Recovery after mass extinction: evolutionary assembly in large-scale biosphere dynamics

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Biotic recoveries following mass extinctions are characterized by a process in which whole ecologies are reconstructed from low-diversity systems, often characterized by opportunistic groups. The recovery process provides an unexpected window to ecosystem dynamics. In many aspects, recovery is very similar to ecological succession, but important differences are also apparently linked to the innovative patterns of niche construction observed in the fossil record. In this paper, we analyse the similarities and differences between ecological succession and evolutionary recovery to provide a preliminary ecological theory of recoveries. A simple evolutionary model with three trophic levels is presented, and its properties (closely resembling those observed in the fossil record) are compared with characteristic patterns of ecological response to disturbances in continuous models of three-level ecosystems.

Keywords: biodiversity recoveries; assembly dynamics; mass extinctions; food web structure; macroevolutionary model

1. INTRODUCTION

The dynamics of the biosphere involves temporal scales spanning millions of years with a nested hierarchy of different processes taking place at different temporal and spatial scales. Ecological and evolutionary responses are strongly correlated across scales, and ecosystems constrain further evolution due to a number of emergent properties that are characteristic of mature communities, which are typically resistant to the invasion of new species and display a high degree of homeostasis (Pimm 1991; Morin 1999; see Levine & D'Antonio (1999) for a recent review of the discussion community maturity/diversity–invasibility). But existing ecologies are also the result of evolutionary forces that go beyond the pure ecological scenario: path dependence, innovation and the response to strong perturbations.

Although most models of large-scale palaeoecologies do not consider real evolutionary responses, it seems obvious that an important ingredient in the evolution of the biosphere through the Phanerozoic is the presence of irreversible qualitative changes in ecosystem function associated with the aftermath of mass extinctions (Erwin 2001).

Despite the variety of causes of mass extinctions they all share a common trait: they reflect perturbations which stress ecosystems beyond their resilience. Ecosystems reflect long-term assembly processes in which individual species come and go, but eventually a functional whole

emerges. The final system tends to be stable (in some sense, e.g. very resistant to new invaders, high biodiversity levels, characteristic trophic structure or low turnover rates between species), but such stability is context dependent and has been built up under a given set of conditions and historical constraints. Despite the heated topics concerning the complexity–diversity–stability debate (see McCann (2000) for a review), it is commonly accepted that new perturbations, or perturbations that are greater in magnitude or duration than the system can accommodate, can disrupt it (Margalef 1968, 1997; Yodzis 1997).

The ecological and evolutionary impacts of different extinction events differ between extinctions and the same happens with recovery patterns (Hallam & Wignall 1997; Erwin 1998a). Some mass extinctions had little immediate ecological effect, or long-term evolutionary consequences (end-Ordovician, end-Triassic). Others, such as the end-Permian event, dramatically shifted the course of evolution (Erwin 1993, 1994). Recovery patterns provide a unique window to explore the structure and evolution of palaeoecosystems. Ecological links do not fossilize, but many aspects of the underlying structure of ancient food webs can be inferred from the fossil record.

Several examples illustrate this claim. Estimations of carbon fluxes (particularly carbon isotopic ($\delta^{13}C$) differences) have shown that the ecological recovery in oceans after the K–T event involved the rebuilding of higher trophic levels (D'Hondt et al. 1998). By tracking the time evolution of carbon isotopes, D'Hondt and his colleagues showed that primary productivity quickly returned to previous levels over thousands of years. However, the final recovery of the open-ocean ecosystem structure required the evolution of new species and more than

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Table 1. *Comparison between different trends displayed by ecological succession and those observed in recovery dynamics.*

(ss, small size; PP, primary production; CPP, constant primary production. No information is available in relation to the degree of predictability or the probability of invasion for fossil record data.)

|	ecological succession	recovery pattern
initial condition	species-poor	low-diversity
initial groups	generalists, ss, short-lived	common sp., opportunistic, ss
final groups	specialist, larger, longer-lived	Lazarus sp., larger
trophic features	trend constant CPP, omnivory	increase predation
functions developed	trend to CPP	increase in PP
niche dynamics over time	colonization	colonization + construction
final system/community	mature community	functional ecology
path dependence	present, moderate	important
predictability	possible (at the community level)	?
probability of invasion	decreasing with time	?
external species pool	conserved	evolving
diversity trends	increasing	increasing
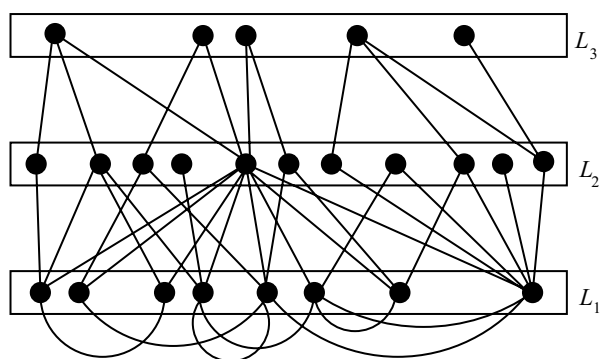
Figure 1. Trophic structure of the evolutionary model of recovery. The basal level (L_1) includes primary producers competing for some underlying resources. The second (L_2) and third (L_3) levels are connected to the lower layers through trophic links.

3 Myr. The late Cenomanian event gives a similarly well-defined example of marine food-chain recovery (Hart 1996). Late Cenomanian ecosystems have been reconstructed prior to the start of the event and followed through the subsequent changes. Changes in the oxygen minimum zone through the water column triggered the later changes, which can be followed in their effects on the abundances of different groups (over thousands of years). Similar evidence is also available from terrestrial ecosystems (see Erwin 2001).

