

Simulations of recovery after mass extinctions

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Abstract

Mass extinctions played a crucial role in the evolution of species. They disrupted some evolutionary lines and started or altered others. After a short discussion of the impact of mass extinctions on the evolution of species, a simple model of evolution with three trophic levels will be discussed. This model was used by Solé and Montoya [1, 2] to measure the fragility of ecological networks, and to simulate the recovery of ecosystems after mass extinction events.

Introduction

Five big mass extinction events are known at present day. From fossil records we understand that these events gave evolution completely new twists and turns. The responses of surviving species range from unbroken continuity, over setbacks, to survival without recovery, and unbridled diversification [4]. Besides geographical effects, which will not be discussed here, it turns out that the properties of the trophic networks in an ecosystem play an important role in determining the fate of the single species as well as the system as a whole.

Here I will review the work of Solé and Montoya [1, 2] who analyzed trophic networks and their stability. This provides a better understanding of the effect of secondary extinction and the *'insurance effect'* in species-rich ecosystems. Also based on trophic networks a simulation of the response of an ecosystem after a mass extinction event was developed. Finally, I will briefly discuss, how these results were related to paleoecological data and fossil record.

A simple model for evolution

Three trophic levels

For modelling the time evolution of species diversity on an ecological time-scale, one has to group the species in the ecosystem. A reasonable minimal model

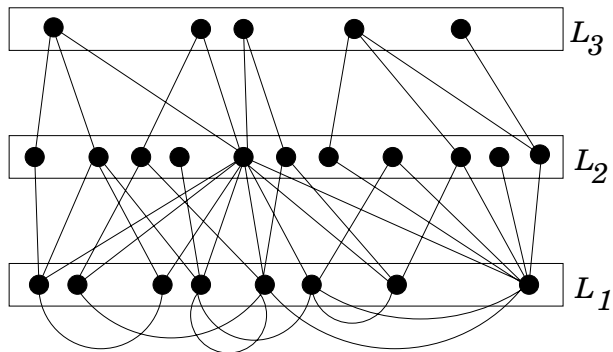


Figure 1: The three trophic levels of the evolutionary model. The labels L1, L2, and L3 refer to primary producers, herbivores, and predators, respectively. From: Solé and Montoya [1]

consists of only three layers (see Fig. 1), the three trophic levels: primary producers, herbivores, and predators. For the sake of simplicity let us not consider omnivores. Each species is connected to species in the other layers as either predator or prey. This is called a food network. In order to understand, why the three level approximation makes sense, we must take a closer look at the properties of these networks.

Food networks

It is known that complex networks can have a ‘*small world*’ (SW) behavior. In some of the networks the links are also distributed scale-free (SF), which means that the frequency of nodes, P_k , with k connections follows a power-law distribution, $P_k \approx k^{-\gamma}$. Most of the nodes are connected to only a few other nodes, whereas only a minority of nodes have a high connectivity. Networks with SW behavior and SF distributions exhibit a characteristic response to successive removal of their nodes. If the nodes are removed randomly, the SW network responds quickly and shows homeostasis. On the other hand, if the most-connected nodes are successively removed, network fragmentation will take place. In a study of the three best-documented food networks Solé and Montoya [2] found that the networks show either a SF or other fat-tail distribution of the P_k ’s, see Fig. 2. In their simulations they saw that there was little secondary extinction or network fragmentation, when species were removed randomly. Highly connected, or *keystone* species were found in all three layers that correspond to the minimal model. The extinction of a highly connected predator species can have as big an impact on the ecosystems as the removal of a highly connected primary producer. This reflects the phenomenon that the prey species population can now grow unhindered eating up a too large a share of the resources available in the ecosystem.

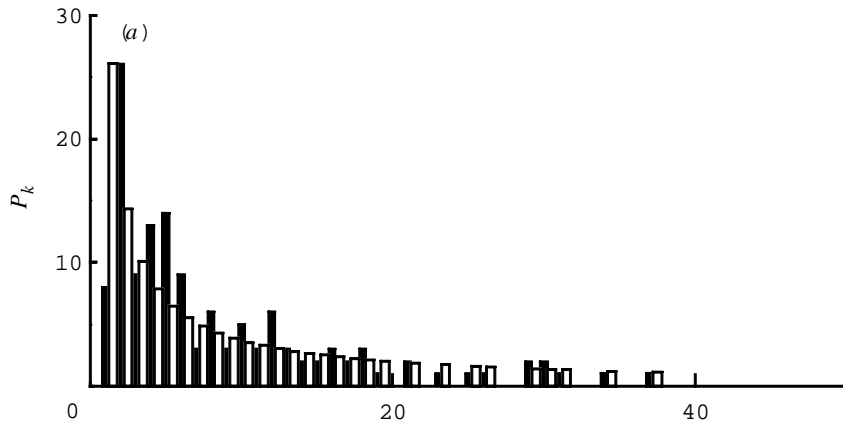


Figure 2: Histogram of the distribution of the total number of links k per number of species, P_k (black bars), for the Ythan Estuary food network (ref in [2]). The white bars show the best power-law fit. From: Solé and Montoya [2]

