Diversity Evolution

Russell K. Standish

School of Mathematics, University of New South Wales
2052, Sydney, Australia
R.Standish@unsw,.edu.au
http://parallel.hpc.unsw.edu.au/rks

Abstract

Bedau has developed a general set of evolutionary statistics that quantify the adaptive component of evolutionary processes. On the basis of these measures, he has proposed a set of 4 classes of evolutionary system. All artificial life sytems so far looked at fall into the first 3 classes, whereas the biosphere, and possibly the human economy belongs to the 4th class. The challenge to the artificial life community is to identify exactly what is difference between these natural evolutionary systems, and existing artificial life systems.

At ALife VII, I presented a study using an artificial evolutionary ecology called *EcoLab*. Bedau's statistics captured the qualitative behaviour of the model. *EcoLab* exhibited behaviour from the first 3 classes, but not class 4, which is characterised by unbounded growth in diversity. *EcoLab* exhibits a critical surface given by an inverse relationship between connectivity and diversity, above which the model cannot tarry long. Thus in order to get unbounded diversity increase, there needs to be a corresponding connectivity reducing (or food web pruning) process. This paper reexamines this question in light of two possible processes that reduce ecosystem connectivity: a tendency for specialisation and increase in biogeographic zones through continental drift.

Introduction

During the Phanerozoic (540Mya–present), the diversity of the biosphere (total number of species, also known as biodiversity) has increased dramatically. The trend is most clear for intermediate taxonomic levels (families and orders), as fossil species data is too incomplete and higher taxonomic levels (phylum and class diversity) have been fairly constant since the Paleozoic. A recent review is given by Benton(2001). The most completely documented diversity trend is amongst marine animals, which exhibits a plateau during the Paleozoic (540-300Mya), followed by an accelerating diversity curve since the end of the Permian. The corresponding trend amongst continental, or land animals is characterised by a clear exponential growth since the first species colonised dry land during the Ordovician. Benton argues that the terrestrial trend is more characteristic than the marine trend, owing to the far greater diversity shown amongst land animals, even though the marine fossil record is more complete. Similar trends have been reported for plants(Tiffney & Niklas 1990).

Bedau *et al.*(1998) introduced a couple of measures to capture the amount of adaptation happening in a general evolutionary system. The basic idea is to compare the dynamics of the system with a neutral shadow system in which adaptation is destroyed by randomly mixing adaptive benefits amongst the components of the system (think of the effects ultra-Marxism might have on an economy!). The amount of adaptive activity (numbers of each component in excess of the shadow model integrated over time) and adaptive creativity (numbers of speciations per unit time exceeding a threshold of activity) is measured. Bedau has also introduced a general neutral shadow model that obviates the need to generate one on a case by case basis(Rechtsteiner & Bedau 1999).

Using these measures, it is possible to distinguish 3 classes of activity:

1. unadaptive evolution, when the mutation rate is so high that organisms have insufficient time to have their adaption tested before being killed off by another mutation

2. adapted but uncreative evolution, when species are highly adapted, but mutation is so low that ecosystems remain in perpetual equilibrium

3. creative, adaptive evolution, when new species continuously enter the system, and undergo natural selection

The Biosphere appears to be generating open ended novelty — not only is it creative, but it is *unboundedly* creative. Evidence for this exists in the form of the intricate variety of mechanisms with which different organisms interact with each other and the environment, and also in the sheer diversity of species on the planet. Whilst there is no clear trend to increasing organismal complexity(McShea 1996), there is the clear trend to increasing diversity mentioned above, which is likely to be correlated with ecosystem complexity. Bedau takes diversity as a third evolutionary measure, and distinguishes between *bounded* and *unbounded creative*

evolution, according to whether diversity is bounded or not. All artificial evolutionary systems examined to date have, when creative, exhibited bounded behaviour[1]. This was also the case of the $Ec\varrho_{ab}$ model (Standish 2000). Bedau has laid down a challenge to the artificial life community to create an unbounded, creative evolutionary system.

