populations of different species over very large time scales. By analyzing the behaviour of this simulated ecosystem, and comparing it with empirical evidence derived from the fossil record, it is intended that further light can be shed on the problems associated with this study of extinction dynamics.

Empirical Extinction Data

In order to establish biological credibility for a computational simulation, it should ideally be possible to make direct quantitative comparisons between the results of the simulation and the actual available empirical data. In the case of the simulation to be presented here (and the other related computational and mathematical models which will be considered in the next section), the appropriate empirical data is derived primarily from the fossil record.

Trends and Patterns in the Fossil Record

There are several key statistical trends in the fossil record which are potentially of relevance to the models and simulations considered here. Of greatest importance is the distribution of extinction events of a particular size. One of the important features that almost all of the existing models of extinction dynamics share, is that they predict a power law distribution of extinction sizes. The fossil data (as drawn from compiled databases of the times of origination and termination of taxonomic groups such as those given by Sepkoski [33] and Benton [9]) can then be plotted to test this conjecture. It does indeed turn out that the available data is compatible with a power law distribution. Specifically, the probability of a given size of extinction event $p(s)$, in a given time step in the fossil record can be approximated by the formula $p(s) \propto s^{-\tau}$, with $\tau = 2.0 \pm 0.2$.

Other Empirical Data

Further empirical evidence for this power law distribution of extinction sizes can be found in the studies of Hawaiian avifauna by Keitt and Marquet [19]. In this work, the distributions and population sizes of various species of native and introduced birds across a range of Hawaiian islands were analysed. The introduction of new species in these cases resulted in increased levels of extinction, such that sufficient data could be collected on which to perform statistical analyses. Their conclusion is that in the case of the Hawaiian avifauna, extinction patterns do indeed appear to follow a power law form.

Recent Models of Extinction

Over the past ten years or so, a number of methods have been proposed to model the statistical macroevolution-

ary dynamics described above. In this section, some of these models will be briefly reviewed.

The Bak-Sneppen Model

The Bak-Sneppen model [7] is a simple model of large-scale coevolution. The system organises itself to a critical point at which 'avalanches' of evolutionary activity propagate throughout, giving a power law distribution of avalanche sizes. Although extinction is not addressed explicitly, these avalanches of activity can be interpreted as a possible biotic basis for extinction. The scale-free, power law behaviour seen is one characteristic of such self-organised critical systems. This suggests, therefore, that macroevolutionary extinction dynamics may themselves arise through a self-organised critical process, as indicated by the power law distribution of extinction sizes across the fossil record.

There are many problems with the Bak-Sneppen model as a simulation of extinction dynamics. Most obviously, there is no explicit notion of extinction at all in the system. The assumption is simply made that extinction patterns will be in some way correlated to general patterns of evolutionary activity. Additionally, only coevolutionary factors intrinsic to the system are considered, extrinsic factors are ignored. However, external environmental factors are widely held to be a primary cause of extinction events. This is largely due to the influential work of Alvarez[5] which examined evidence of an extra-terrestrial bolide impact at the time of the end-cretaceous mass extinction. Hallam and Wignall [15], in their summary of the proposed causes of the main Phanerozoic extinction events, list only the following, all extrinsic, possibilities: Bolide impact, volcanism, global cooling, global warming, marine regressions, and marine anoxia. More exotic theories, such as extinction through the ionising effects of cosmic ray jets as proposed by Dar, Laor, and Shaviv [12] are still being suggested.

Another possible distortion of the dynamics of the system is the lack of any speciation mechanism. The number of species is artificially maintained at a fixed level, whereas in biological systems species diversity is free to fluctuate. It seems reasonable to assume that the number and density of different species could have some affect on the probabilities and sizes of extinction events.

A good discussion of the Bak-Sneppen model, its weaknesses as a model of extinction dynamics, and its variants, can be found in Newman [26].

Environmental Stress Models

Extensions to the Bak-Sneppen model incorporating the effects of environmental stress have been proposed in Newman & Roberts [27], and Roberts & Newman [32]. These variants are also an improvement over the Bak-Sneppen model for describing extinction dynamics through the use of an explicit extinction mechanism.

Newman [25] has also investigated the same model, but using only environmental stress – no co-evolutionary mechanism is employed. This model produces near identical dynamics to the earlier version, suggesting that it is the dynamics caused by external stresses which are dominant. What is particularly interesting about this, is that Newman's model is demonstrably not self-organised critical. However, it still produces extinction dynamics that are power law in form. This suggests that the power law form of the fossil record data is not necessarily indicative of a self-organised critical extinction mechanism.

The models of both Newman and Roberts, and Newman, both still suffer from significant problems. For example, as with the Bak-Sneppen model, there is still no explicit speciation mechanism.

Speciation Models

Vandewalle and Ausloos [36] and Head and Rogers [16] have both proposed models which are derived from the Bak-Sneppen model but incorporate explicit speciation mechanisms. A further model, Wilke and Martinetz [37], incorporates speciation based on Newman's environmental stress model. Additionally, Amarel and Meyer [6] includes a speciation mechanism, which will be considered separately below. A brief mention should also be made here of the speciation mechanism used in the biogeographical model of Pelletier [28].