As a first approximation, it seems reasonable to consider the underlying ecological networks as a three-layer structure (figure 1) involving primary producers, herbivores and predators. Although trophic-level interactions in evolutionary recovery studies are starting to be addressed (Hart 1996; D'Hondt *et al.* 1998; Erwin 2001), earlier evolutionary models based on competitive interactions among organisms have not considered the importance of networks of feeding relationships on recovery patterns.

On an ecological time-scale, a consideration of different trophic levels is required for understanding successional patterns, as it is for a rebound in primary productivity (Valentine 1973). For instance, algal succession in the rocky intertidal zone of California was accelerated in the presence of herbivores, because herbivores removed early-successional species and allowed late-successional species

to become established. By contrast, there is only anecdotal evidence for terrestrial ecosystems (Morin 1999).

In this paper, we try to provide a preliminary ecological theory of recoveries. In doing so, we first investigate possible similarities and differences between ecological succession and recoveries from mass extinctions. Then, we explore the behaviour of two dynamic models where trophic structure is present: a simple ecological model that is Lotka–Volterra based and a new evolutionary model of recovery where speciation is present. In both cases, recovery patterns after different magnitudes of disturbance on primary producers are explored, searching for similarities in diversity rebounds observed in the fossil record.

2. ECOLOGICAL SUCCESSION VERSUS RECOVERY

Succession (in a strict sense, secondary succession) includes the processes that co-occur after disturbances to established communities, but that do not destroy regional species pools. Although the specific species and their relative abundances may change from pre-disturbance communities, no new species evolve and the composition of successional communities will be drawn from the regional species pool and occasionally colonization from other regions. It has been widely observed that a mature community where niches are occupied is highly resistant to the colonization of new species belonging to a different regional species pool (Elton 1958; Pimm 1991; Margalef 1997; Levine & D'Antonio 1999; and references cited therein). The establishment of new species sometimes occurs, but it is often due to different kinds of human-induced disturbances affecting mature communities (see Mooney & Hobbs (2000) for a review). Empty ecospace is also present after mass extinctions, but the greater magnitude of the disturbance creates opportunities for new species as well as colonization by surviving species. The number of species in a single assemblage increases after disturbance in both cases, but for different reasons. Ecological disturbances are followed by recolonization from surrounding areas or regions, depending on the magnitude of the disturbance. By contrast, post-extinction rebounds are characterized by colonization, delayed increases in abundance, speciation, and for the largest events, evol-

utionary innovation. One of the outstanding issues in understanding ecological disturbance concerns the similarities and differences between the local, ecological scale of succession and the global and evolutionary scale of post-mass extinction recovery.

Many field studies on ecological succession focus on plant succession, but only a few consider whole-ecosystem patterns. This has led to an overemphasis on the role of plant competition (a special type of primary producer) in explaining successional patterns (Drury & Nisbet 1973). The few studies dealing with trophic levels other than primary producers include the data from breeding birds in different secondary successional sites in the piedmont of Georgia, USA (Johnston & Odum 1956). Recovery of the original vegetation was accompanied by bird replacements. The composition of the bird community in sites at early successional stages was very different from that present in sites with mature vegetation. One of the features of biodiversity recoveries on evolutionary timescales is the common presence of opportunistic clades just after the perturbation, followed by their gradual replacement by non-opportunistic clades. Examples include the lycopside *Isoetes* and the bivalve *Claraia* in the Early Triassic and *Gumbelitria* in the earliest Tertiary. These taxa are both locally highly abundant and geographically widespread immediately following mass extinctions. In some cases, these taxa may have been well adapted to the unusual environmental conditions of the time. For example, *Claraia* is common in dysaerobic marine environments as may have predominated in the earliest Triassic. Priority effects are actually observed in ecological succession along with species replacements (Rosenzweig & McCord 1991).

From an ecological point of view, there are two recovery phases: (i) productivity rebound (a quick return in richness and abundance of primary producers), and (ii) whole ecological functions rebound. Both are observed in the fossil record (Hart 1996; D'Hondt *et al.* 1998). Successional dynamics tend to stabilize primary production, as well as primary production equals total respiration (Margalef 1997; D'Hondt *et al.* 1998).

Before introducing our two basic models, it is worth explaining why it is important to use an ecological–community level analysis, and what are the more relevant (and sometimes controversial) issues to explore through this approximation. First, there is compelling evidence from the fossil record that (as it occurs today) fossil communities from similar environments have similar ecomorphological structures (see Valentine (1973) and references cited therein). In spite of the different species composition of two ecosystems, one can usually identify close ecological analogues between them. Similarities found in diversity (both morphological and taxonomic) are actually far more impressive than the differences observed between major biotic crises (Bambach & Bennington 1996). This and other examples suggest that functional patterns of community organization might be replicated under similar conditions, as happens when comparing modern ecosystems (e.g. food-web patterns and ecosystem functions related, Polis & Winemiller (1996)). The similarities exhibited allow us to conjecture that similar ecological constraints to community organization are at work.

Another important issue is to what extent community-level influences can be a major force in macroevolution. In this context, it has been argued that ecological networks actually provide a possible source of decoupling between micro- and macroevolutionary dynamics (Solé *et al.* 1996, 1999). Such a decoupling naturally emerges as a result of the importance of network-level responses, as cascade and indirect effects can be as important as direct, pairwise interactions among species (Pimm 1991; Yodzis 1997; Wooton 1998; Morin 1999). However, this picture requires a consideration of environmental stochasticity (see Newman 1997) and other sources of change, such as evolutionary innovation.