Ecosystem Complexity

The heart of the idea of unbounded creative evolutionary activity is the creation and storage of information. The natural measure of this process is *information based complexity*, which is defined in the most general form in(Standish 2001). The notion, drawing upon Shannon entropy and Kolmogorov complexity(Li & Vitányi 1997) is as follows:

A language $\mathcal{L}_1 = (S, \mu)$, is a countable set of possible descriptions S, and a map $\mu : S \to \{0, 1\}$. We say that $s, s' \in S$ have the same meaning iff $\mu(s, s') = 1$. Denote the length of s as $\ell(s)$ and $S_n = \{s \in S : \ell(s) = n\}$. The information content (or *complexity*) of a description s is given by:

$$\mathcal{C}(s) = -\lim_{n \to \infty} \log_2 \frac{\text{card}(\{s' \in S_n : \mu(s, s') = 1\})}{\text{card}(S_n)} \quad (1)$$

In the usual case where the interpreter (which defines μ) only examines a finite number of symbols to determine a string's meaning, $C(s)$ is bounded above by $\ell(s) \log_2 B$ where B is the size of the alphabet. This is equivalent to the notion of *prefix codes* in algorithmic information theory.

Now consider how one might measure the complexity of an ecosystem. Diversity is like a count of the number of parts of a system — it is similar to measuring the complexity of a motor car by counting the number of parts that make it up. But then a junkyard of car parts has the same complexity as the car that might be built from the parts. In the case of ecosystems, we expect the interactions between species to be essential information that should be recorded in the complexity measure. But a simple naive counting of food web connections is also problematic, since how do we know which connections are significant to a functioning ecology?

To put the matter on a more systematic footing, consider a tolerance ε such that $x, y \in \mathbb{R}$ are considered identical if $|x - y| < \varepsilon$. Now two different population dynamics $\dot{x} = f(x)$ and $\dot{x} = f'(x)$, where

$$x \in \mathbb{R}^{n+} \equiv \{x \in \mathbb{R}^n : x_i \geq 0\},$$

can be considered identical (i.e. $\mu(f, f') = 1$ iff[2]

$$|f(x) - f'(x)|_\infty < \varepsilon, \ \forall x \in \mathbb{R}^{n+}. \quad (2)$$

At this point for the sake of concreteness, let us consider Lotka-Volterra dynamics:

$$\dot{\mathbf{x}} = \mathbf{r} * \mathbf{x} + \mathbf{x} * \beta\mathbf{x} \quad (3)$$

where $*$ refers to elementwise multiplication, $\mathbf{r}$ is the net population growth rate and β is the matrix of interspecific interaction terms.

Over evolutionary time, the growth coefficients r_i, the self-interaction coefficients β_{ii} and the interspecific interaction coefficients $\beta_{ij}, i \neq j$ form particular statistical distributions $p_r(r_i), p_d(\beta_{ii})$ and $p_o(\beta_{ij})$ repectively.

Since inequality (2) must hold over all of the positive cone $\mathbb{R}^{n+}$, it must hold for population density vectors $|x| \ll 1$ and $|x| \gg 1$. In which case eq. (2) can be broken into independent component conditions on $\mathbf{r}$ and β can be written:

$$|r_i - r_i'| \leq \varepsilon, \forall i \quad (4)$$
$$||\boldsymbol{\beta} - \boldsymbol{\beta}'||_\infty \leq \varepsilon. \quad (5)$$

Since these conditions are independent, they contribute additively to the overall complexity (1). The term for the growth coefficients is given by:

$$\begin{aligned} \mathcal{C}_r &= -\log_2 \prod_i \int_{|r_i - r_i'| \leq \varepsilon} p_r(r_i') dr_i' \\ &\approx -\sum \log_2 p_r(r_i) - D \log_2 2\varepsilon \quad (6) \end{aligned}$$

where $\varepsilon \ll 1$, and D is the ecosystem diversity.

