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THE ENGAGEMENT OF THE RED QUEEN AND KING MIDAS IN THE PHYLOGENERATOR MODEL*

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Abstract. Two alternatives of the Phylogenerator (Vida *et al.* 1989), describing ceoevolution of abstract asexual, clonal communities, based on explicit multispecies dynamics, are presented along with some preliminary results. The model works in the sense that speciation and extinction lead to variously connected communities comprising all sorts of interactions, including mutualism. Abstract phylogenetic trees generated by the Phylogenerator are shown. Examples of self-inflicted and externally elicited diversity collapses are presented. Commonly used pairwise models of mutualism are not adequate representations in a community evolution context. Hints for further development, such as microevolutionary fine-tuning or rigorous food-web analysis, are outlined.

Introduction

Evolution in the living world is usually a coevolutionary process in the sense that most populations undergo some genetic change simultaneously due to natural selection and drift. Although this situation is the natural one, evolutionary theory could not start with the description of coevolution: it is far too complex to begin with. In fact, analytical approaches have emerged as generalizations of one- and two-population evolutionary models (reviewed by Slatkin and Maynard Smith 1979; and Roughgarden 1983). The goal would be to obtain general analytic results of models including frequency- and density-dependence as well as all kinds of possible ecological interactions. The sad fact is that such complicated models are analytically intractable.

Another approach to coevolution has been pioneered by Van Valen's (1973) Red Queen hypothesis. He has argued that due to the prevalent antagonistic interactions in nature, the gain in one species' fitness due to some evolutionary advancement is exactly balanced by the total loss in other species' fitness. Thus he, similarly to Fisher's (1930) conviction, sees the biotic environment as constantly deteriorating. The assumed steady state evolution is indeed a consequence of the zero-sum assumption about fitnesses (Maynard Smith 1976a). Without this, evolution can come to a halt or proceed at an increasing speed.

A definite advancement in the field comes from Maynard Smith's (1976a) adoptation of Felsenstein's (1971) lag load into coevolutionary modelling. Imagine that you know the fitness of the best *possible* (not necessarily actually present) genotype of the population in the *given, fixed* (abiotic and biotic) environment and denote it by $\hat{\omega}$. If the actual average fitness of the population is ω, then the lag load of the population is expressed as $L=(\hat{\omega}-\bar{\omega})/\hat{\omega}$. Evolution by natural selection drives the population toward a decreased lag load. However, if antagonistic species are also present, the lag load does not trivially decrease in all species simultaneously.

A clearer understanding of coevolution has come from a more detailed model (Stenseth and Maynard Smith 1984; reviewed in Stenseth 1986) incorporating species turnover and the average lag load at the same time. The possible outcomes are steady state evolution (Red Queen) and stasis, provided the physical environment does not change. Which of these is characteristic for actual populations cannot be deduced from first principles yet. The paleontologic study by Hoffman and Kitchell (1984) slightly favours the Red Queen, but in the face of other results (Wei and Kennett 1983), the situation is even less clear (reviewed by Benton 1985, 1987). The curious fact is that these models do not represent ecological processes, despite the observation that the theatre in which evolution is played is essentially ecological in nature (Hutchinson 1965).

If one considers ecological interactions explicitly, it becomes clear that antagonism is not the only possible interaction between species. Commensalism and mutualism are definitely not antagonistic. Students in the field are increasingly aware of the importance of mu-

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tualism in nature (reviewed in Boucher 1985). In particular, the evolution of mutualism results in an improvement rather than deterioration of the environment. It is worth quoting Law (1985, pp. 146-148) in full: "... consider species A in an environment in which the only other species (B) is one with which it interacts in a mutualistic manner. As before species A, being a component of the mutualist's environment, will act as a selective force on B, with phenotypes at high frequency in A exerting the strongest pressures. Thus, in species B, one expects to find selection for phenotypes which are particularly successful in partnership with the frequent phenotypes of species A... if these selected mutualists are genetically different from their less successful counterparts, the environment will tend to improve for the high frequency phenotypes of species A. We therefore expect the deterioration arising from antagonistic interactions to be replaced by a tendency towards improvement in the environment. Extending Van Valen's regal metaphor, this could be likened to King Midas, since, whenever species A encounters an environment of this kind, it tends to transform it into a state from which greater rewards are reaped." Also, it is selectively favourable to stabilize this "golden" environment (Law 1985).

Bearing these in mind, we set out to model coevolution without the lag load and population genetic details, but incorporating various ecological interactions, including mutualism. This 'Phylogenerator model' was first presented at a Budapest meeting in 1987 (Vida *et al.* 1989). A similar but simpler model, having two predetermined trophic levels and no mutualism, was presented at the same meeting by Stenseth (1987).

Here we present some new, but still preliminary, formulations of and results from the Phylogenerator. We do not pretend to be conclusive; rather, we would like to call attention to this approach and urge others to make their own versions. Due to the inherent complexity and numerical nature of this modelling, one cannot expect too many results from a single group anyway.

In Section 2, we summarize the first version of the model along with our reservations which lead us to construct the second version incorporating a different formulation of mutualism and clearer representation of predator-prey and host-parasite relations (Sect. 3). Finally, we discuss arguments for further modification of the model (Sect. 4).

2. The Phylogenerator: version one

Here we present the first version (Vida *et al.* 1989) of the model, along with some results and considerations.

The model

The ecological machinery of the model is described by the following equations:

$$dx_i/dt = x_i\ k_i\ S/(Ks_i + S) + x_i \sum_{j \neq 1}^{N} a_{ij}\ x_j/(1 + g_{ij}\ x_j + h_{ij}\ x_i) - \\ - x_i\ d_i - x_i^2\ \delta_i \tag{1}$$

where x_i is the population density of the ith species, S the concentration of a primary substrate, k_i is the resource utilization coefficient of species i_j, a_{ij} is the action coefficient of species j on species i_j, d_i is the death rate, and δ_i the intraspecies interference coefficient of species i. Ks_i is the saturation coefficient affecting primary substrate consumption, g_{ij} influences the saturation effect by species j on the $j \rightarrow i$ action, and h_{ij} does the same for species i. N is the number of species present The signs are as follows:

$$a_{ij} = +,\ 0; \qquad a_{ji} = +,\ 0,\ - \tag{2a}$$

$$d_{ij},\ \delta_{ij},\ K_{si},\ g_{ij},\ h_{ij} > 0, \tag{2b}$$

i.e. direct interspecies interference is excluded; species compete for resources only. The primary resource changes according to the following dynamic:

$$dS/dt = k_s - S \sum_{i=1}^{N} k_i x_i/(k_{si} + S). \tag{3}$$

The rules of speciation and extinction are as follows. Extinction is simple: we assume that a species disappears when its density sinks below 0.001. Speciation is more complicated. We allow for speciation at the end of regular (arbitrary) time intervals T. We have a fixed, aspecific probability P for each species to undergo speciation. The value of a random number between 0 and 1 decides if speciation actually happens or not. If it does, the rules are as follows. We calculate the ecological parameters of the offspring species from those of the ancestor by Gaussian distributions centred around the latter. There are some constraints, however. Direct interaction in terms of a_{ij} and a_{ji} between the ancestor and its descendant is excluded. Some additional numerical constraints are:

$$|a_{ij}| < m_i \tag{4a}$$

$$\sum_{i=1}^{N} |a_{ij}| < m_2 \tag{4b}$$

here m_1 and m_2 are maxima such that $m_1 < m_2$. If every condition is fulfilled, the new species with the new parameters is introduced at a density 0.1 times that of the ancestor, while the ancestor's density becomes 0.9

times its pre-speciation value. This procedure is repeated for all species, and then the functioning of the altered ecological machinery is ready to start.

Rationale

Here we comment on the particulars of the ecological machinery and the speciation rules.

The primary resource is renewable. It is clearly not sunlight, since sunlight cannot accumulate. We imagine an environment such as the neighbourhood of deep-sea hydrothermal vents (Edomond and von Damm 1983) where reduced chemicals (such as hydrogen-sulphid) are ejected, and the living of the whole community rests on the oxydation of these compounds. The consumption of our primary resource is described by the Monod-type (1950) equation (3), which basically reflects the dynamics of the assimilating metabolism.

In (1) all interspecific action terms are modulated by double saturation. For predator-prey interactions, Holling (1959) has argued that the quadratic "mass action" interaction term in the corresponding Lotka-Volterra formalism is inadequate, as the prey sooner or later saturates the predator, quite similar to the Monod model. However, the efficiency of prey capture and consumption by the predator cannot linearly depend on the predator's density either. Recognizing this fact De Angelis et al. (1975) introduced the double-saturation formalism adopted here.

Saturation is even more important in the case of mutualism, since the Lotka-Volterra formulation easily blows up; the populations approaching infinite densities in finite time (Hallam 1986). Vandermeer and Boucher (1978) pointed out that for stability in obligate mutualism models curved isoclines were necessary. Wells (1983) conformed to this requirement by introducing double saturation into his plant-pollinator model. Note that our formalism would describe strictly obligate mutualism if only a single mutualist pair were present. However, as the various interactions figure additively in (1), the situtation is more complicated. A mutualist may or may not die out without the mutualist link, depending on whether it consumes other resources and at which rate. This is not a wholly satisfactory account, however (cf. the next version of the model).

The incorporation of intraspecies interference and the deliberate neglect of interspecies interference may seem puzzling. In fact, we did not want to incorporate the former either, but it proved to be a very good control ensuring that population densities do not become excessive.

To sum up, equations (1-3), without speciation, describe a community succession without immigration and emigration.

From an evolutionary theoretical point of view, the exclusion of population genetics may be annoying. However, tractability forces one to make this decision; the system is complicated enough anyway. Yet the system is per definitionem evolutionary: it reflects that the individuals in the modelled populations have multiplication, heredity, and variation (cf. Maynard Smith 1987). For practical purposes, heredity is exact for T long, then it becomes non-exact when speciation occurs, and so on.

It is apparent that we have clones rather than species proper, since "good" species are predominantly sexual (Maynard Smith 1978), and we do not have representations of the dynamic and genetic aspects of sexuality. The fixed speciation probability P per species is a first choice and is not intended to be realistic.

We conclude that speciation and extinction turn our model from an ecological into an evolutionary one. The

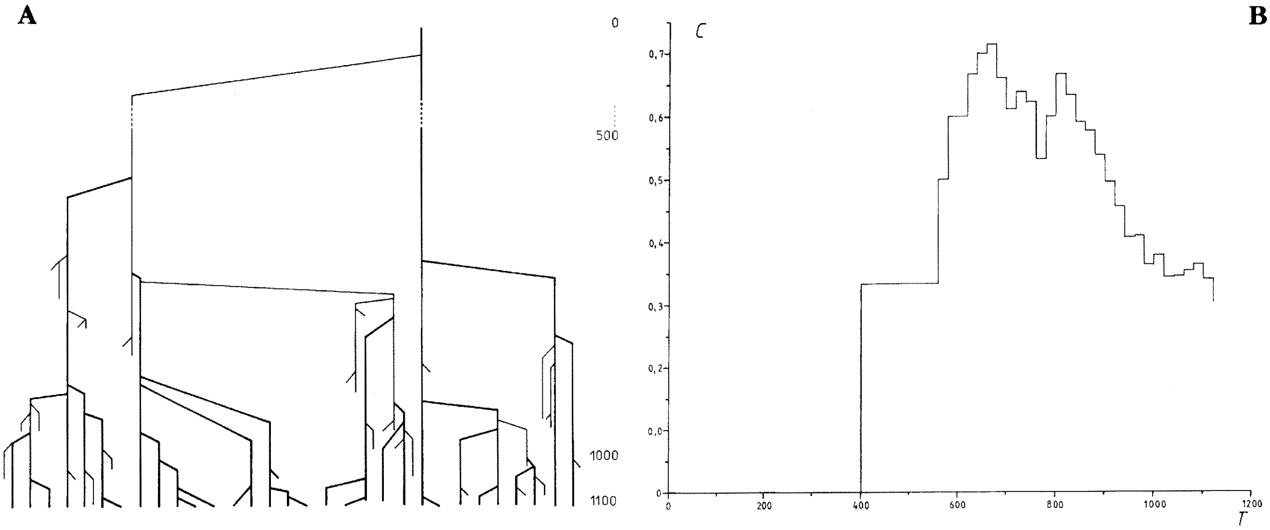


Fig. 1. A phylogenetic tree generated by the Phylogenerator (A, reproduced from Vida et al. 1989) and the associated change of connectance (B). $k_s = 2$, $P = 0.15$, σ (standard deviation of the Gaussian used in speciation) = 0.2.