How much of the Phanerozoic patterns of extinction and diversification is due to biotic responses, such as escalation (Vermeij 1987), or to stochastic driving of species from interaction stress is not known, but both need to be included in the whole picture (Benton 1996; Sepkoski 1996). In many ways, chance and necessity meet in the aftermath of mass extinctions, and models can help to understand how they interact.

3. A SIMPLE ECOLOGICAL MODEL

How will species populations recover when we subject them to a transient shock? Disturbance plays an important (sometimes leading) role in determining the abundance and diversity of species in ecosystems. Models of the effects of disturbance on ecological communities usually deal with communities of competing species at a single trophic level. But in most real ecologies the dynamics of one species affects the dynamics of other species across trophic levels, often in unpredictable ways (Yodzis 1997; Wooton 1998). In this section, we use a very simple ecological model that could yield some insight into the ecological mechanisms occurring after a perturbation acting on primary producers, including time-lags to recover population densities for each trophic level or the nature of the response under different perturbation intensity.

The model consists of three species at three different trophic levels, whose interactions are described through Lotka–Volterra dynamics. We have three different equations describing the population dynamics of the primary producer (X_1), the herbivore (X_2) and the predator (X_3) species. These variables refer to the number of individuals (i.e. population abundances) in each trophic level. Omnivory is not present, that is, the herbivore feeds on the primary producer and the predator on the herbivore. Primary producers compete among themselves (intraspecific competition, parameter a_{11}), whereas herbivores and predators only compete indirectly via predation on primary producers and herbivores, respectively. The model (Pimm 1999) is defined as:

$$\frac{\mathrm{d}X_1}{\mathrm{d}t} = X_1(b_1 - a_{11}X_1 - a_{12}X_2), \tag{3.1}$$

$$\frac{\mathrm{d}X_2}{\mathrm{d}t} = X_2(b_2 - a_1X_1 - a_{23}X_3), \tag{3.2}$$

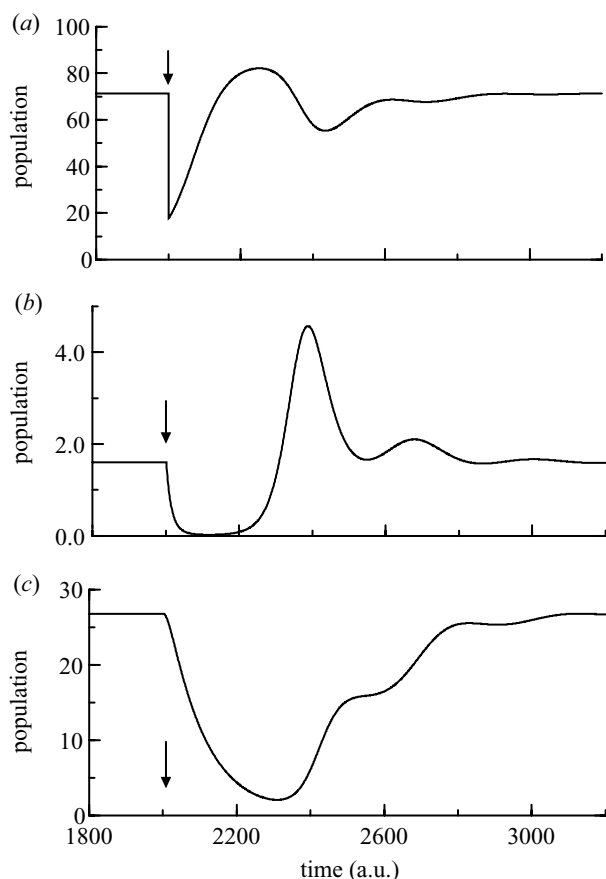$$\frac{\mathrm{d}X_3}{\mathrm{d}t} = X_3(-b_3 + a_{32}X_2). \tag{3.3}$$

Figure 2. Recovery pattern of population densities in the ecological model for (*a*) primary producers, (*b*) herbivores, and (*c*) predators. The perturbation (marked by the arrow), eliminates 75% of the population of the primary producer. Although the primary producer population recovers quickly, both herbivores and predators experience a well-defined delay. Here we use: $b_1 = 0.85$, $b_2 = 2.9$, $b_3 = 0.4$, $a_{11} = 0.01$, $a_{12} = 0.085$, $a_{21} = 0.05$, $a_{23} = 0.025$ and $a_{32} = 0.25$. The basic patterns observed here (particularly the patterns of delay) are highly robust under other parameter values.

Each equation contains a growth or death term in the absence of other species (b_i) and interation terms for every interspecific interaction. These terms are of the form $a_{ij} X_i X_j$, that derives from the assumption that species collide with each other randomly like molecules in a gas.

The set of parameters b_i, a_{ij} and a_{ji} has been chosen in order to have a fixed point as the system attractor (see figure 2 for parameter values). We let the population densities arrive at equilibrium, and then we disturb primary producers by removing a percentage of their equilibrium density. Here, our plots start from the species densities at equilibrium (after a transient of 2×10^3 steps has been discarded) and then the system is perturbed.

Disturbances affecting primary producers cascade into other trophic levels, often with some time-delay (see figure 3) on both herbivore and predator populations. Understanding the population dynamics of the species just after an extinction event would help us discern why some species survive whereas others go extinct. For instance, if ecosystem dynamics kept some species or clades below some critical population value over a long time, these organisms would be more prone to extinction. Other ecosystem functions, like primary production, are closely related to population densities (Tilman 1999). Although there is insufficient time resolution in the fossil record to observe population dynamics (Behrensmeyer *et al.* 2000), recent studies on biodiversity recoveries based on carbon isotopic ($\delta^{13}C$) analysis are opening a feasible test for such theoretical observations (D'Hondt *et al.* 1998; Erwin 2001).