The complexity term for the interaction terms is given by

$$\begin{aligned} \mathcal{C}_\beta &= -\log_2 \int_{\sum_j |\beta_{ij} - \beta_{ij}'| < \varepsilon} \prod_{i \neq j} p_o(\beta_{ij}') \prod_i p_d(\beta_{ij}') \prod_{i,j} d\beta_{ij}' \\ &\approx \sum_{i \neq j} \log_2 p_o(\beta_{ij}) + \sum_i \log_2 p_d(\beta_{ii}) + \\ & \quad D^2 \log_2 2\varepsilon - 1 \quad (7) \end{aligned}$$

If ε is chosen very small, the total ecosystem complexity is proportional to D^2. This is because the zeros of the interaction matrix are encoding information. However, if $\varepsilon = \frac{1}{2p_o(0)}$, then (7) becomes:

$$\mathcal{C}_\beta = D^2 C \langle \log_2 p_o(\beta_{ij}) \rangle + D \langle \log_2 p_d(\beta_{ii}) \rangle + o(D) \quad (8)$$

This gives flesh to our intuitive notion that complexity should somehow be proportional to the number of connections making up the food web.

Empirically, Lotka-Volterra dynamics has been shown to exhibit an inverse relationship between connectivity

---

[1]Channon(2001) claims his Geb artificial life system exhibits unbounded creative behaviour

[2]As an anonymous referee pointed out, trajectories described by f and f' may diverge exponentially in time, and that a better definition of equivalence would also require similarity of the attractor sets as well. The results derived here would only be a lower bound of the ecosystem complexity under this more refined definition of equivalence.

and diversity $D \propto C^{-1}$(Standish 1998). May(1972) demonstrated this relationship in connection with dynamical stability. However, it seems unlikely that an ecology undergoing evolution is often stable. If this result holds more generally, it implies that complexity is directly proportional to diversity, so that diversity indeed is a good proxy for ecosystem complexity. Although earlier foodweb studies demonstrated this hyperbolic diversity-connectivity relationship, more recently collected data suggests a relationship of the form $D \propto C^{-1+\epsilon}$, with $\epsilon \approx$0.3–0.4 (Drossel & McKane 2002). If complexity indeeds scales superlinearly with diversity as suggested by latter data, then a system displaying open-ended diversity growth is indeed growing in complexity, however a system displaying bounded diversity growth may still be growing in complexity.

Ec𝒬ab

Ec𝒬ab is an evolutionary ecology, and is to my knowledge the first published account of population dynamics being linked to an evolutionary algorithm(Standish 1994). The next model to be developed in this genre is Webworld(Drossel, Higgs, & McKane 2001), which features a more realistic ecological dynamics, and handles resource flow issues better. Other models in this genre have appeared recently (Christensen *et al.* 2002; Anastasoff 2000).

Ec𝒬ab is also the name of a software package used for implementing this model, as well as other models. The software is available from http://parallel.hpc.unsw.edu.au/rks/ecolab.

The model consists of Lotka-Volterra ecology:

$$\dot{\boldsymbol{n}} = \boldsymbol{r} * \boldsymbol{n} + \boldsymbol{n} * \boldsymbol{\beta n} + \texttt{mutate}(\boldsymbol{\mu}, \boldsymbol{r}, \boldsymbol{n}) + \boldsymbol{\gamma} * \nabla^2 \boldsymbol{n}. \quad (9)$$

$\boldsymbol{n}$ is the population density vector, $\boldsymbol{r}$ the growth rates (net births-deaths in absence of competition), $\boldsymbol{\beta}$ the interaction matrix, $\boldsymbol{\mu}$ the (species specific) mutation rates and $\boldsymbol{\gamma}$ the migration rate. In the panmictic case, the $\boldsymbol{\gamma}$ term is left out, and $\boldsymbol{n}$ refers to total populations, rather than population densities.

The mutation operator randomly adds new species i into the system with phenotypic parameters (r_i, β_{ij}, μ_i and γ_i) varied randomly from their parent species. A precise documentation of the mutation operator can be found in the *Ec𝒬ab* Technical Report(Standish).