Vandewalle and Ausloos [36] and Head and Rogers [16] are primarily models of branching in phylogenetic trees. The models produce a number of interesting dynamics, but, like the Bak-Sneppen model, there are no explicit extinction mechanisms. This limits their direct relevance to the current study.

Wilke and Martinetz [37] take Newman's environmental stress model as a starting point. In each time step the number of expected new species is calculated, based on the current number of species and a proposed ceiling to the total number of species that the ecosystem can support. This number of new random species is introduced. Although the formula used does describe the growth in numbers of species in biological systems well, it is also somewhat arbitrarily imposed.

The biogeographical model of Pelletier [28] incorporates an interesting speciation mechanism. Pelletier bases his mechanism on the observation that genetic drift occurs at a faster rate in smaller populations. This leads him to adopt a speciation mechanism in which the rate of speciation of a species is inversely proportional to the population size of that species. However, this would be reasonable only if speciation rates could be directly correlated to rates of genetic drift, which seems at best a questionable assumption.

Ecology Based Models

Of most direct relevance to the model to be presented here are two food web based models, Amarel and Meyer

[6], and Abramson [1]. The belief is that this finer-grained ecological level is more appropriate for modeling the fundamentals of macroevolutionary dynamics than the more abstract representations used by the models described above. There is good supporting evidence for this importance of ecological factors in macroevolutionary dynamics. Maynard-Smith [24] gives a number of examples of ecological factors that are the direct cause of extinctions. Further discussion of the relevance of ecological factors, such as inter-species competition and trophic position, to macroevolutionary dynamics can be found in Jablonski [17], Sepkoski [34], and Lawton [20].

Abramson's model [1] is based around the population dynamics of a simple one-dimensional food chain, as described by a Lotka-Volterra type equation. The model does produce periodic cascades of extinction that propagate along the food chain in a manner that Abramson claims to be similar to that of mass extinction events.

The Amarel and Meyer model [6] involves more complex food webs, consisting of multiple trophic levels. The species are arranged on a two-dimensional lattice. One dimension represents trophic levels, the other represents ecological niches in that level. Although the Amarel-Meyer model lacks the population dynamic level of detail of the Abramson model, it does produce results more in line with the fossil data. Further analysis of this model can be found in Drossel [13].

Other Relevant Models

Brief mention should be made of two other relevant lines of research. The first is the work done by Adami [4, 3] based on Ray's *Tierra* system [31], in which evolutionary patterns in populations of self-replicating computer code were studied. Adami looked at the duration of different 'species' of code in extended runs of *Tierra*. He found a good fit to a power law distribution (apart from a fall-off towards high values) similar to that observed in the fossil record. Like Bak and Sneppen, Adami took this power law form as evidence of self-organised criticality in the system.

One further piece of work has had some influence in the development of the model presented here – the macroevolutionary algorithms of Marin and Solé [23]. Marin and Solé have developed an evolutionary optimisation algorithm similar in some ways to the genetic algorithm. However, instead of operating at the level of individual genomes, the macroevolutionary algorithm operates at the level of species. The traditional genetic algorithm operators of mutation and crossover are replaced by species level operators of diversification and extinction. Solé and Manrubia [35] have studied extinction dynamics in a model of species interactions closely similar to that used for macroevolutionary algorithms.

An Ecological Model of Macroevolutionary Extinction Dynamics

The model presented here is based around the evolutionary and ecological dynamics of populations of species in a simulated ecosystem. Predator-prey relationships, as represented by Lotka-Volterra type equations, form the basis for the ecological interactions of the system. In addition to the ecological interactions inherent in the ecosystem, the populations of each species are also affected by external environmental stresses, generated at random. The system is driven by low background levels of phyletic transformation and speciation that gradually change species over time and introduce new species, replacing those driven to extinction by ecological or environmental factors.

With the exception of Abramson [1], all the models discussed in the previous section considered species as the fundamental ecological unit. The Amarel-Meyer model [6], for example, defines the food web explicitly and only in terms of which species feed on which other species. However, the population based model used here, (and that used by Abramson) operates at a more appropriate level. As Eldredge [14] points out, there are two distinct sorts of biological hierarchy – genealogical and ecological. A species is a unit of genealogical organisation, an evolutionary lineage. It is a single layer in a hierarchy consisting of the various taxonomic ranks – order, family, genus etc. The fundamental organisational unit of an ecosystem (above the level of individual organisms) is, however, a population of conspecifics (Eldredge uses the term 'avatar' to describe such a population). In the ecological hierarchy it is these populations that constitute local ecosystems, which in turn build up regional ecosystems, and so on. It is, therefore, more appropriate to model ecological processes at this level of populations drawn from species, rather than treating a species as a discrete ecological unit on its own.