4. EVOLUTIONARY MODEL OF RECOVERY

The problem of modelling complex ecological systems, including trophic interactions of different types (such as competition and predation), is far from trivial. Adding evolutionary changes simply increases the difficulty. Some previous models have explored this issue with variable success (see Solé *et al.* (1999) and references therein). Models of interacting or non-interacting species were used in the analysis of extinction patterns through the interplay of biotic and abiotic causes (Sepkoski 1978, 1979, 1984; Kauffman & Johnsen 1991; Raup 1991, 1996; Plotnick & McKinney 1993; Newman 1996, 1997; Solé *et al.* 1996, 1999). These models are very simple but their dynamic outcomes can sometimes give unexpected results and provide a quantitative formalization for different scenarios of macroevolutionary dynamics.

Most of these models lack a multi-trophic, layered structure, and thus cannot be properly used to compare the responses of different parts of the ecology, such as primary producers or top predators. An exception is the work of Amaral and Meyer, who developed a model of large-scale evolution with a layered structure (Drossel 1998; Amaral & Meyer 1999; Camacho & Solé 2000). The model is able to reproduce some interesting patterns displayed by the fossil record (such as some long-range correlations in the fluctuations of species numbers), but all the influences and cascade effects are bottom-up: species at higher layers depend on the presence of other species in their immediate lower level and become extinct if all their prey at the lower layer disappear.

Here, we consider a similar model in which three layers of sites (that can be occupied by new species) are defined, involving primary producers, herbivores and predators (figure 1). Instead of using a simple model where links have no weights or signs (as in the Amaral–Meyer model) we introduce weighted interactions in order to gain some realism and provide the system with the opportunity of self-organizing with no other constraint than the layered structure. Besides, top-down and bottom-up control can emerge and extinctions can happen if prey in the bottom layer are gone, but also under pressure from the top predators (May 1974; Pimm 1991). Other sources of species coextinction can include overcompetition between prey after a predator with a wide diet of species is removed (Bronmark *et al.* 1992; Persson *et al.* 1996; Schmitz 1997).

Our model is an oversimplified picture of reality, and for simplicity we represent species as present (1) or absent (0). Also, the time-scale in our simulations is assumed to be very large. The state of the ith species at the kth layer at a given time t will be indicated as $S_i^k(t)$. Layers two and three (L_2, L_3) exploit species at lower layers and thus they do not compete directly. The interactions between layers L_1-L_2 and layers L_2-L_3 are indicated by C_{ij}^1 and C_{ij}^2, respectively. Producers at the lower level exploit some
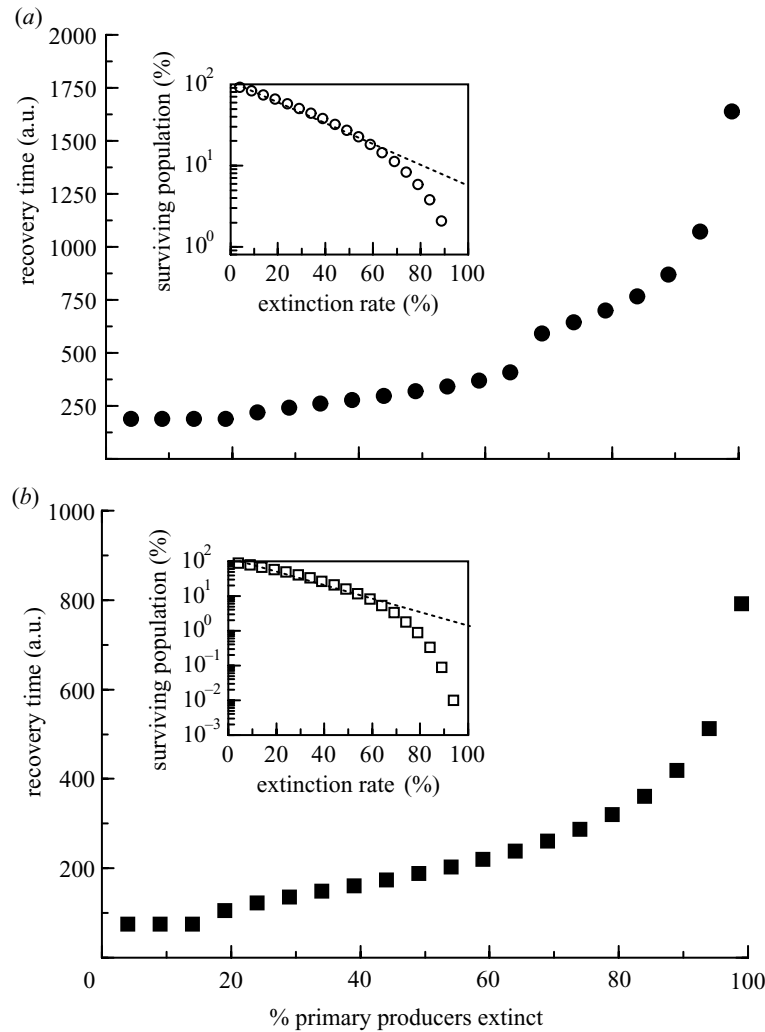
Figure 3. Recovery times of predators (*a*) and herbivores (*b*) after different perturbation intensities on the primary producer equilibrium population for the ecological model. Recovery times reflect the time since the end of the perturbation until recovery of 75% of the pre-extinction population. Insets show the survival population (i.e. the minimum value it reaches) in relation to the percentage of primary producers that are extinct. A quick change in the response of predators to perturbation is observed for 65–70% of primary producers that are extinct.

underlying, limiting resource and thus compete among themselves. Their interactions are defined by a competition matrix $\beta = (\beta_{ij})$.