The $\boldsymbol{n}$ vector has integral valued components — in assigning a real valued vector to it, the values are rounded up *randomly* with probability equal to the fractional part. For instance, the value 2.3 has a 30% probability of being rounded up to 3, and a 70% probability of being rounded down. Negative values are converted to zero. If a species population falls to zero, it is considered extinct, and is removed from the system. It should be pointed out that this is a distinctly different mechanism

than the threshold method usually employed to determine extinction, but is believed to be largely equivalent.

Diversity D is then simply the number of species with $n_i > 0$, and connectivity is the proportion of interspecific connections out of all possible connections:

$$C = \frac{1}{D^2} \sum_{i,j \,|\, \beta_{ij} \neq 0, \, n_i > 0, \, \& \, n_j > 0}$$

Spatial *Ec𝒬ab* is implemented as a spatial grid, with the ∇^2 term being replaced by the usual 5-point stencil.

Specialisation

A *specialist* is a species that only depends on a restricted range of food sources, as opposed to a *generalist* which might depend on many food sources. A specialist has fewer incoming predator-prey links in the food web than does a generalist. Much evolutionary variety is expressed in sophisticated defence mechanisms that serve to suppress outgoing predator-prey links. In this context, I will use the term *specialist* in a more general sense to refer to species with a small number of food web links. In order for the panmictic EcoLab model to generate an increasing diversity trend, a corresponding specialisation trend must also be present (which it isn't in the case of the usual mutation operator). Interestingly, specialisation is usually considered to be the default mode of evolution(Vermeij 1987). Generalists only exist because they happen to be more robust against environmental perturbation.

This experiment involves modifying the mutation operator to bias it towards removing interaction terms. The usual *Ec𝒬ab* mutation operator operator adds or removes connections according to $\lfloor 1/r \rfloor$, where $r \in (-1, 1)$ is a uniform random variate(*Ec𝒬ab* Technical Report). In this experiment, a new experimental parameter $g \in (-1, 1)$ (gen_bias) is introduced such that $r \in (-1 + g, 1 + g)$ and the number of connections added or deleted is given by $\lfloor (1 + \text{sgn}(r)g)/r \rfloor$. By specifying a very negative value of g, the mutation operator will tend to produce specialists more often than generalists. The code for this experiment is released as *Ec𝒬ab* 4.2.

A typical run with $g = -0.9$ is shown in Figs. 1–4. As described in (Standish 2000), activity is weighted by the population density, not just presence of a particular species. The results show unbounded creative evolutionary activity (Class 4 behaviour). As can be seen from Fig. 4, the system remains close to the hyperbolic critical surface, yet the dynamic balance has been removed by the specialisation trend. If we assume that $D \leq C_0/C(D)$, then unbounded diversity growth can only happen if C vanishes at least as fast as $1/D$ (see Fig. 5). An ecosystem consisting entirely of specialists has a constant number of foodweb links per species, or $C \propto 1/D$. The presence of generalists in the ecosystem damps the growth in diversity, and unbounded growth is
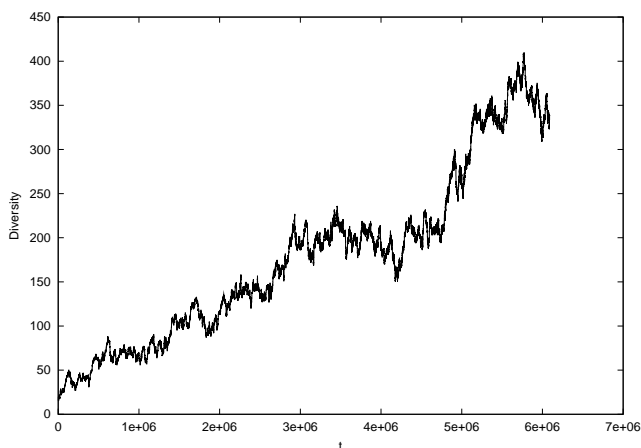
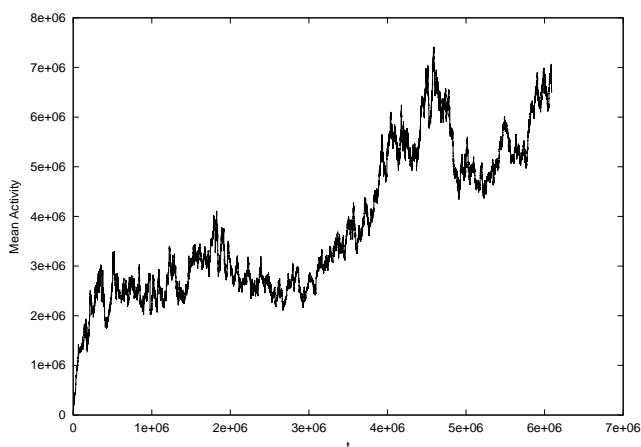Figure 1: Diversity growth for a typical run with $g = -0.9$
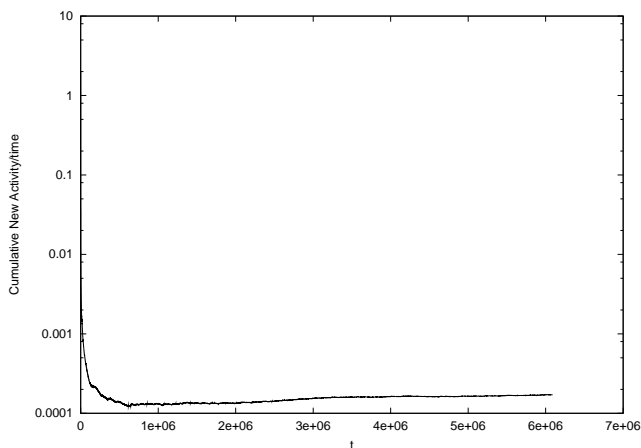