Structure of the Ecosystem

As in the Amarel-Meyer model, the ecosystem is structured around a two dimensional lattice. The vertical axis is representative of trophic levels within the system, while the horizontal axis is representative of individual ecological niches within each trophic level. Note that on the horizontal axis, physical proximity is not necessarily correlated with phyletic similarity – the arrangement of niches is quite arbitrary. Note also that although the word 'niche' is used to designate particular locations within the lattice, the true 'niche' of a species (in the usual sense of the word) is determined also by its trophic interactions. The word 'niche' will henceforth be used only in the former sense, unless specified otherwise. Populations from each level feed on one or more populations from the next lowest trophic level. Species from the lowest trophic level are assumed

to be autotrophic, deriving their energy directly from the environment.

The maximum number of trophic levels and niches per level are set at fixed values. The maximum number of trophic levels was set based on data from biological food webs taken from Cohen [11]. As will be seen later, the simulated food webs rarely develop to maximum possible trophic depth. Thus, the arbitrarily imposed limit is largely irrelevant – even if additional trophic levels were allowed, it is unlikely that food webs would ever evolve sufficient complexity to make use of these additional levels.

The justification for fixing the maximum number of ecological niches per level is based largely on studies of island biogeography (e.g. MacArthur [22], and Begon, Mortimer and Thompson [8]). Species-area curves can be plotted of numbers of species occurring on islands of varying sizes. From these curves, it can be seen that there is an apparent fixed maximum number of species that any given area can harbour. Although the number of available niches in the model is set arbitrarily, changing this value would simply result in the model being a simulation of the dynamics of species over varying geographical ranges.

Each species is parameterised in three ways: population density, predator/prey interactions, and tolerance to environmental stress. Population density is simply an integer value assigned on an arbitrary scale. Predation and prey interactions are modeled using two vectors, one each for interactions with predators and prey. The vectors map on to the trophic levels directly above and below that of the species, as appropriate. Each element in each vector contains a floating point value in the range $[0, 1]$ representing the strength of the interaction. Values of 0 indicate that no interaction between the two species takes place. Note that the values in each predator vector are kept coherent with the values in the corresponding prey vector. If a predation value is reduced to 0 (through phyletic transformation), then the corresponding prey value is also automatically reduced to 0. Tolerance to environmental stress is represented by one or more floating point values in the range $[0, 1]$, with a separate value being assigned for each environmental stress (see below for more details on environmental stress).

The ecosystem is initially seeded with a single randomly generated autotrophic species. It is then updated in discrete time steps by repeatedly applying the following operators, which are described in more detail in the following sub-sections. First, a reproduction operator updates the population density of each species. This is done using Lotka-Volterra type equations based on each population's interactions with its neighbouring trophic levels, modified by the effects of environmental stress. An extinction operator then removes any species whose population density has dropped below a critical threshold.

A phyletic transformation operator is then applied to each species with some fixed low probability, altering that species' environmental stress tolerances and trophic interactions. Finally, a speciation operator is applied to each species with some fixed low probability, resulting in the generation of new species.

The Reproduction Operator

The population density of each species is updated according to the following Lotka-Volterra type equation, derived from those used by Abramson [1], [2], and those given in Begon, Mortimer, and Thompson [8]:

$$\Delta n_z^i(t) = \sum_{j=1}^{N_{(z-1)}} k_z^{ij} n_{(z-1)}^j(t) - \sum_{j=1}^{N_{(z+1)}} g_z^{ij} n_{(z+1)}^j(t) - \sigma_z^i(t) n_z^i(t)$$

The term $n_z^j(t)$ gives the population density of species n in niche j of trophic level z at time t. N_z is the total number of niches in trophic level z. Predator and prey relationships are given by the variables k and g where k_z^{ij} is the jth element in the prey vector of the ith niche of trophic level z, and g_z^{ij} is the jth element in the predator vector of the ith niche of trophic level z. Environmental stress is given by the function $\sigma_z^i(t)$, the proportion of the population of niche i of trophic level z at time t being eliminated by environmental stress.

In essence this means that population growth of each species will be in proportion to the population density of its predators and prey times the ability of the species to exploit their prey and resist their predators respectively (modified by environmental stress).

For autotrophic species, it is assumed there is some fixed level of available environmental resources. The prey vector of an autotrophic species simply reflects its ability to exploit these resources. Population increases for autotrophic species are then calculated by multiplying the species' ability to exploit environmental resources by an assigned constant value.

The system is assumed to undergo some fixed number of different environmental stresses. In each time step, each stress is assigned a global value according to some probability distribution (linear, normal and bimodal distributions were used in various different runs). To calculate population decreases due to environmental stress, the tolerance levels of each species are compared in turn to the appropriate global stress levels. If tolerance exceeds stress for all stresses, then the population suffers no additional losses. If any stress exceeds the associated tolerance level, then a proportion of the population is killed off, based on the difference between stress and tolerance (as represented by the function σ in the equation above).

The Extinction Operator

After population densities have been updated by the reproduction operator, the extinction operator then removes any species whose population density has dropped below a critical threshold value. There are two reasons why this threshold is applied. The first is simply a matter of computational implementation. If population densities are allowed to become arbitrarily small, it makes it very difficult to reduce a population to a density of zero due to rounding of the integer values used. However, from a biological point of view there are minimum viable population sizes, as described for example in Raup [29]. A species dropping below its minimum viable population will almost inevitably be driven to extinction regardless of any other factors. For this reason, the use of an extinction threshold, as a representation of the minimum viable population size, seems justified.