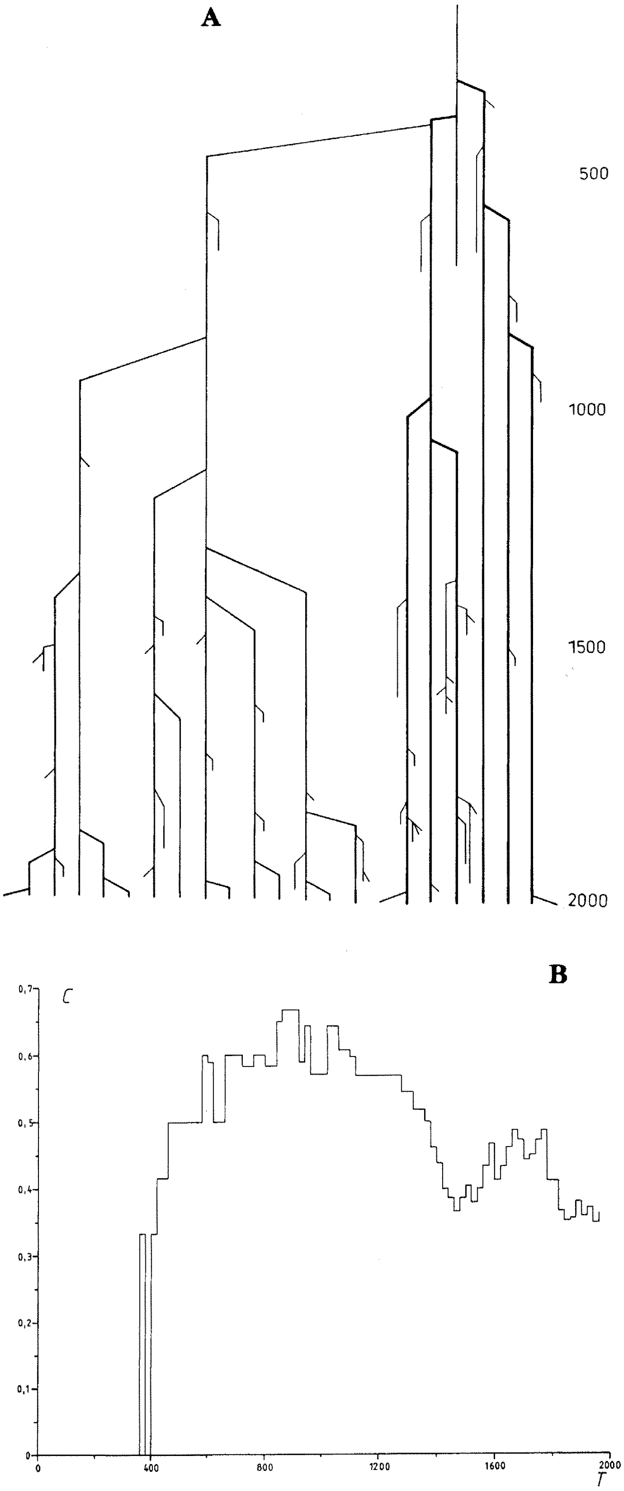


Fig. 2. Another phylogenetic tree (A, reproduced from Vida et al. 1989) and the associated change in connectance (B). $k_s = 2$, $P = 0.8$, $\sigma = 0.2$. Due to the reduced speciation probability, the community builds up slower than that in the previous figure.

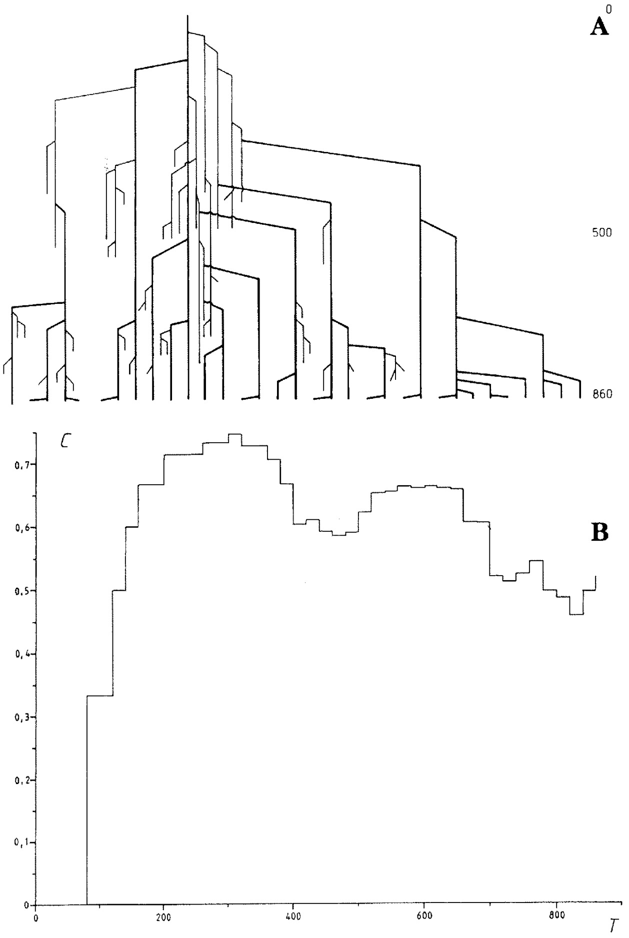


Fig. 3. A third phylogenetic tree (A, reproduced from Vida et al. 1989) and the associated change in connectance (B). $K_s = 2.5$, $P = 0.15$, $\sigma = 0.1$.

link with island biogeography is as follows: both approaches have extinction, but we have speciation replacing immigration (cf. Stenseth and Maynard Smith 1984).

Simulation and a few preliminary results

Numerical solutions were obtained on an R-40 and an R-45 mainframe computer by the predictor-corrector algorithm. We have used compiled FORTRAN language. Run time can be quite long, especially when the equations become "stiff", meaning that the time derivatives differ from each other considerably.