Figure 2: Mean cumulative activity $\bar{A}_{\text{cum}}(t)$

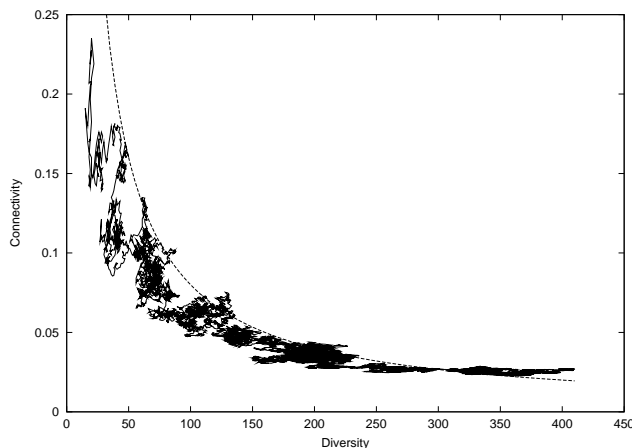Figure 3: Cumulative New Activity over time $\frac{1}{t}\int_0^t A_{\text{new}}(t)dt$

Figure 4: Connectivity vs Diversity for the same run depicted in Figs. 1–3. The dashed curve is $8/D$.

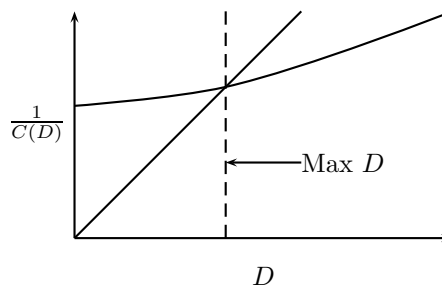

Figure 5: Diversity is constrained to lie under the curve $1/C(D)$. The intersection of this curve with line $y = D$ gives the maximum possible diversity in the ecosystem. If $C(D) \leq o(D^{-1})$, then diversity is unbounded.

only possible if the proportion of generalists continually diminishes over time.

Continental Drift

In (Standish 2000), I suggested that one possible explanation for the diversity growth since the end of the Permian was the breakup of the supercontinent Pangaea. A simple estimate given in that paper indicated that the effect might account for a diversity growth of about 3.5 times that existing during the Permian. This was remarkably similar to the growth reported by(Benton 1995), however it is worth noting that Benton's data referred to families, not species. It is expected that the numbers of species *per family* also increased during that time(Benton 2001). Furthermore, when continental organism are included, familial diversity today is more like 5 times the diversity during the Permian.