A species whose population drops below the threshold value has its population density reduced immediately to zero. Additionally all trophic interactions involving the niche occupied by the newly extinct species are removed from the system.

The Phyletic Transformation Operator

In each time step, each species will be phyletically transformed with some given probability. Phyletic transformation potentially changes species in up to three ways. Firstly, the species' tolerance to environmental stress can be altered. Secondly, the strengths of a species' interactions with its existing predators and prey can change. Finally, the species can acquire new prey, randomly selected from the next lower trophic level, or lose existing prey. Note that any acquisition or loss of prey will also result in a corresponding acquisition/loss of the predator to the prey's predation vector.

The phyletic transformation operator uses a simple hill-climbing algorithm to determine whether phyletic transformation occurs in a selected species. Once a species has been selected for phyletic transformation, a variant on that species is generated. The two species are compared by looking at the expected population changes in the next time step assuming the rest of the ecosystem and environment remains constant. If the newly generated species has the higher expected population growth of the two, then it is assumed to be the 'fitter' and replaces the original. This is supposed to be broadly representative of microevolutionary selective forces acting to improve the overall fitness of the species.

Note, however, that this hill-climbing process will not necessarily act to maximise all of a species' parameters. During times of low environmental stress, there is no selective advantage to high stress tolerance levels. Selective forces on ecological interactions will instead dominate, with phyletic drift pulling down stress tolerances. Likewise, during periods of intense environmental stress, increases in stress tolerance will dominate, with drift weakening the ecological position of the species.

To generate a new phyletically transformed species, each of the parameters of the original species is examined in turn. Each is then assigned a new random value with some given low probability.

The Speciation Operator

The final stage in each time step is the application of the speciation operator. Each species is selected to undergo speciation with some given low probability. The speciation operator then works as follows. A new niche is selected at random from the same or a neighbouring trophic level. If this niche is empty then a speciation event will occur. If a speciation occurs, then a new species is generated to occupy the vacant niche. The new species will be a phyletically transformed version of the original. In the case of a speciation event causing a species to be formed on a different trophic level than its progenitor, it will be assigned a single random prey from the next lower trophic level. It will initially have no predators.

Some further justification of this speciation mechanism (which is essentially the same as that used by Amarel and Meyer [6]) should be given. In absence of any limiting factors, it would be expected that biodiversity (e.g. the total number of species in an ecosystem) would increase exponentially. Speciation mechanisms such as geographical isolation of sub-populations, or runaway sexual selection, are equally applicable no matter high many species are present. Therefore the more species an ecosystem contains, the faster would be the total rate of speciation across the ecosystem. However, there are of course limitations. In a finite ecosystem with only a limited amount of resources, competition for these resources will inevitably limit the number of species the ecosystem can support. If a speciation event were to occur such that the new species would occupy an ecological niche already occupied by an existing species, one of two things will occur. Most likely, the new species will simply not manage to establish itself, and the speciation will fail. The alternative is that the new species will usurp the extant species, driving it to extinction and taking its ecological position. The assumption is made in the model that this sort of competitive niche invasion happens only rarely, and for computational efficiency can be ignored altogether as being irrelevant to the macroevolutionary dynamics. Thus, speciation is only allowed to occur into vacant niches. Some justification for this is needed, however.

This mechanism of extinction through competitive replacement was of course the principal extinction mechanism envisioned by Darwin, and this influence remained dominant for some considerable period. However, more modern studies suggest that it is not a significant factor in evolutionary dynamics, and the decision here to omit
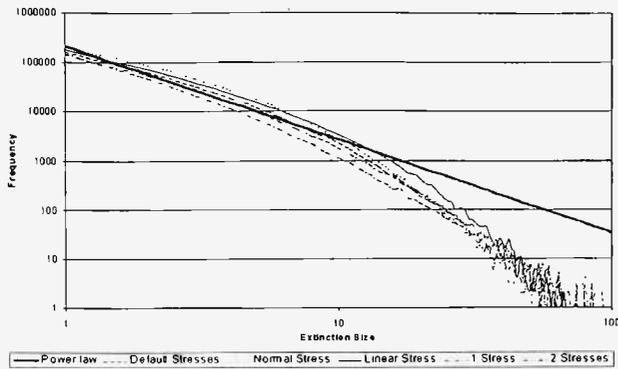
Figure 1: Graph of extinction rates for five simulation runs varying numbers and types of environmental stress. The power law here has an exponent of $\tau = 1.90$.
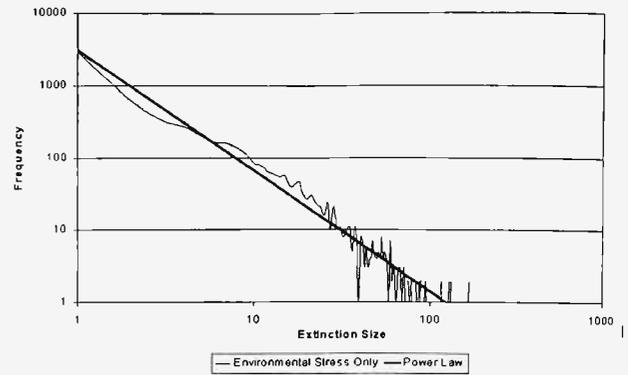