Simulation naturally raises the problem of different (ecological and evolutionary) time scales (cf. Stenseth and Maynard Smith 1984). In our case this boiled down to the appropriate choice of T, the time interval between two speciations. If the community reaches an almost stationary state during this time, the time scales are set satisfactorily. T=20 is arbitrary, but consequent units proved to be appropriate.

In Figs. 1-3 we present three phylogenetic trees and the associated connectances, measured as

$$C = \frac{\text{number of nonzero } a_{ij} \text{ actions}}{N\,(N-1).}$$

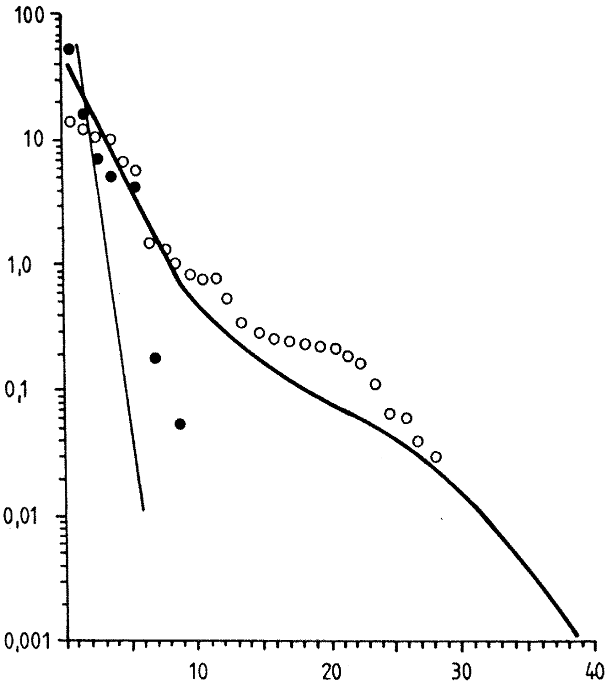


Fig. 4. Species-abundance relations from an early (black circles) and a later (open circles) stage of the same coevolved community. Horizontal axis: species rank order of abundance; vertical axis: abundance on logarithmic scale. The straight line is the exact geometrical, the curved line the lognormal distribution.

It can be seen that species number N tends to increase and connectance C tends to decrease with time. This is understandable since constraint (4) tends, in effect, to limit the number of interactions.

For the community evolutions shown the Law of Constant Extinction (Van Valen 1973) does not seem to apply. This should not lead us to far-reaching conclusions, however, because simulation was quit before an apparent steady state species number could be established.

Fig. 4. displays the species-abundance relations from an early and an evolved stage of the same run. The former case fits a geometric, the later a lognormal distribution better. This is in agreement with findings on real communities (May 1975): within early communities, a few dominant factors exert control (niche preemption), while in established ones there are many independent effects, following roughly a normal distribution, on growth rate; this in turn leads to the lognormality of relative abundances.

It is noteworthy that, although population densities were explicitly displayed for several runs, sustained regular oscillations or chaos were not detected. We conjecture that the lack (non-prevalence) of these behaviours is some epiphenomenon of natural community organisation, despite the fact that for large differential equation systems in general chaos is the probable behaviour (cf. Schaffer and Kot 1986). Many more runs and advanced analytical approaches are needed to settle this question.

Rigorous tests for patterns of connectance and extinctions are under way.

Reservations

Here we present some considerations which made us to construct the second version of the Phylogenerator, to be discussed later.

The major problem is the representation of mutualism. Inspection of (1) reveals that cycles of mutualistic interactions of any length may arise in which every member is an obligate mutualist. This is equivalent to saying that these species live on the "air". While such kind of modelling is adequate when we extract a mutualist pair from a community (Hallam 1986), in our context this leads to nonsense. Though we have not encountered such a paradox system in our runs, we cannot be sure of their absence since the search for them was sporadic. The mere possibility of such cycles is discouraging enough.

An analogous case is cyclic food chains. Although it is possible that the bottom species in a food chain is a parasite of the top species, but the former presumably cannot be a predator of the latter. Such relationships must be expressed by appropriate rate constants incorporating yields, etc. This requires the application of certain constraints.

The a priori set value of P conceals the fact that speciation should somehow relate to population size, for example.

3. The Phylogenerator: version two

Considering the above detailed reservations, we have constructed a modified Phylogenerator.

The model

Instead of equation (1), the basic ecology is now specified by the following dynamics:

$$dx_i/dt = x_i\, k_i\, S/(K_{si}+S) + \tag{5}$$

$$+ x_i \sum_{j \in A_i} a_{ij}\, x_j/(1+g_{ij}\, x_j + h_{ij}\, x_i) -$$

$$- x_i\, d_i - x_i^2\, \delta_i/(1+\sum_{k \in M_i} \mu_{ik}\, x_k),$$

where A_i is the set of species antagonistic to species i and M_i is the set of mutualists of the same species. μ_{ik} is the strength of the beneficial effect of species k on species i in the mutualistic interaction. The ranges of parameter values are as follows:

$$a_{ij} = -,\ 0; \qquad a_{ji} = +,\ 0,\ - \tag{6a}$$

$$\mu_{ik}=0, +; \quad \mu_{ki}=0, + \tag{6b}$$

$$d_i, \delta_i, K_{si}, g_{ij}, h_{ij}>0. \tag{6c}$$

It is apparent that here we allow for interspecific interference as well.

Predator-prey and parasite-host interactions (specified by a_{ij} $a_{ji}<0$, $i=j$) obey the following constraints (there is a size s_i assigned to each species):

$$\text{if } s_j>s_i, \text{ and } a_{ji}>0, \text{ then } a_{ji}'=a_{ji}\ s_i/s_j \tag{7a}$$

$$\text{if } s_i>s_j, \text{ and } a_{ij}>0, \text{ then } a_{ji}'=a_{ij}\ s_j/s_i \tag{7b}$$

$$\text{if } s_j<0.1\ s_i, \text{ and } a_{ji}>0, \text{ then } a_{ij}'=a_{ij}\ s_j/s_i \tag{7c}$$

$$\text{if } s_i<0.1\ s_j, \text{ and } a_{ij}>0, \text{ then } a_{ji}'=a_{ji}\ s_i/s_j \tag{7d}$$

Cases (7a, b) are predator-prey and (7c, d) are host-parasite relationships. Otherwise, the interaction is cancelled.