A second property of a food network has to be looked at when dealing with extinction: the *insurance effect*. One single large food network is favorable over many small sub-networks under variable environmental conditions and perturbations, because different species will react differently and a higher functional redundancy in the species results in a higher probability that one species can step in for another that becomes extinct. There is a species pool.

Ecological succession vs. recovery

It has been argued that mass extinction is qualitatively different from ‘background’ extinction, Jablonski (1986), reference in [1]. See also [3]. Here a spectrum of different scales of species extinction is considered and the effect on the time-scale of recovery is observed. The difference between these two effects will be manifest only in such a way that ‘background’ extinctions will cause other species from the regional species pool to fill the empty ecospace, but in case of mass extinction there is much more free ecospace, which will result in a two phase recovery process:

1. productivity rebound (quick return in richness and abundance of primary producers by successional dynamics), followed by
2. whole ecological rebound (delayed increase in abundance, speciation, evolutionary innovation).

Algorithmic realization of the model

For the simulation a very simple realization of the ecological model was chosen. A species is represented by a binary bit. At a very large time-scale the state of

the i -th species at the k -th layer at time t will be described by $S_i^k(t)$. The layers interact by virtue of the matrix elements C_{ij}^1 and C_{ij}^2 . The producers at the lower level also compete among each other. This is modelled by a competition matrix β . The evolution equations then become

$$\begin{aligned} S_i^1(t+1) &= \Theta \left[1 - \sum_{j \in L_1} \beta_{ij} S_j^1 - \sum_{j \in L_2} C_{ij}^1 S_j^2 \right], \\ S_i^2(t+1) &= \Theta \left[\sum_{j \in L_1} C_{ij}^1 S_j^1 - \sum_{j \in L_3} C_{ij}^2 S_j^3 \right], \\ S_i^3(t+1) &= \Theta \left[\sum_{j \in L_2} C_{ij}^2 S_j^2 \right], \\ \Theta(z) &= \begin{cases} 0, & z \leq 0, \\ 1, & \text{otherwise;} \end{cases} \quad \text{and } i = 0, \dots, N. \end{aligned}$$

The model has the basic structure of a *Lotka-Volterra* model, although there is no population size defined. Also notice that the model includes a response of the lower levels for the case that a predator becomes extinct (secondary extinction) in a straight forward way.

From the study of fossils we know that communities from similar environments have similar ecomorphological structures. Thus we might find functional patterns to be replicated after the recovery from a mass extinction event, quite like in the succession scenario, when a different species steps into the ecological niche that was left vacant after another species died out. These two observations can be used to add speciation events to simulation by simply adopting a new rule: After updating the system, vacant species sites can be filled with new species at a certain rate α . The newly created species inherits the connections from its ancestor, which is chosen at random from the same trophic level. The connection parameters C_{ij} for the new site i are then altered by adding a small amount of noise, e.g. $C_{ij}^\alpha = C_{kj}^\alpha + \xi_i^\alpha$, or establishing and deleting connections completely.

Simulation parameters and procedure

Solé and Montoya [1] used a $N = 500$ species system in their simulations. The simulation parameters were chosen to allow the ecological system to come to an equilibrium state. After $T = 3000$ simulation steps, when the equilibrium had been established, a pulse perturbation was applied removing a fraction E of the species from the system. The parameter E is called extinction size. The system was then allowed to come into equilibrium again and the equilibration time was measured as the amount of time that the system needed to regain 75% of its initial diversity.