The state of each species at each layer is updated following simple rules. First, species from the bottom layer can become extinct with some probability p_d. Then the states are updated as follows:

$$S_i^1(t + 1) = \Phi\left[1 - \sum_{j \in L_1} \beta_{ij}S_j^1 - \sum_{j \in L_2} C_{ij}^1 S_j^2\right], \quad (4.1)$$

$$S_i^2(t + 1) = \Phi\left[\sum_{j \in L_1} C_{ij}^1 S_j^1 - \sum_{j \in L_3} C_{ij}^2 S_j^3\right], \quad (4.2)$$

$$S_i^3(t + 1) = \Phi\left[\sum_{j \in L_2} C_{ij}^2 S_j^2\right], \quad (4.3)$$

where $i = 1, \ldots n$, $\Phi(z) = 0$ if $z \leqslant 0$ and $\Phi(z) = 1$ otherwise. A maximum number of n sites per layer is considered. The

first equation corresponds to producers and involves three terms: (i) a constant term Θ, which guarantees that it will survive if no other species are present; (ii) a competition term; and (iii) a third term involving pressure from grazers. Grazers experience the pressure from predators through C_{ij}^2 and a positive predation term on producers through another matrix C_{ij}^1. The final layer of top predators has only one term from their predation on level L_2.

In spite of their discrete character, we can easily recognize the basic features of (three-level) Lotka–Volterra models, although no population size is defined for each species and species come and go. As we will see, however, some surprisingly common features are shared with the behaviour of the previous continuous, ecological model.

The rules are completed by introducing speciation into the system. After the previous updating is applied (in a sequential way) then new species can be created from existing ones. This rule is introduced as follows: at each layer we look for empty niches (i.e. using vacant sites (such that $S_i = 0$)) and with some probability of origination α, a new species can be generated from one of the already present species at the same layer. The new species is
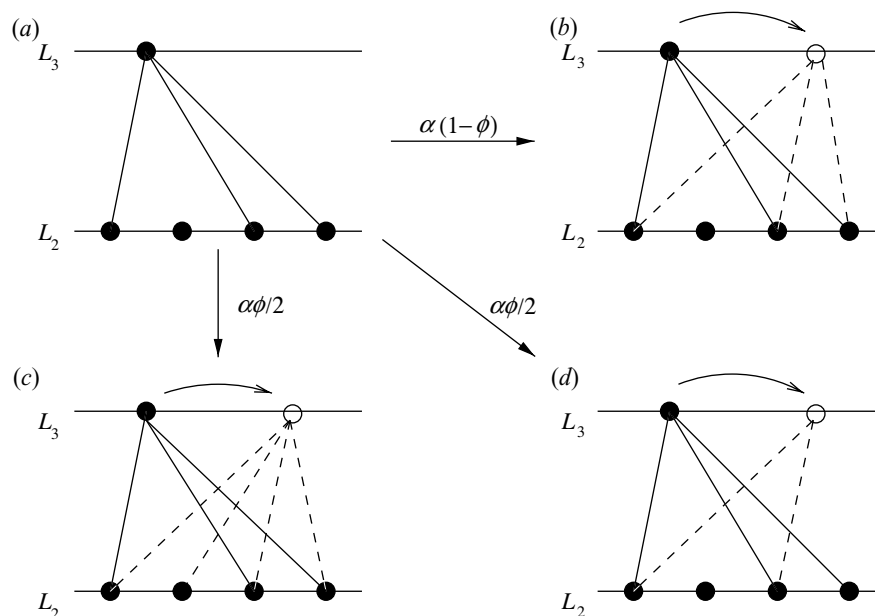
Figure 4. Diversification into empty sites: at each level (here layers L_2 and L_3 are shown as examples) a new species (open circle) can emerge at empty sites through diversification of a present species at another site (solid circles). With probability α, the new species is generated by copying the connections of its ancestor. The copy (b) will maintain the same set of connections (with small changes in their strengths) with probability $1 - \phi$. Two more possibilities are allowed: (c) a new link (with random strength) is added or (d) one of the inherited links is deleted. Both events take place with probability $\phi/2$.

obtained by copying its ancestor's set of connections, and adding a small amount of noise to the new connections. Assuming that the chosen species is S_k, the new connections of the new species (say from level L_2) are inherited from the parental one as

$$C_{ij}^1 = C_{kj}^1 + \xi_{ij}^1, \qquad (4.4)$$

$$C_{ij}^2 = C_{kj}^2 + \xi_{ij}^2, \qquad (4.5)$$

and similarly for other levels. The copy process can include the addition or deletion of connections (see figure 4). Different variations around these rules gave the same basic results.

The model displays some amount of sensitivity to the type of species removal occurring in the bottom layer. An example of the model dynamics is shown in figure 5, where a system with a maximum of $n = 100$ species per level is used. Instead of introducing high rates of removal at specific times (i.e. pulse perturbations), here we remove, at each step, a small fraction of species from the bottom layer. Looking at the total number of species extinct at each step (figure 6a), we can see that the system is able to amplify the small perturbations introduced at the lower level. By looking at a small period of time, we see in figure 6b that the number of species at the top layer can experience sudden drops associated with cascade events resulting from a small amount of (random) species removal. After each drop, a recovery pattern with some delay is observable. The statistics of total extinction events (inset, figure 6c) are consistent with previous reported analyses (Newman 1996). Specifically, the frequency $n(s)$ of extinctions of size s scales as $n(s) \approx s^{-\gamma}$, with $\gamma \approx 2$. But actually under this regime of small, constant perturbation, the large extinction events cannot reach the larger values observed from the major extinction events. This suggests that a purely internal origin of the very large extinctions

cannot be accounted for under the assumptions considered here.