The dynamics (3) of the primary resource is modified as well:

$$dS/dt=k_s-S\sum_{i=1}^{N} k_i\ x_i/(K_{si}+S)-d_sS, \tag{8}$$

to express that even without consumption by the different species, the concentration of this resource cannot increase indefinitely; d_s is the corresponding spontaneous decay rate constant.

Speciation follows the rules of the previous version except for the probabilities, which are now density-dependent:

$$p\ (x_i)=P\ (x_i-.05)/(50+x_i), \text{ if } x_i\geq .05 \tag{9a}$$

$$p\ (x_i)=0, \quad \text{if } x_i<.05, \tag{9b}$$

where P is the aspecific, fixed maximum probability of speciation (usually = 0.15). Constraint (4) is lifted. Otherwise, the model is identical with the first version.

Rationale

The conspicuous difference between equations (1) and (5) is in the modelling of mutualism. The latter version obviously prohibits the possibility of exclusively mutualistic communities living on nothing, since mutualism does not contribute with a positive growth term but decreases the strength of intraspecific interference. The approach was first mentioned by Whittaker (1975), and it is known that the effect of a simple death rate d_i, ensures curved isoclines and hence stability in a pairwise case (Wolin and Lawlor 1984). For two species this formulation can express facultative mutualism only.

Rules (7) imply that species with large individuals can prey on species with small individuals. Although this statement deliberately neglects the possibility of varying predation depending on age, for example (cf. Hastings 1988), it seems overall reasonable. It implies a "pecking order" or hierarchy in trophic interactions (Cohen and Newman 1985).

The speciation probability rule (9) has been chosen to reflect the assumption that the rate of speciation depends on the rate of evolution within a species, otherwise neglected in our model. For sexually reproducing haploid populations, Maynard Smith (1976b) has obtained that the rate of evolution, measured as the rate of

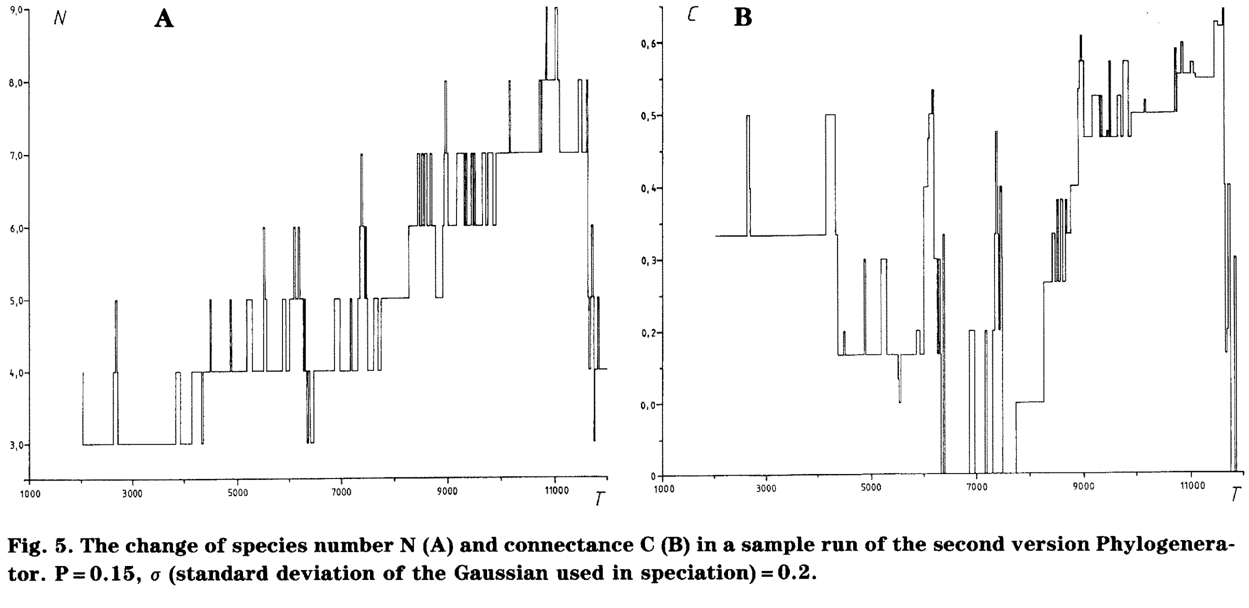


Fig. 5. The change of species number N (A) and connectance C (B) in a sample run of the second version Phylogenerator. P = 0.15, σ (standard deviation of the Gaussian used in speciation) = 0.2.

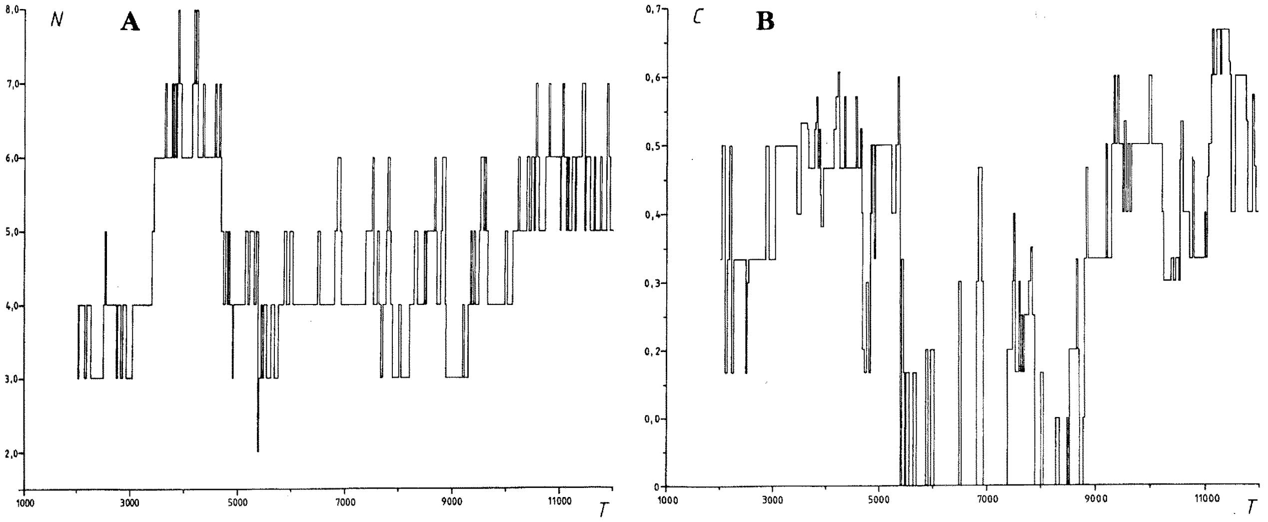


Fig. 6. The change of species number (A) and connectance (B) from another run. P = .3, $\sigma = 0.2$.