Unbeknownst to me at the time, Vallentine(1973) had proposed essentially the same theory, called *biogeographic provincialism* (the notion that the number of biological provinces is increased through rearrangement of the continents). The idea received some serious support by Signor(1990), although in a later review he was less

enthusiastic(Signor 1994). Tiffney and Niklas(1990) examined plant diversity in the northern hemisphere and concluded that plant diversity correlated more with the land area of lowlands and uplands, rather than continental breakup. Benton(1990) is characteristically sceptical of biogeographic provicialism as an explanation of the diversity trend through the Phanerozoic. Biogeography theory depends on an assumed dynamic balance between speciation and extinction[3], which appears to be contradicted by the fossil data for continental animals(Benton 2001), which shows a strong exponential increase in diversity through the Phanerozoic.

Since the *EcoLab* model has this dynamic balance between speciation and extinction when the dynamics self-organise to the critical surface $D \approx (Cs^2)^{-1}$, I experimented with the spatial version of *EcoLab* reported in (Standish 1998). The maximum migration rate $|\gamma|_\infty$ was swept up and down exponentially in time according to $0.9^{t/1000}$, *i.e.* with a time constant of about 9500 timesteps, by scaling γ by 0.9 every 1000 timesteps (and then inverting the scaling factor every 174,000 timesteps). It is a little hard to relate *EcoLab* figures to biological evolution. The maximum growth rate in *EcoLab* is 0.01, so the doubling time for the fastest organism in the ecosystem is around 100 timesteps. This might correspond to a year or so of real time. So migration rates are being forced much faster than is typical in the real world. However, in EcoLab we also tend run the mutation rate quite high, with adaptive speciations happening every 1000 timesteps or so. If the mutation rate is too high, natural selection has no chance to weed out non-adaptive species, if too low, too much computing resource is need to obtain interesting dynamics. In practice, the mutation rate is set about 2 orders of magnitude less than the critical amount needed for adaptation. In terms of speciation rates, the migration rate time constant might correspond to something of the order of 10^4 years, instead of the 10 years or so one gets from considerations of doubling times.

This code is released as EcoLab 3.5. Due to a design flaw, performance of this code scales poorly with diversity, unless the code is run in parallel with one cell per execution thread. For this experiment, the runs took place on a 2×2 spatial grid, on a four processor parallel computer supplied by the Australian Centre for Advanced Computing and Communications, apart from one run of a 3×3 grid on a 9 processor system. Work is currently underway to implement a spatial version of the *EcoLab* 4.x code, which does not suffer from this performance problem.
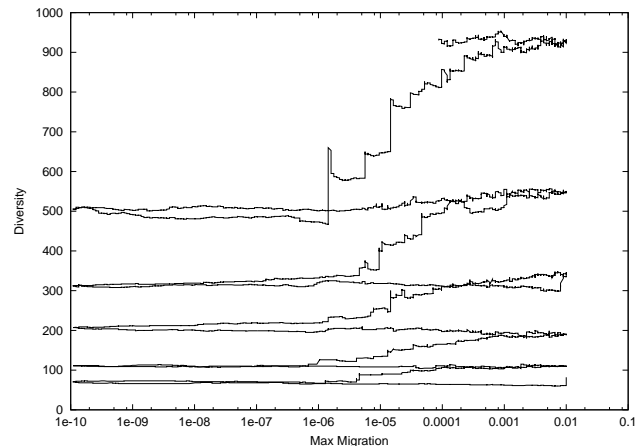
The results of a typical run is shown in figure 6. The

Figure 6: Typical run sweeping the maximum migration rate $|\gamma|_\infty$. The migration operator was applied every 100 time steps, so the units of the x-axis are 0.01 cells per timestep

run started with a maximum migration rate of 0.01 at the bottom right hand corner of the figure and swept down to 10^{-10} before increasing. The migration rate was swept back and forwards 5 times over the 18 million time steps in the run.