Our analysis of recovery patterns will assume that the ecosystem has reached some equilibrium state (under the previous set of rules) and that stationary diversity levels are present before the pulse perturbation is introduced. The parameters used are chosen accordingly in order to guarantee stable levels. The stability conditions we are assuming in the model do not refer to the absence of compositional variability, but to aggregate variability (Micheli *et al.* 1999). Changes in species composition through removal, addition and replacement are present at equilibrium states (in lower rates than those observed over recovery periods), as many palaeontologists suggest is the rule over time (Valentine & Jablonski 1993), whereas certain overall, aggregate properties of the ecosystem remain constant, as diversity levels, trophic structure or productivity. Several studies on biodiversity recoveries deal with these sorts of aggregate properties to assess the pace of the rebounds (Valentine 1973; D'Hondt *et al.* 1998; Jablonski 1998; Kirchnner & Weil 2000) Thus, stationary states where pulse perturbations take place in our evolutionary model are non-equilibrium conditions under the perspective of compositional variability.

In figure 7, the basic results obtained from extensive simulations of the evolution model are shown. Here, an $n = 500$ system has been used, and is run over $T = 3000$ steps in order to get a stable ecology. Then a pulse perturbation is introduced on the first layer, killing a fraction of the species present. Species removed are randomly chosen and the fraction removed is called the extinction size (E) at this level. Then, the system recovery is followed over other $T = 3000$ steps. Two quantities are shown in this plot. One is the time required in order to re-establish 75% of the initial diversity before the extinction. We can see that there seems to be a threshold of *ca.* 20% of removal
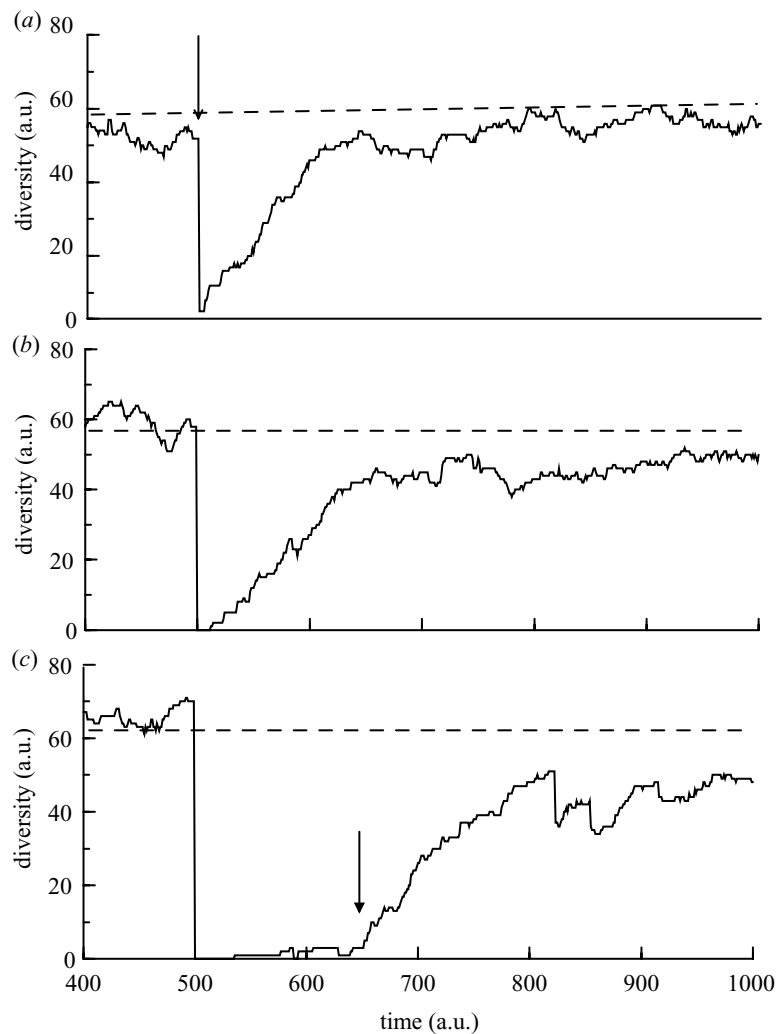
(a)

(b)

(c)

Figure 5. Recovery pattern displayed by the evolutionary assembly model after a pulse extinction introduced at $T = 1000$. Here, the diversity levels of: (a) primary producers, (b) herbivores and (c) predators are shown. We can appreciate different recovery curves associated with each level. A clear lag occurs at the two upper levels, as happened in the recovery of populations in the ecological model.

in which recovery proceeds very quickly (only the intermediate level seems to experience some delay). For $0.2 < E < 0.4$, top predators recover faster than herbivores. This is due to the emergence of predators that have many, but weak, connections (i.e. generalist species), preventing them from being removed and favouring further diversification. However, after $E_c \approx 0.5$, predators require larger times, reflecting the fact that their buffering against extinction associated to broad trophic requirements no longer enhances recovery.

These different regimes can be also observed by looking at the inset of figure 7: here, the fraction of species surviving immediately after the mass-extinction event is shown. As expected, for the bottom layer we find a linear relationship between input and response (further effects involving competition are not shown). But the response of herbivores and predators is far from linear. Actually, we can see that $\Gamma(E)$ drops to nearly zero for $E \approx E_c$ at the intermediate level, and a corresponding drop in the top layer is also observable around this value. Variations to the previous model gave very similar results.