change in mean fitness, depends on the population size according to a saturation function for fixed mutation rate. Although, as mentioned already, we do not have an adequate representation of sexuality in our model, we have "good" species in mind. Whether the rate of speciation depends positively or negatively on intraspecies evolution is a largely empirical issue. Interestingly, our choice of positive dependence implies the Red Queen (stationary) case only in the lag load model (Stenseth and Maynard Smith 1984), for the following reasons:

1. We assume that speciation probability obeys a saturation function of population density.

2. This rule is thought to be the result of microevolution in the species.

3. The rate of microevolution, understood as the rate of change in mean fitness, is proportional to the lag load of the species (Maynard Smith 1976b).

4. The rate of speciation may increase or decrease with the increase of the average lag load of the community.

5. The former case implies the Red Queen in the lag load model.

Nevertheless we emphasize that (9) is conjectural.

Simulation and a few preliminary results

The numerical method is the same as before. Species numbers and connectances of four parallel runs are displayed in Figs. 5-8. In Fig. 6, the maximum probability of speciation per species, P, is doubled relative to the case shown in Fig. 5. Speciation-extinction events become more frequent. If, however, the standard deviations of the Gaussian, applied in the calculation of

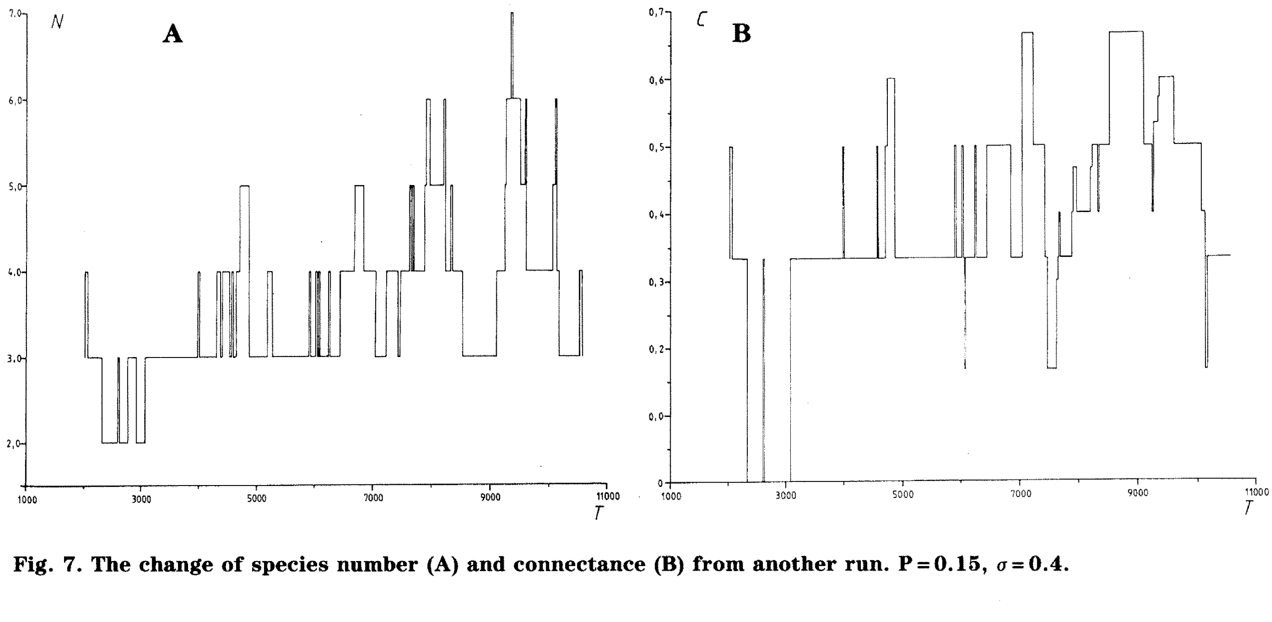


Fig. 7. The change of species number (A) and connectance (B) from another run. P = 0.15, $\sigma = 0.4$.

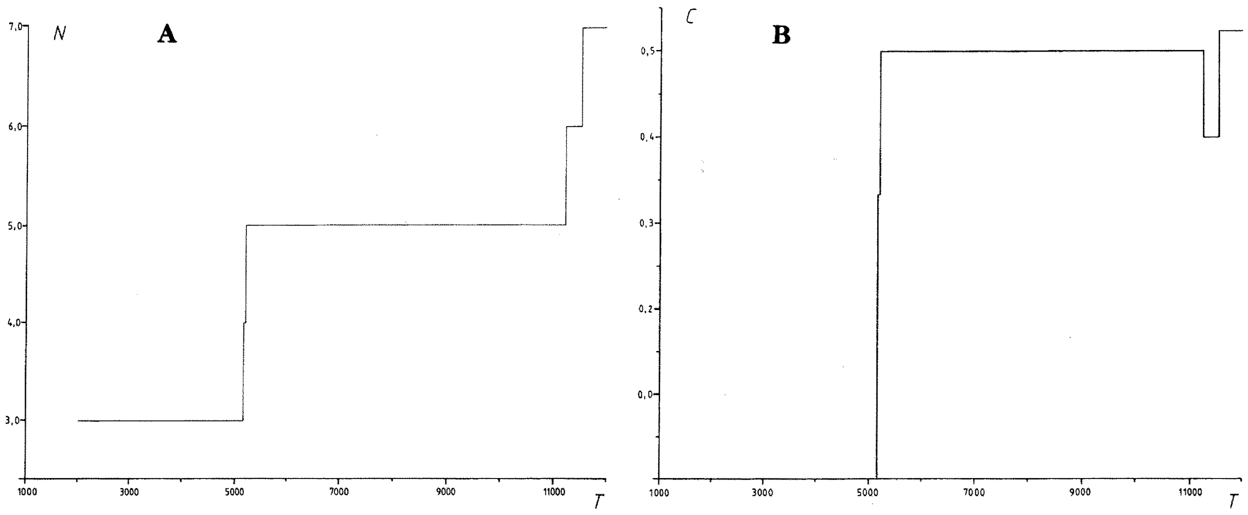


Fig. 8. The change of species number (A) and connectance (B) from a run having the same parameters as that in Fig. 5, except for the start position of the random number generator.