Figure 2: Graph of extinction rates for simulation run in which only environmental stress was used. The power law here has an exponent of $\tau = 1.67$.

it is well supported by palaeobiological evidence. See Raup [30] for some broad consideration of the issues involved, and Benton [10] for more detailed work. Benton performed an analysis of 840 families of tetrapods, concluding that "competitive replacement was apparently rare in the evolution of tetrapod families, and family originations were most often associated with expansion into new niches." ([10], pg. 204).

Results from a Number of Extended Runs of the Simulation

The simulation was run a number of times to test the effects of various parameter settings on the resultant dynamics. Except where noted, the following default principle parameter settings were used: 6 trophic levels with 500 niches per level; 4 environmental stresses using a bimodal probability distribution; an autotrophic level of 1000; extinction threshold of 50; a 0.02 probability of phyletic transformation per species per time step; and a 0.01 probability of speciation per species per time step. Each run consisted of 1,000,000 iterations. In each run data was collected on the number of extinction events per time step, the lifetime of species at the point of extinction, levels of environmental stress in each time step, mean tolerance to environmental stress across each trophic level and the ecosystem as a whole, number of species in each trophic level, mean number of prey species per predator species, and mean interaction levels between predators and prey. However, only selected results from the total collected will be presented and discussed here. Extinction rates were also calculated over periods longer than a single time step, and at very low resolutions. In the latter case, only partial

data was recorded, to reflect the low resolution of the fossil record. Both these data sets indicated potentially interesting avenues for further investigation, but are not directly relevant to the discussion below, and so will not be considered any further.

In addition to conducting runs varying the default parameter settings, several runs were also conducted in which only ecological or environmental factors were considered.

Extinction Rates

Figure 1 shows extinction rates (number of extinctions occurring in a single time step against rate of occurrence of an event of that size) using the default values given above, as well as four additional runs using various numbers and types of environmental stress. The results are plotted log-log, on which a power law form will appear as a straight line.

As can be seen, all five runs produced statistically very similar sets of results, suggesting that the dynamics of the system are robust to the type and number of environmental stresses. A power law with an exponent $\tau = 1.9$ has also been plotted, a value well within the range of available fossil data $\tau = 2.0 \pm 0.2$. Although the simulation curves initially follow this trend line very closely, higher extinction rates can be seen to be somewhat under-represented in the data according to the power law.

Figure 2 displays data from a run of the simulation in which only environmental stress was used. This data fits a power law form, with an exponent of $\tau = 1.67$, as has been plotted on the graph. This value is slightly lower than the range compatible with the fossil data.
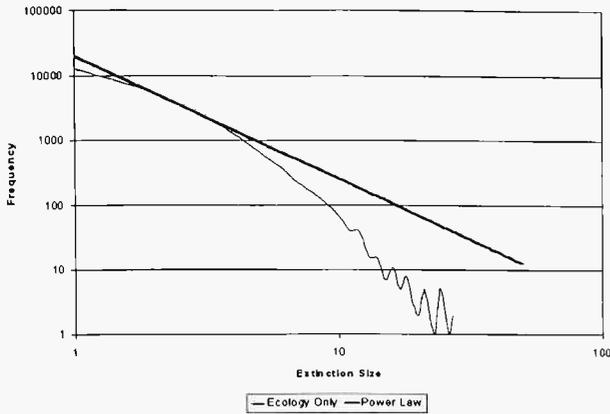
Figure 3: Graph of extinction rates for simulation run in which environmental stress was disabled. The power law here has an exponent of $\tau = 1.90$.

Figure 4: Graph of extinction size against lowest level of environmental stress at which an extinction event of that size occurred.

The data for figure 3 is drawn from a run in which the system was driven by ecological interactions alone, with environmental stress being held constant. Without the effects of environmental stress, the total number of species in the ecosystem was able to rise to considerably higher levels than in the other runs. Due to the increased computational demands that this entailed, the 'ecology-only' runs were limited to only 50000 generations. However, even on this shorter time-scale it is still clear that the statistical dynamics of the system remain almost constant when environmental stress is disabled. The same power law form as before, with $\tau = 1.9$, has been added to the graph. The simulation data again follows the pattern seen in figure 1, initially following a power law form closely with large extinction events being under-represented.