5. DISCUSSION

The evolutionary trophic model presented here has some clear implications for studies of real biotic recoveries. For pulse extinctions, we predict a progressively greater lag in recovery as one moves from primary producers through herbivores to predators. This can be tested by comparing carbon isotopic analyses with detailed palaeoecological studies, and available evidence, although sketchy, is consistent with this prediction (Erwin (2001) and references therein). For extinctions below about 20% of diversity, recovery proceeds very quickly, reproducing a pattern similar to the episodic turnover in community structure that is commonly documented by palaeontologists. For more severe extinctions, the model shows differences in the recovery time between herbivores and predators. We suggest that the faster recovery of predators for extinctions between 20% and 40% may reflect their numerous, weak connections. This prediction is amenable to testing by comparing (across numerous clades) the recovery rates of
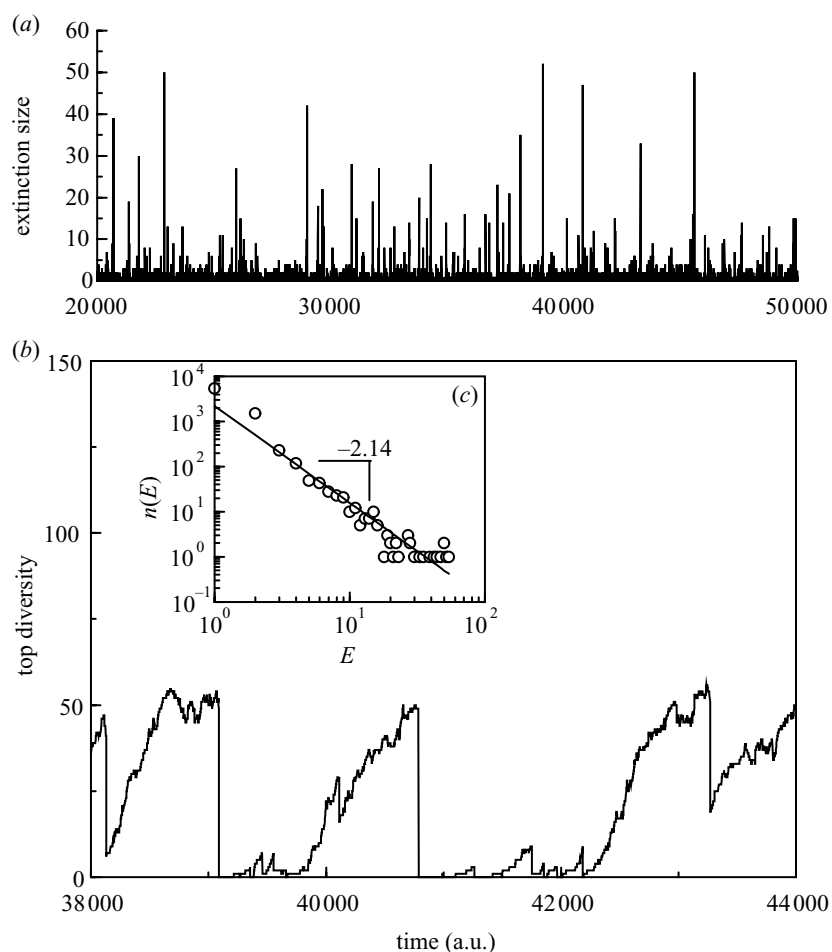
Figure 6. Extinction and diversification in a long-run evolution of the recovery model. Here, a system with $n = 150$, $\alpha = 0.003$, $\phi = 0.002$ and a constant probability of removal at the bottom layer of $P_d = 0.01$, is constantly applied through the process. Here, we show (*a*) the statistics of extinction events (for all layers), and (*b*) diversity dynamics for the upper layer, where a delayed response is observable after each large extinction event. In (*c*) the frequency distribution of (total) extinctions is shown to be a power law.

specialist and generalist predators. Weak interactions between species have important consequences for community stability and species persistence because of two underlying mechanisms: (i) the weak-interaction effect generates negative covariances between resources (prey) that promotes community-level stability, and (ii) these negative covariances ensure that the species that interact weakly dampen the destabilizing potential of strong interactions (McCann 2000).

Is there a correlation between the magnitude of extinction and the pace of recovery? That is, is the duration of the recovery lag proportional to the magnitude of the diversity drop? As Erwin (2001) notes, this relationship has been proposed, but there is no good evidence of such a proportional lag from the fossil record. This may simply reflect a lack of sufficiently precise geochronologic dating and palaeontological analysis.

In our evolutionary trophic model there is a threshold of about 75% removal of primary producers before the appearance of a lag in recovery proportional to the magnitude of extinction (figure 7). In ecological models with nonlinear dynamics, the pace of the response to long-term perturbations in terms of population recoveries is far from being known. At short-term scales, where perturbations of low intensity take place, linear relationships between

magnitude of perturbation and magnitude of response are exceptional. Non-monotonic responses, critical transitions and even discontinuous responses are thought to be more realistic (Yodzis 1997).