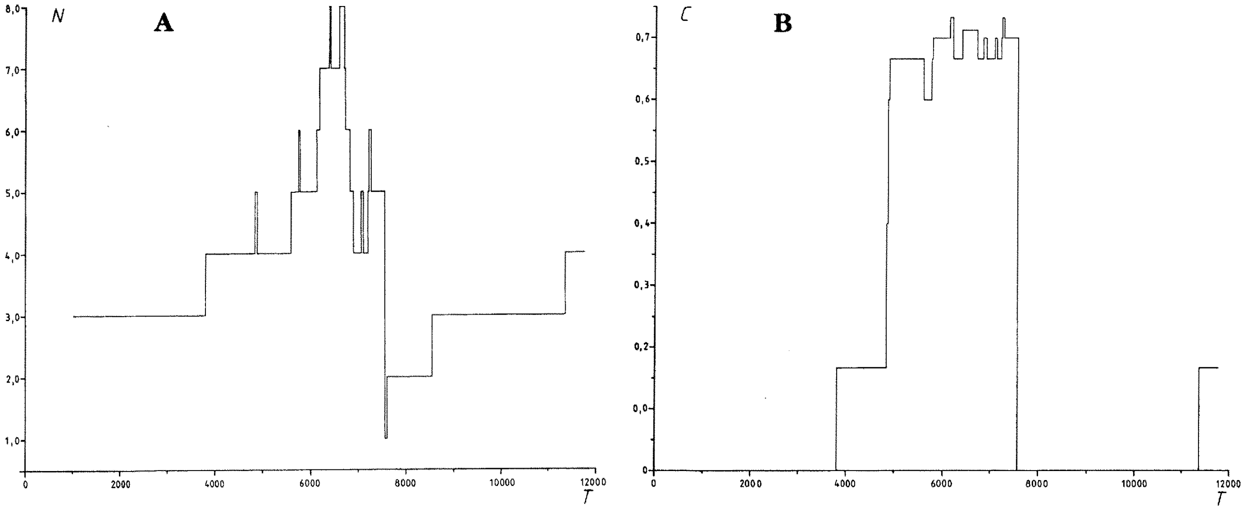
new parameter values, is double, speciation-extinction seems to be slowed down somewhat (Fig. 7), suggesting perhaps that closely related species can invade more easily.

Extreme care should be exercised in evaluating such outputs. Comparing Fig. 8 with the previous ones one could think that the speciation probability was greatly reduced. Not so. The only difference between the runs in Fig. 5 and Fig. 8 is that the random number generator, used frequently in the speciation algorithm, was launched from a different number!

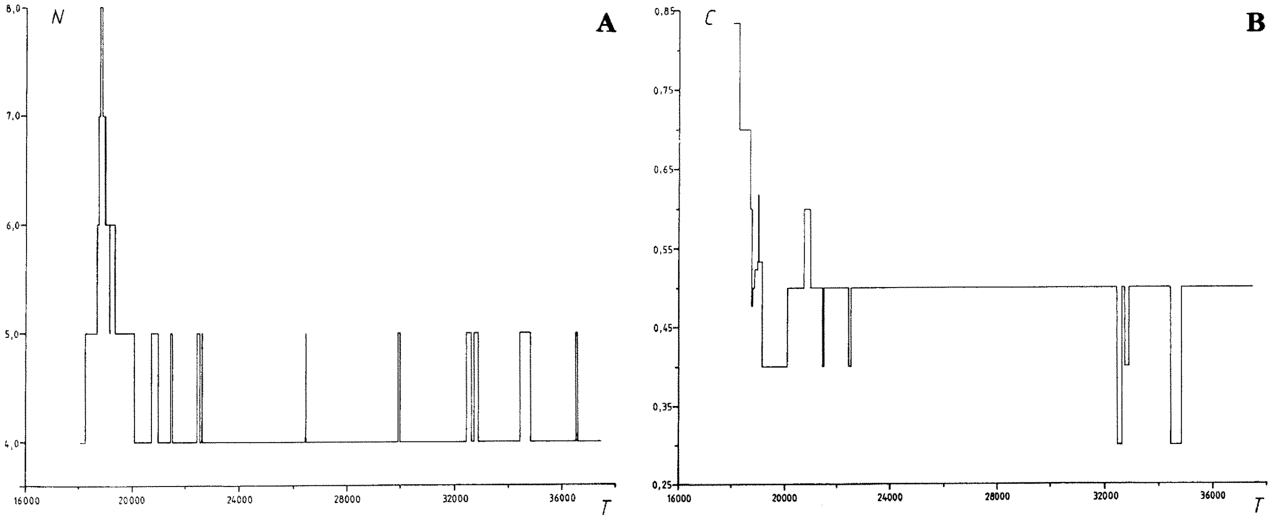
A conspicuous difference in species dynamics between the Phylogenerators based on (1) and (5) is that the number of species remains quite low in the latter case. This is attributable to the difference in the modelling of mutualism. Pairwise facultative mutualisms do not have such a strong influence on the community as pairwise obligate ones have. This again leads to the conclusion that the nature of mutualism is decisive for community evolution.

Larger or smaller fluctuations in species number are seen everywhere. More drastic coevolution-inflicted catastrophes can also occur (Fig. 9). This may suggest that larger extinctions in a community do not necessarily call for an extrinsic explanation.

Extrinsically driven bursts of extinction can be simulated by a sudden, drastic reduction of the production of the primary substrate (Fig. 10). Species number and connectance both decrease, but biomass (the sum of population densities) suffers the most severe reduction. Thus the model can imitate externally induced extinctions.



An intrinsic catastrophe in the Phylogenerator. Note the sudden buildup and destruction of the community as measured by connectance (B).