The first thing to note was that the expected response of diversity to migration rate was not there. We would expect a response of the form $D \propto A^c$, with $A = 4$ in the 2×2 case, and c varying smoothly between 1 for the infinite migration (panmictic) case and 2 for zero migration. These results tentatively indicate that possibly c does not vary smoothly at all, but is nearly constant for most values of $|\gamma|_\infty$. This needs to be resolved with further study.

The second thing to note is the completely unexpected "resonance" at about 1×10^{-5}. It is not peculiar statistical aberration, since the same result was obtained with completely different random number seeds, and fixing the migration rate at the resonance value produces an exponential growth in diversity (Figure 7).

3 more tests were performed to determine if this result is an artifact of discretisation, or a feature of the dynamics. The first involved changing the grid to a 3×3 grid, which did not affect the location of the resonance. The second involved scaling all parameters in the model $(\mathbf{r}, \boldsymbol{\beta}, \boldsymbol{\mu})$ by 0.1, which is equivalent to changing the timescale. If the effect was purely due to dynamics, one would expect the resonance to shift one order of magnitude higher on the scale, however little qualitative different was observed. The third test involved performing the migration operator every 1000 timesteps, instead of 100. This did change the resonance value by 1 order of magnitude, ruling out certain classes of software faults.
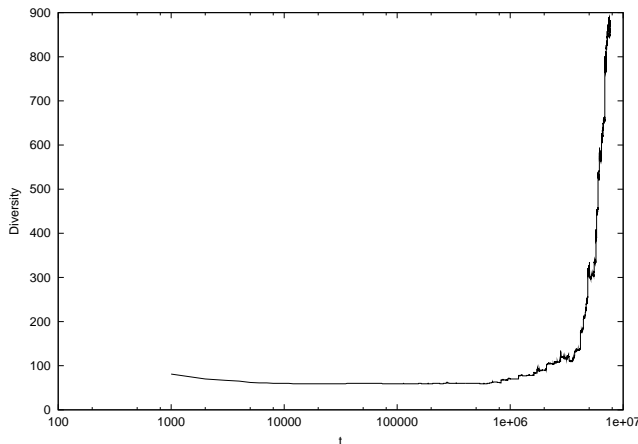
---

[3]Benton calls this a *dynamic equilibrium*, although it is nothing like what the term equilibrium denotes in dynamical system theory, and characterises biogeorahic theories as *equilibrial*

Figure 7: Diversity growth on a 2×2 grid, with $|\gamma|_\infty = 1 \times 10^{-6}$.

Conclusion

The choice of diversity as a proxy measure for ecosystem complexity is a good choice. Complexity is obviously constrained by diversity, so that bounded diversity dynamics also implies bounded complexity dynamics. However, in the case of evolutionary Lotka-Volterra dynamics, the system will tend to self-organise to a critical surface where speciation is balanced by extinction. This surface defines the maximum allowed complexity for a given diversity value, which turns out to be proportional to the diversity. The analysis presented in this paper could be extended to other evolutionary ecologies as well.

Whilst there is still debate about whether the biosphere is exhibiting unbounded complexity growth, I am persuaded by Benton's(2001) argument that the growth is nothing short of spectacular. In this paper I examined two possible mechanisms for diversity growth — *specialisation* which proves capable of delivering unbounded creative evolution in $Ecolab$, and *biogeographic provincialism*. Whilst I was only expecting biogeographic changes to deliver a modest impact on diversity, $Ecolab$ delivered a unexpected result of a "resonance", where if the migration rate was tuned to this value, diversity grew exponentially.

Acknowledgements

References

Anastasoff, S. J. 2000. Ecology and extinction — macroevolutionary extinction dynamics in a simulated ecosystem. In Bedau et al. (2000).

Bedau, M. A.; McCaskill, J. S.; Packard, N. H.; and Rasmussen, S., eds. 2000. *Alife VII: Proceedings of the Seventh International Conference.* Cambridge, Mass.: MIT Press.