Our ecological model tries to explore these responses under a wide range of magnitudes of extinction that affect primary producers, incorporating both short-term and long-term perturbations. A linear response is followed by an exponential increase of recovery times (for both herbivores and predators) after a critical threshold of magnitude of perturbation (figure 3). This threshold is also observed in the evolutionary model, now in terms of species diversity. Some ecologists advocate focusing on short-term perturbation experiments with small disturbances because it is easier to interpret the response of the system. This has led to a paucity of long-term perturbation experiments in ecological systems. But, in order to construct a valuable theoretical framework of biodiversity recovery in evolution under an ecological perspective, we need to improve our understanding of large perturbations that disrupt ecological systems on long time-scales. In doing so, new approximations, such as those presented here, need to be developed. In this context, future models should also consider the differences in the patterns of recovery in several different biogeographic provinces (Erwin 1998*b*; Jablonski 1998).
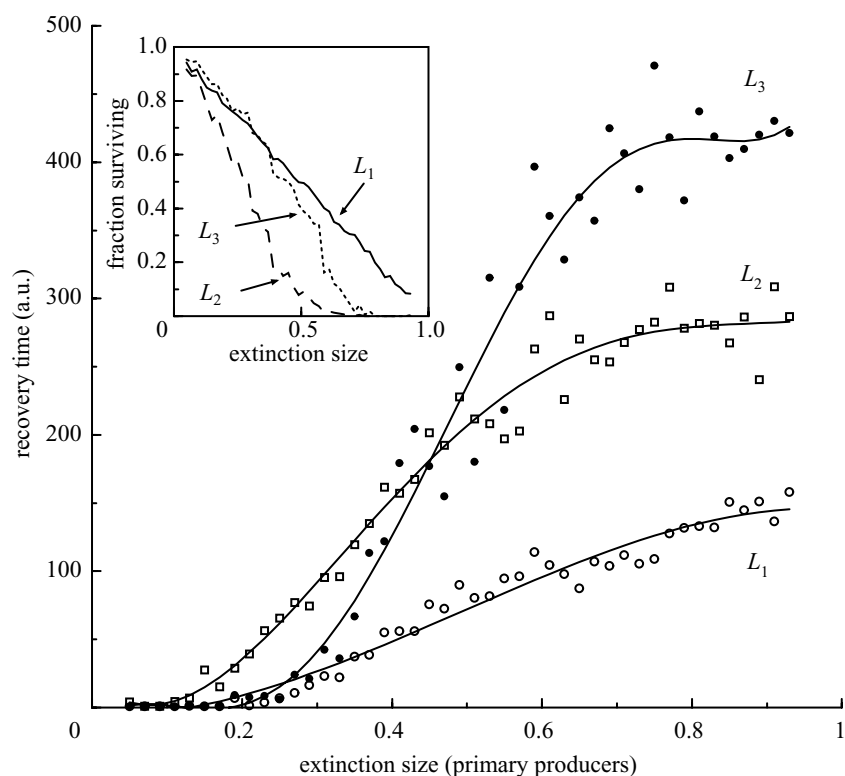
Figure 7. Patterns of recovery against the intensity of the mass extinction level on primary producers (see text). Here, we used $P_d = 0.005$, $\alpha = 0.004$ and $\phi = 0.002$. Inset: fraction of surviving species right after the mass-extinction event is introduced at the bottom layer.

Are long-term responses a lack of regularities? A few studies concerning long-term perturbations have shown that food-web structure plays a fundamental role in the way ecosystems react. For instance, it has been shown that the removal of the most trophically connected species (i.e. generalists) triggers many coextinctions of other species from the community (Pimm 1980; Solé & Montoya 2001). In this manner, observing how food-web structure is modified, the long-term responses of ecosystems to large perturbations (such as those affecting mass-extinction events through evolutionary history) could be partially predicted.

One of the outstanding issues in palaeontology involves the relationship between mass extinctions and background extinction (those extinctions occurring between mass extinctions). While Jablonski (1986) argued that mass extinctions are qualitatively, as well as quantitatively, distinct from background extinctions, Raup (1996) and Miller (1998), among others, have viewed the palaeontological record as more consistent with a primary role for periodic physical disturbances at a variety of scales, with a continuum between smaller events and mass extinctions. There is far less information on the similarity and differences in pattern and process during biotic recoveries following mass extinctions, and no evidence that any dichotomy between mass and background extinctions necessarily occurs during the recovery phase.

Some of the great mass extinctions (e.g. the K–T boundary), and other events where biodiversity dropped in a substantial manner (e.g. the late Cenomanian event), involved a reduction in primary production (Sheehan & Hansen 1986; Arthur *et al.* 1987; Rhodes & Thayer 1991).

Disturbing the basal species layer affects the whole ecosystem through trophic interactions between species, resulting in characteristic extinction and recovery patterns.

Feeding types and the position of species within food webs appear to be determining factors for the selective survival or extinction of many taxa. Examples include, for the K–T boundary, sea urchins (Smith & Jeffery 1998; Eble 2000), tetrapod families (Fara 2000), ammonites, belemnites and marine reptiles (Sheehan & Hansen 1986), and dinosaurs and mammals (Sheehan & Hansen 1986). If trophic dynamics were shown to be a key ingredient to explain extinction dynamics throughout the history of life, it should be also one of the main factors in explaining post-extinction rebounds.

The close similarities (and some important differences) exhibited by ecological succession and recovery patterns are summarized in table 1. Future models of evolutionary assembly and biodiversity recoveries should consider different feeding strategies on primary producers and the dynamics of nutrient cycling (DeAngelis 1992). For instance, differences between feeding on living plants or on dead plant matter played an important role in the survivorship of clades during the K–T mass extinction (Sheehan & Hansen 1986; Rhodes & Thayer 1991). Food chains that were dependent directly on living plant matter crashed at the end of the Cretaceous, whereas food chains constructed over detritus experienced high survival rates. That is because the dramatic drop of photosynthesis for several months had few effects on the latter, which had a food supply adequate for that interval due to the death of many plants and animals that might actually have increased the amount of detritus available.

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GLOSSARY

K-T: Cretaceous—Tertiary
Myr: million years