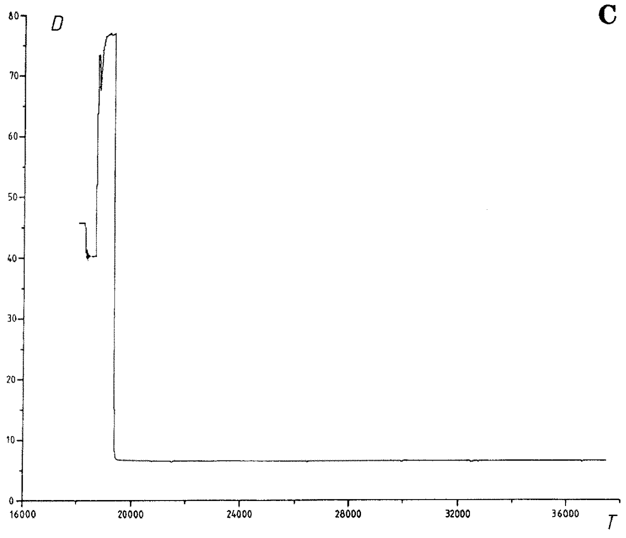


Fig. 10. An extrinsic catastrophe in the Phylogenerator. Just after the highest peak of the species number (A) the equilibrium density of the primary resource S was decreased to 10%. Associated changes of connectance (B) and biomass (C) are also displayed.

4. Discussion

We present some considerations which will force us to modify the Phylogenerator in the near future, along with some hints for doing this.

The representation of mutualism in (5) is still not satisfactory. Note that both in (1) and (5) obligate mutualism is not robust: a species can always become facultative through speciation, without any constraint; consumption of a prey may always happen. This is due to the fact that the different interactions of the same species are represented in an additive and independent manner. The common dynamic models of mutualism (see Wolin 1985, for review), when inserted into a community model, cannot adequately represent obligate mutualism.

There are two possible escapes: to introduce higher order non-linearity (cf. Roughgarden and Diamond 1986), or to introduce separate dynamic equations for the "complexes" of mutualists (Kostitzin 1934). The latter approach is mechanistically clear and satisfactory, but is not very rewarding from a pragmatic point of view; the further increase of the number of variables in a model which is already complex enough is undesirable. Higher order nonlinearities should preferably be avoided as well. We do not know at the moment how to go around this problem.

As regards ecology, the Phylogenerator depicts a homogeneous, deterministic environment. We think that the first thing to give up is homogeneity; we know too well how important spatial variation is for coexistence (Levin 1986) and speciation (White 1978). In the present model we have a single "island", one ought to have at least two.

A more reliable ecosystem model calls for some account of the conservation of matter/energy (Austin and Cook 1974). Then, having in mind results like that in Fig. 10, one could test the hypothesis that available energy limits species richness (reviewed by Moore

1987). This more adequate representation could enable us to rigorously analyze the coevolved food-webs and compare them with real ones. In particular, do rather short food-chains appear? How does a consistent diversity-connectance relationship emerge? We shall make an effort to give an answer to these questions (Pimm 1982) in the context of the Phylogenerator. Sizes, as already used in model II, should be used to indicate the biomass/individual. If these are set to have integer values only (reflecting the particulate nature of chemistry: Austin and Cook 1974), then a formal "stoichiometry" for interactions based on biomass exchange can be calculated, constraining the corresponding population dynamics in the form of formal reaction kinetics. If we assume that the total matter available for the entire ecosystem is constant, there is no way that the model can blow up (Maynard Smith, J., pers. commun.).

The present Phylogenerator works without intraspecies (microevolutionary) fine-tuning. This drawback should somehow be altered, still without the incorporation of (intractable) population genetics. Also, sexuality must be given some representation. An obvious thing to do is to have a larger width of the Gaussians used in speciation for sexuals than for apomicts. With at least two islands and the possibility of local intraspecies fine-tuning, allopatric speciation can be modelled if two populations differing from each other more than a given threshold are assumed to have become reproductively isolated. An interesting question is if sexuals will do on the average better then asexuals in the coevolutionary setting (cf. Maynard Smith 1978). The introduction of fine-tuning would make the application of three time-scales (those of population dynamics, within-population evolution, and species dynamics: Valentine 1972) rigorous.

Some constraints replacing the crude ones in (4) should be established. For example, prey defense and predator effect should be made costly in terms of overall gowth or death. Microevolutionary adjustment would then drive prey-predator pairs towards a coevolutionarily stable state, other things being equal (Roughgarden 1983). The problem of choosing sensible specific submodels is a difficult one, however.

An interesting aspect of this work relates to the modelling of cladogenesis. In contrast to our enquiry into the nature of cladogenetic mechanisms, previous models (cf. Raup et al. 1973, Gould et al. 1977) did not incorporate detailed ecological mechanisms. These models of cladogenesis were based on patterns of speciation and extinction different from those of the Phylogenerator. In consequence, the explanation of the fascinating similarity between real and randomly generated clades, merely in terms of speciation and extinction, without explicit ecology is rather incomplete.

The elucidation of the origin of evolutionary trends merely in terms of variable (biased) species birth and death processes, as suggested by Gould (1983, see his Fig. 2 on p. 156), seems to be oversimplified. This attitude is probably due to the desire to uncouple microevolution and macroevolution and to favorize species selection. However, this desire may well be doomed to extinction (cf. Maynard Smith 1988, Eldredge and Gould 1988). Based on empirical evidence as well as the Phylogenerator model we think that ecological interactions play a cardinal role in the assembly and geometrical transformations of clades. We have similar reservations concerning the illumination of the "asymmetry of lineages and the direction of evolutionary time" as presented by Gould et al. (1987).

In sum, we emphasize the joint treatment of speciation, various ecological interactions, and extinction in modelling of cladogenesis, diversity patterns, and evolutionary trends. These are surely main ingredients of a careful macroevolutionary approach.

We have expressed our definite desire and have outlined some ways to achieve more realism in future versions of the Phylogenerator. Yet, in a sense even irrealistic models are useful: they show how certain rules lead to different patterns in the evolution of "artificial life". "The most important problem for research on artificial life is how to design worlds of self-reproducing interacting entities with emergent collective properties, that are robust to noise, and have the spontaneous capability to co-adapt and produce functional structures." (Farmer and Kauffman 1988, p. 391).

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