

Food Webs and the Evolution of Organism Complexity

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Abstract

This paper investigates the role of ecological interactions in the evolution of organism complexity. Webworld is a robust model of evolution in food webs. Here it is extended for variability of organism complexity under evolution. Webworld organisms interact by comparing organism features. We assume a more complex organism has more features, and find that the rate of feature length increase is greater when all features are used to calculate interactions than when only a fixed number of features are used (i.e. compared to a passive diffusion control). Since in both cases the rate of feature addition is the same, passive diffusion cannot be a sufficient explanation for increasing complexity. However, no increase in the complexity baseline is observed.

Introduction

Natural selection predicts survival of the fittest, not survival of the complex, (Maynard Smith and Szathmary, 1995), so what accounts for the macro-evolutionary trend to increasing organism 'complexity', (McShea, 1996)? The causes of increasing complexity are probably many. Can increasing organism complexity ever purely be due to passive diffusion against a left wall below which organisms can no longer replicate, (Gould, 1996) (McShea, 1994), or must there be an adaptive benefit to increased complexity, e.g. reduced decay rates during periods of resource limitation (Fernando, 2005), the capacity to exploit novel energy sources or resources (Williams and Frausto da Silva, 2005), (Lenski et al., 1999) or cope with environmental variety. Presumably, if a complexity-increasing feature incurs any metabolic cost, passive diffusion is insufficient, unless some compensating adaptive benefit re-asserts neutrality. It is certainly such metabolically costly features, e.g. brains, to which we generally allude when referring to organismal complexity. Note of course that left walls can exist, even if there is a driven increase in complexity rather than a passive diffusion. Such left-walls can move to the right due to the process of contingent-irreversibility, where symbiotic organisms lose the ability to revert to an independent existence (Maynard Smith and Szathmary, 1995). However organism-level contingent irreversibility does not explain the existence

of a far left wall but rather it concerns the left wall of specific symbiotic species, e.g. mitochondria cannot replicate independently, and eukaryotes cannot revert to prokaryotes. A far-left wall on the other hand may arise from ecosystem level constraints preventing the re-emergence of simple life forms.

This paper is concerned with one possible influence on the evolution of organismal complexity; the stability of organisms in an ecosystem as a function of their complexity. Our conjecture is that ecological interactions have a core role in the process of complexification. Within an ecosystem, a species must adapt to numerous relationships with predators, prey, competitors, and mutualists. Surviving within such variety could seemingly require more complex adaptations. In turn, the increasing complexity of species could lead to more stable, intricate ecosystems. The feedback of this process of organism and ecosystem adaptation may lead to ever increasing complexity.

We are not concerned with measures of 'network complexity', but only 'organismal complexity', however, incidentally, dynamics resulting in increasing food web 'complexity' through disconnection are also observed, e.g. 'bovers' that create new niches and allow increased diversity (Wilson, 1992). Using the Webworld model, ??, organisms are described by a set of features, e.g. sharp teeth, quick wits etc. A feature is defined by its capacity to obtain resources when pitted against the features present in another organism. Organism complexity is synonymous here with the number of features that a species has. Our intuition is that an organism with higher complexity may have more opportunities to gain resources from other organisms, but may also have more Achilles heels that simpler species can use to exploit. We compare the passive diffusion case, in which there is no effect of the extra features, with the active case, in which extra features may influence the stability of an organism in its food web. We find that under a wide range of parameter settings, organisms with more features tend to arise in the ecosystem at a rate greater than through passive diffusion alone. Ecosystems show a macro-evolutionary trend to containing more complex organisms.

The Webworld Model

The Webworld model has been jointly developed by several researchers, over years of work aimed at combining predator-prey-population dynamics with an evolutionary process of food web assembly (McKane, 2004). Webworld has been used to examine questions on the stability and network structure of food webs, as well as long term evolutionary trajectories and extinction events in an ecological context (Quince and McKane, 2004b) (Quince and McKane, 2004a). The resulting model is robust, and in particular, the predator response equation has been shown to enable construction of biological realistic food web structures (Drossel et al., 2004). While portions of the model have been criticized as too complex (Dunne et al., 2004), the evolutionary process is more elegant than the artificially restrictive assembly models based on cascades and niches. We highlight key portions of the model below; for a thorough introduction to the model see (Drossel et al., 2001) and (Maron, 2004), and for a survey of food web modelling see (Drossel and McKane, 2003).

First, the population dynamics are described briefly. The population of a species in a food web, $N_i(t)$, is updated according to the equation

$$\frac{dN_i(t)}{dt} = -N_i(t) + \lambda \sum_j N_j g_{ij}(t) - \sum_j N_j g_{ji}(t) \quad (1)$$

The first term is the constant death rate, independent of interaction with other species. The second term represents the amount of resources transferred to species i , from predation on other species. $g_{ij}(t)$ is the 'functional response' equation, or the rate at which species i consumes species j . λ is the ecological efficiency constant, the percentage of resources incorporated in a higher trophic level, here 0.1. The final term represents predation by other species on species i .

The response function incorporates ratio-dependent predation, foraging, and interspecies competition.

$$g_{ij}(t) = \frac{S_{ij} f_{ij}(t) N_j(t)}{b N_j(t) + \sum_k \alpha_{ki} S_{kj} f_{kj}(t) N_k(t)}. \quad (2)$$

S_{ij} is the rate of predation, described in depth below. The constant b controls the level at which predation saturates on high prey populations, set to 0.005 in these simulations. α_{ki} is interspecies competition, dependent on species similarity.