Figure 4 is derived from the default parameter settings described earlier. This figure shows the size of extinction events against the environmental stress level during the time step in which the extinctions took place. The graph has been generated from 10000 random data points taken from throughout the course of the run, by plotting the minimum level of stress during which an extinction event of that size occurred. A clear relationship can be seen here between the size of an extinction event and the level of environmental stress at the time at which that event occurred. A best-fit logarithmic curve has also been plotted, which can be seen to be a reasonable fit for the relationship between the two data sets. Note that the scale on the environmental stress axis is entirely arbitrary, and is here in the range $[0, 1.4]$.
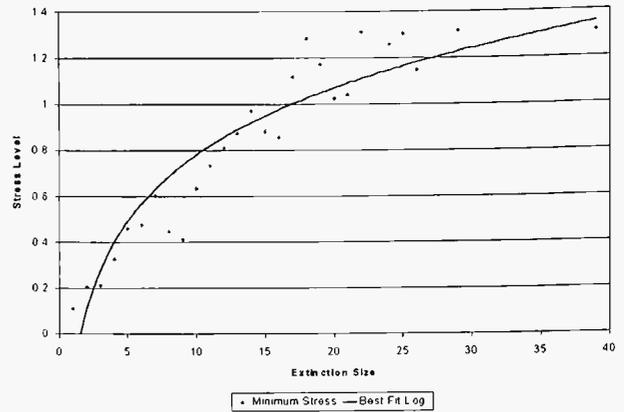
Ecological Data

Additionally, data on the ecological interactions occurring during the default parameter run was taken. The primary purpose of recording this data was to assess the biological credibility of the assumptions underlying the simulation mechanisms. However, some ecological data will be also be relevant to the discussion of macroevolutionary dynamics in the next section.

So far, all results have been tested as robust to minor changes in rates of speciation and phyletic transformation. However, due to the very high computationl demands of the simulation, comprehensive parameter sweeps have yet to be completed.

Discussion

Methodological Issues

There are several methodological issues which the use of a simulation-based model, such as the one described here, raises. Given sufficient degrees of freedom (and the model here has plenty) almost any desired results may be achievable, not through the intrinsic dynamics of the simulation, but rather just through careful control of parameters. This is particularly evident when modelling extinction patterns, due to the low resolution and extent of the empirical data to be modelled. Almost any simulation resulting in a power law distribution of some result set could purport to be a simulation of extinction dynamics in good accord with the empirical evidence. Several precautions must therefore be considered.

In the first place, the mechanisms of the simulation must generally be justifiable in terms of the system being simulated. For example in this case, it would be very easy to justify the finite number of ecological niches by

referring to the finite memory capacity of the computers on which the simulation is to be run. This would not, however, be satisfactory. This sort of problem is most evident in analytic models, which are intrinsically grounded by the requirements of solvability, rather than biological credibility. If the assumptions on which a model is based cannot be justified outside of that model, then it is difficult to see how a link of explanatory relevance can possibly be established between simulation and reality.

Secondly, the analysis of the model should extend throughout the domain being modelled, and not be limited to a single parameter. For example, as discussed below, measurements were taken of ecological factors in this simulation, such as lengths of food chains, in addition to the specific measurements of extinction events. A good simulation should be representative of the simulated domain in whichever way the data is to be considered.

Finally, a good simulation based model should be able to make predictions concerning the domain being simulated. This final point is perhaps the most important of all. The predictive power of a scientific theory has long been held as a cornerstone of its usefulness and validity. For a simulation based model to establish scientific credibility, it too should conform to this standard. Although no predictions will be presented here, there is certainly a large predictive scope for this simulation. For example, predictions could be made concerning the distribution of extinctions throughout different trophic levels, e.g. what proportion of autotrophic species are driven to extinction in a given size of extinction event?

Ecological Considerations in the Simulation

The data recorded included various measures of the ecological factors in the simulation. These can be compared with ecological data from biological systems in order to establish the credibility of the assumptions underlying the model. The data to be considered here include: maximum length of food chains; numbers of prey species per predator species; and relative abundance of species in different trophic levels. Some further discussion of issues regarding the comparison of simulated food webs with actual ecosystems can be found in Lindgren & Nordahl [21].

Begon, Mortimer and Thompson [8] point out that food chains rarely consist of more than four or five trophic levels. The data recorded here is in good accordance with this. For approximately 80% of the time, no food chains longer than five trophic levels occur in the ecosystem. Even at those times when food chains of six trophic levels do develop, they are few in number compared to shorter food chains (note that these values represent maximum chain lengths across the whole ecosystem).

The mean number of prey species per predator in a given time step was measured across the system at 1.64, with a standard deviation of 0.1, for the default parameter settings. This can be compared with the extensive data compiled in Cohen [11]. The value obtained from the simulation does appear to be very much on the low side when such a comparison is made – the mean value for all of Cohen's data is listed as 2.2. The simulation value is by no means implausible, however. The Georgia Salt Marsh food web, for example, contains only 1.75 prey species per predator, and that of the Florida Gastropods only 1.67.

Cohen also observes that the number of species in each trophic level is proportional to the number of species in the next lower trophic level. Cohen measures the constant of proportionality at 0.77 based on a limited sub-set of the available data. A constant of ≈ 0.5 was observed in the simulation – a not implausible value. The food webs of Costa Rican gastropods and lake-dwelling triclads both have values of exactly 0.5, for example, again as taken from Cohen's compilation.