Bedau, M. A.; Snyder, E.; and Packard, N. H. 1998. A classification of long-term evolutionary dynamics. In Adami, C.; Belew, R.; Kitano, H.; and Taylor, C., eds., *Artificial Life VI*, 228–237. Cambridge, Mass.: MIT Press.

Benton, M. J. 1990. The causes of the diversity of life. In Taylor, P. D., and Larwood, G. P., eds., *Major Evolutionary Radiations.* Oxford: Clarendon. 409–430.

Benton, M. J. 1995. Diversification and extinction in the history of life. *Science* 268:52–58.

Benton, M. J. 2001. Biodiversity on land and in the sea. *Geological Journal* 36:211–230.

Channon, A. 2001. Passing the alife test: Activity statistics classify evolution in geb as unbounded. In Kelemen, J., and Sosík, P., eds., *Advances in Artificial Life*, volume 2159 of *Lecture Notes in Computer Science*, 417. Berlin: Springer.

Christensen, K.; di Collobiano, S.; Hall, M.; and Jensen, H. 2002. Tangled nature: A model of evolutionary ecology,. *J. Theor. Biol.* 216:73–84.

Drossel, B., and McKane, A. J. 2002. Modelling food webs. In Bornholdt, S., and Schuster, H. G., eds., *Handbook of Graphs and Networks.* Berlin: Wiley-VCH. arXiv:nlin.AO/0202034.

Drossel, B.; Higgs, P. G.; and McKane, A. J. 2001. The influence of predator-prey population dynamics on the long-term evolution of food web structure. *J. Theor. Biol.* 208:91–107.

Li, M., and Vitányi, P. 1997. *An Introduction to Kolmogorov Complexity and its Applications.* New York: Springer, 2nd edition.

May, R. M. 1972. Will a large complex system be stable. *Nature* 238:413–414.

McShea, D. W. 1996. Metazoan complexity and evolution: Is there a trend? *Evolution* 50:477–492.

Rechtsteiner, A., and Bedau, M. A. 1999. A genetic neutral model for quantitative comparison of genotypic evolutionary activity. In Floreano, D.; Nicoud, J.-D.; and Mondada, F., eds., *Advances in Artificial Life*, volume 1674 of *Lecture Notes in Computer Science*, 109. Berlin: Springer.

Signor, P. W. 1990. The geologic history of diversity. *Annual Reviews of Ecology and Systematics* 21:509–39.

Signor, P. W. 1994. Biodiversity in geological time. *American Zoologist* 34:23–32.

Standish, R. K. Ecolab documentation. Available at http://parallel.acsu.unsw.edu.au/rks/ecolab.

Standish, R. K. 1994. Population models with random embryologies as a paradigm for evolution. In *Complex Systems: Mechanism of Adaption.* Amsterdam: IOS Press. also *Complexity International*, **2**.

Standish, R. 1998. Cellular Ecolab. In Standish, R.;

Henry, B.; Watt, S.; Marks, R.; Stocker, R.; Green, D.; Keen, S.; and Bossomaier, T., eds., *Complex Systems '98 — Complexity Between the Ecos: From Ecology to Economics*. http://life.csu.edu.au/complex: Complexity Online. 80. also in *Complexity International*, **6**.

Standish, R. K. 2000. An Ecolab perspective on the Bedau evolutionary statistics. In Bedau et al. (2000), 238–242.

Standish, R. K. 2001. On complexity and emergence. *Complexity International* 9.

Tiffney, B. H., and Niklas, K. J. 1990. Continental area, dispersion, latitudinal distribution and topographic variety: A test of correlation with terrestrial plant diversity. In Allmon, W., and Norris, R. D., eds., *Biotic and Abiotic Factors in Evolution*. Chicago: Univ. Chicago Press. 76–102.

Vallentine, J. W. 1973. *Evolutionary Paleoecology of the Marine Biosphere*. Englewood Cliffs, NJ: Prentice-Hall.

Vermeij, G. J. 1987. *Evolution and Escalation*. Princeton, NJ: Princeton UP.