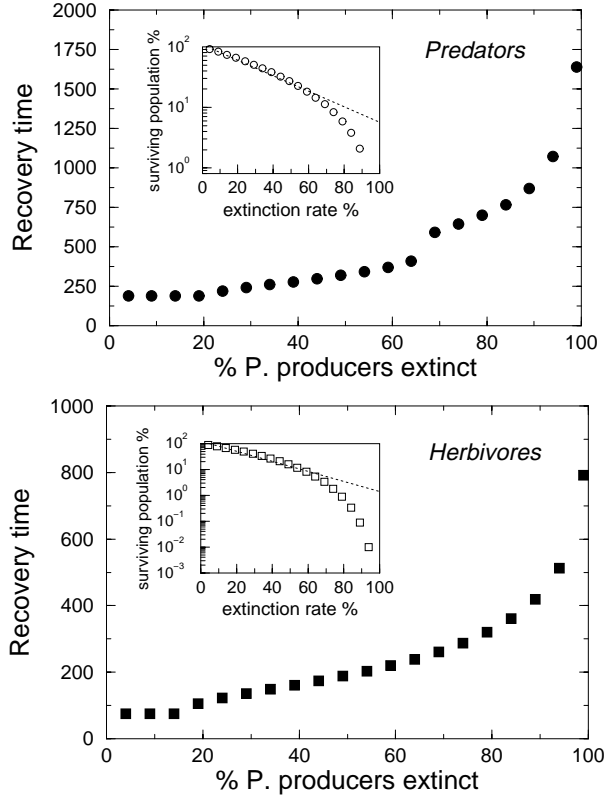


Figure 3: Recovery times of predators and herbivores for different extinction intensities on the level of primary producers. Observe the jump in the response of predator recovery time when 65 to 70% of the primary producers extinct. From: Solé and Montoya [1]

Results of the simulations

The simulations show that there is a threshold value of 20% for species removal from which the system can recover quickly. In the range $0.2 < E < 0.4$ the top predators recover faster than herbivores. See Fig. 3. This is because of the emergence of generalists. These are predators that have many weak connections, which prevents them from secondary extinction and favors further diversification. However, this advantage does not persist once a critical value $E_c \approx 0.5$ of the extinction size is surpassed.

The inset of Fig. 4 also shows the same regimes by comparing the number of surviving species of each layer immediately after the mass extinction event. The response of primary producers is linear with the perturbation size, whereas the other layers show non-linear behavior. At $E \approx E_c$ the number of survivors in the intermediate level drops almost to zero.

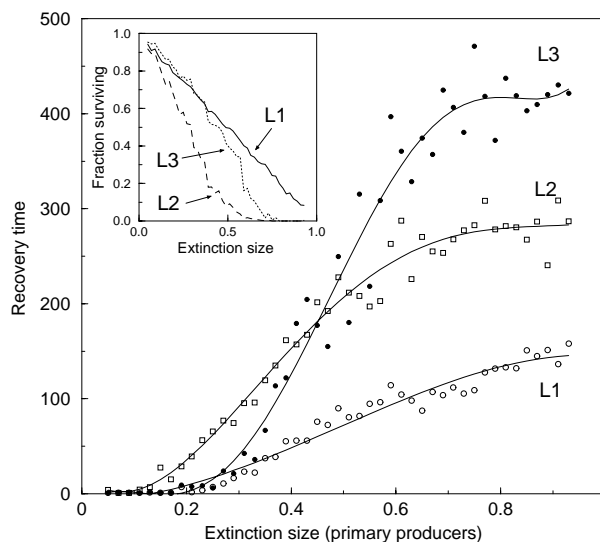


Figure 4: Recovery pattern as a function of the intensity of the mass extinction on the level of primary producers. The labels L1, L2, and L3 refer to primary producers, herbivores, and predators, respectively. From: Solé and Montoya [1]

Discussion

The results obtained by simulation can be compared with carbon isotopic analyses in paleoecological studies. The quick recovery after extinctions of size smaller than 20% can be identified with the episodic turnovers in community structure that were documented by paleontologists. There are also hints for the lags of recovery in herbivores and predators that were observed in the simulations. A correlation of magnitude between recovery lag and magnitude of the diversity drop has not been found in the fossil record, but this can also be due to insufficient resolution of geochronologic dating methods.

In primary producers the three layer model has a threshold of 75% removal of species before it shows a lag in recovery. However, in ecological models we do not expect a strict linear behavior. Non-linear or even discontinuous responses seem to be more realistic.

Future simulations could include differences in pattern recovery for different biogeographic provinces (Jablonski, 1998, ref. in [1]). Other issues are different feeding strategies on primary producers and the dynamics of nutrient cycling, e.g. feeding on living plants vs. dead plants will play an important role in surviving when there is a drop of photosynthesis for several months.

It is of great importance to further investigate the dynamics of (mass) extinctions and recovery in ecosystems since the exploitation of the resources of the planet Earth by the species man lead us to the brink of a biotic crisis [4]. It is expected that a large loss in species diversity will occur on a scale that is

surpassed only by the five big mass extinctions. We will have to adopt strict conservation policies based on this research to protect the global bio-diversity and ourselves from the fate of extinction.

References

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