Rates of Extinction – The Roles of Ecology and Environment

The distribution of sizes of extinction events is the single most important data set from the simulation. Although the data is highly suggestive of a power law form, it clearly does not take this form closely and consistently, with a notable under-representation of large extinction events. It should be noted that the finite bounds of the simulation might serve to distort the data, as pointed out for example in Kauffman [18]. The imposed limit on the maximum number of species the ecosystem can contain may result in a reduced number of large extinction events, since the system cannot expand to a point where the largest extinctions would occur. However, this under-representation of large extinctions is in fact in closer accord with the empirical fossil data than a straight power law form, also as observed in [18].

What is more interesting is a comparison of the curves for those runs in which environmental stresses were running in tandem with ecological factors, and the run in which environmental stress was the sole driving mechanism for the simulation. In all the runs in which the ecological factors were allowed to play a part, the resulting dynamics were near identical (see figure 1). In each case the curve follows the pattern described above, with exponents for the power law curve of $\tau \approx 1.9$ with under-representation of large extinction events. This same pattern was evident regardless of the number of environmental stresses, the probability distribution of those stresses, or even if there was any environmental stress at all. In part, this robustness of the dynamics to environmental stress is in line with the results from Newman [25]. In particular, the results were also highly robust to the particulars of stress generation. However, what is more sur-

prising, and where these results differ from Newman's, is that the statistical properties of the system continue to remain the same even when there is no environmental stress at all. The only time at which the dynamic changes is when the simulation is run with no ecological factors. This strongly suggests that it is the ecological factors, and not the environmental stresses, which are the sole contributory force to the extinction dynamics of the complete system. (If x appears to remain the same regardless of y then it is a fair assumption that x is independent of y). However, matters are not that simple.

Figure 4 shows why. There is a direct correlation between the size of an extinction event and the minimum level of stress occurring in the same time step as an event of that size. Were it not for the robustness to the presence or absence of various types of stress described above, this would be taken as a strong indicator that it is environmental stresses that are the dominant factor in determining extinction patterns. How can these two apparently contradictory dynamics be reconciled?

One way to view the results would be to consider that the long-scale dynamics of the system are governed by ecological factors alone. Thus, when looked at in a long time frame, the extinction statistics of any run in which ecological interactions were enabled would appear the same regardless of environmental stress levels. Under this view, external stresses are responsible only for determining the exact timing of extinction events of a particular size, acting as a sort of 'tempo-keeper' over the effects of ecological interactions. Note that this is opposed to the traditional view of extinctions taken in modern palaeontology (as for example in Raup [29]). This opposing view holds that factors extrinsic to an ecosystem are the direct cause of large scale extinction events, and the dynamics of such events should be determined by the patterns of such extrinsic factors. Ecological factors are typically viewed as generating low levels of background extinction, independently from environmental stresses.

These ideas are, of course, in need of a more formal and rigorous explication. This could perhaps be done in terms of the density of trophic connections, or the saturation level of the ecological niches in the ecosystem. In particular, the dynamics of the simulation need to be examined at a much finer grained level to ascertain exactly what role different factors play in specific individual extinction events.

One advantage of the current simulation over any of the other models considered is that it is driven by sufficiently low level mechanisms that further detailed investigations are easily facilitated. Future work can focus in on extinction dynamics at any required level of resolution, right down to the dynamics of individual populations. This provides scope for developing a thorough and detailed theory of extinction dynamics based around the dynamics of this simulation.

Conclusion

An ecology-based model of macroevolutionary dynamics has been presented. Results from several extended runs of the simulation have been considered, and discussed. The results suggest that patterns of macroevolutionary extinction dynamics are determined by the interactions between intrinsic ecological factors, and extrinsic environmental factors. Intrinsic factors appear to determine the large scale statistical dynamics of the system over long time scales. However, under finer grained analysis, specific extinction events can be seen to be highly correlated with specific levels of environmental stress.

Additionally, the finer-grained resolution of the simulation opens up considerable scope for further investigation. Predictions and analysis may be feasible that go beyond anything that is currently possible using existing models of extinction dynamics.

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References

[1] Abramson, G., 1997. Ecological model of Extinctions. *Phys. Rev. E* 55.

[2] Abramson, G., & Zanette, D. H., 1998. Statistics of extinction and survival in Lotka-Volterra systems. *Phys. Rev. E* 57:4.

[3] Adami, C., 1995. Self-organized criticality in living systems. *Phys. Lett. A* 203:23.

[4] Adami, C., 1994. On Modeling Life. In Maes, M. & Brooks, R., eds., *Artificial Life IV, Proceedings of the fourth conference on artificial life.* Addison-Wesley.

[5] Alvarez, L. W., et al., 1980. Extraterrestrial Cause for the Cretaceous-Tertiary Extinction. *Science* 208:4448.

[6] Amarel, J. A. N. & Meyer, M., 1999. Environmental Changes, Coextinction, and Patterns in the Fossil Record. *Phys. Rev. Lett.* 82:3.

[7] Bak, P. & Sneppen, K., 1993. Punctuated equilibrium and criticality in a simple model of evolution. *Phys. Rev. Lett.* 71.

[8] Begon, M., Mortimer, M., & Thompson, D. J., 1996. *Population Ecology, third edition.* Blackwell Science, Oxford.

[9] Benton, M. J., 1993. *The Fossil Record 2.* Chapman and Hall, London.

[10] Benton, M. J., 1996. On the Nonprevalence of Competitive Replacement in the Evolution of Tetrapods. In Jablonski, D., Erwin, D. H., Lipps, J. H., eds., *Evolutionary Paleobiology.* University of Chicago Press, Chicago.

[11] Cohen, H. E., 1978. *Food Webs and Niche Space.* Princeton University Press, Princeton.

[12] Dar, A., Laor, A., & Shaviv, N. J., 1998. Life Extinctions by Cosmic Ray Jets. *Phys. Rev. Lett.* 80:26.

[13] Drossel, B., 1998. Extinction Events and Species Lifetimes in a Simple Ecological Model. *Phys. Rev. Lett.* 81:22.

[14] Eldredge, N., 1996. Hierarchies in Macroevolution. In Jablonski, D., Erwin, D. H., Lipps, J. H., eds., *Evolutionary Paleobiology.* University of Chicago Press, Chicago.

[15] Hallam, A. & Wignall, P. B., 1997. *Mass Extinctions and their Aftermath.* Oxford University Press, Oxford.

[16] Head, D. A. & Rodgers, G. J., 1997. Speciation and extinction in a simple model of evolution. *Phys. Rev. E* 55:3.

[17] Jablonski, D., 1996. Body Size and Macroevolution. In Jablonski, D., Erwin, D. H., Lipps, J. H., eds., *Evolutionary Paleobiology.* University of Chicago Press, Chicago.

[18] Kauffman, S., 1995. *At Home in the Universe: The Search for the Laws of Complexity.* Oxford University Press, Oxford.

[19] Keitt, T. H. & Marquet, P. A., 1996. The Introduced Hawaiian Avifauna Reconsidered: Evidence for Self-Organized Criticality? *J.theor. Biol.* 182.

[20] Lawton, J. H., 1994. Population dynamic principles. *Phil. Trans R. Soc. London B* 344.

[21] Lindgren, K. & Nordahl, M. G., 1994. Artificial Food Webs. In Langton, C. G., ed., *Artificial Life III, proceedings of the third workshop on artificial life.* Addison-Wesley, Mass.

[22] MacArthur, R. H., 1972. *Geographical Ecology.* Harper Row, New York.

[23] Marin, J. & Solè, R. V., 1999. Macroevolutionary Algorithms: a New Optimization Method on Fitness Landscapes. *IEEE Transactions on Evolutionary Computation.*

[24] Maynard Smith, J., 1989. The causes of extinction. *Phil Trans R. Soc. London B* 325.

[25] Newman, M. E. J., 1997. A model of mass extinction. *J. Theor. Biol.* 189:235.

[26] Newman, M. E. J. & Palmer, R. G., submitted. Models of Extinction: A Review. *Paleobiology,* submitted.

[27] Newman, M. E. J. & Roberts, B. W., 1995. Mass-extinction: Evolution and the effects of external influences on unfit species. *Proc. R. Soc. London B* 260:31.

[28] Pelletier, J. D., 1999. Species-Area Relation and Self-Similarity in a Biogeographical Model of Speciation and Extinction. *Physical Review Letters* 82:9.

[29] Raup, D. M., 1991. *Extinction: Bad Genes or Bad Luck,* Oxford University Press, Oxford.

[30] Raup, D. M., 1996. Extinction Models. In Jablonski, D., Erwin, D. H., Lipps, J. H., eds., *Evolutionary Paleobiology.* University of Chicago Press, Chicago.

[31] Ray, T. S., 1992. An approach to the synthesis of life. In Langton, C. G., Taylor, C., Farmer, J. D., & Rasmussen, S., eds., *Proceedings of Artificial Life IV.* Addison Wesley, Redwood City CA.

[32] Roberts, B. W. & Newman, M. E. J., 1995. A model for evolution and extinction. *Cornell University technical report CU-MSC-8-95-4.*

[33] Sepkoski, J. J., Jr., 1993. A compendium of fossil marine animal families, 2nd edition. *Milwaukee Public Museum Contributions in Biology and Geology* 83.

[34] Sepkoski, J. J. Jr., 1996. Competition in Macroevolution: The Double Wedge Revisited. In Jablonski, D., Erwin, D. H., Lipps, J. H., eds., *Evolutionary Paleobiology.* University of Chicago Press, Chicago.

[35] Solé, R. V. & Manrubia, S. C., 1996. Extinction and self-organized criticality in a model of large-scale evolution. *Phys. Rev. E* 54.

[36] Vandewalle, N. & Ausloos, M., 1995. Physical models of biological evolution. *Proceedings of the Symposium on the Evolution of Complexity.*

[37] Wilke, C. & Martinetz, T., 1997. Simple model of evolution with variable system size. *Phys. Rev. E* 56:6.