$f_{ij}(t)$ is the percentage of effort the predator i is devoting to prey j . A predator must divide the total of its effort among its prey, and will choose a division so to maximize transfer of resources, according to Optimal Foraging Theory (Morin, 1999). It has been shown that the following calculation of efforts results in an Evolutionary Stable Strategy (Drossel et al., 2001).

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)} \quad (3)$$

Since the response and efforts functions are interdependent, results for all prey are calculated iteratively, and will converge on an optimal distribution of efforts. At this point in simulation, population levels are updated. The population change then requires update of the efforts and functional response. The process is repeated until all species population levels converge to stable values.

In Webworld, each species is defined as a list of L unique integers, each representing some abstract morphological or behavioural characteristic, such as "sharp claws", "camouflage body pattern", "fruit bearing", etc. There are K possible features in a simulation. The interaction of two species' sets of characteristics determines the strength and direction of their interaction in the food web. When starting a run, a $K \times K$ "feature matrix" of normally distributed random numbers is calculated. The matrix is set to be antisymmetric, so $m_{\alpha\beta} = -m_{\beta\alpha}$. The entry $m_{\alpha\beta}$ describes how feature α performs against feature β . The score S_{ij} of species i against species j is calculated as

$$S_{ij} = \max\{0, \frac{1}{L} \sum_{\alpha \in i} \sum_{\beta \in j} m_{\alpha\beta}\} \quad (4)$$

where α and β iterate over all features of species i and j . In most of the published work, and here, $L = 10$ and $K = 500$

Essentially, the score is the sum of the performance values of each species' features against the other, and determines the degree and direction of predation. The external environment is represented as species 0, and is assigned a set of unchanging features. Species with a positive interaction score against the environment are primary producers. External resources are input to the food web at a constant rate, R , here set to 10,000.

Competition between two species is calculated from the similarity of their feature lists. q_{ki} is the percentage of features two species have in common. For members of the same species, $\alpha_{ki} = 1$. A minimal level of competition is present between any species; here $c = 0.5$.

$$\alpha_{ki} = c + (1 - c)q_{ki} \quad (5)$$

The evolutionary process is started by creating 10 initial species, with 10 randomly set features, each with a population size of 10. Scores are calculated, and response functions and population levels are updated until the food web is stable. This triggers a speciation event. From one randomly chosen species, a single individual is removed from the population and one of that individual's features is randomly changed, resulting in a new species. Scores for the new species are determined, and the process of calculating response and population levels is started again.

On the introduction of the new species, there are a few possibilities. It can immediately go extinct, under competition from its parent species. Sometimes, it can co-exist with

its parent and its competitors, causing no subsequent extinctions. Other times, the new species out competes its parent or other competitors, over consumes prey, or causes even more indirect effects, leading to a cascade of extinctions. Webworld is run for some number of speciation events, from 1,000 to 100,000, and the resulting webs are used for statistical analysis. An ecosystem undergoing 2000 speciation events requires two hours to simulate on an Itanium processor.

Extending Webworld for Feature Complexity

At a speciation event, this experiment allowed for feature addition or deletion, as well as the usual feature exchange at fixed feature length. This introduces two new parameters to the model: the probability of adding and the probability of deleting a feature during speciation. These probabilities, plus the remaining probability of only changing a feature, sum to one. The initial species still start with a feature list of size 10.

Variable feature list sizes lead to two additional changes to the interaction strength calculation. The number of feature performance values summed for the predation score is now variable. However, all scores for a species will still be normally distributed, when scaled by $\sqrt{L_i * L_j}$. However, the means and variances of these scores will change in a complex manner. We use a control case in which scaling is independent of length, i.e. $1/L = 0.1$ to test the effect of this scaling decision. Second, the competition coefficient is calculated with respect to the shorter of the two feature lists.

It can be questioned whether varying the feature list length corresponds to complexity change. Since the species representation is not a genome, as the list directly interacts with other species, the problem of lack of correspondence between real genomes and species complexity does not apply (Bonner, 1988). The feature list is intended to relate to 'functional' complexity.

Results

Test runs without feature length variation are comparable to published results (Drossel et al., 2001), see Table 1 and real food webs, (Dunne et al., 2002). Having confirmed that our model faithfully captures the standard Webworld results, all further experiments deal with the consequences of allowing feature length variation during speciation.

Where there is an equal probability of 20% for addition or deletion of a feature, there is a tendency for maximum and mean feature length to increase over evolutionary time, see figure 1.

To measure the strength of the tendency towards organisms with increased feature length, a batch of runs was conducted with different ratios of feature addition-to-deletion probability, ranging from 0 to 1. For all ratios there is a pressure towards a smaller feature vector length, i.e. $P(\text{removal}) \geq P(\text{addition})$. The probability of additions

Table 1: Network metrics of a test run, compared against results published in (Drossel et al., 2001)

	Test Run	Published Results
No. of species	41	33
Links per species	2.2	1.76
Av. level	1.75	1.95
Av. max. level	3.0	3.0
Basal species (%)	24	18
Intermediate species (%)	72	80
Top species (%)	4	2

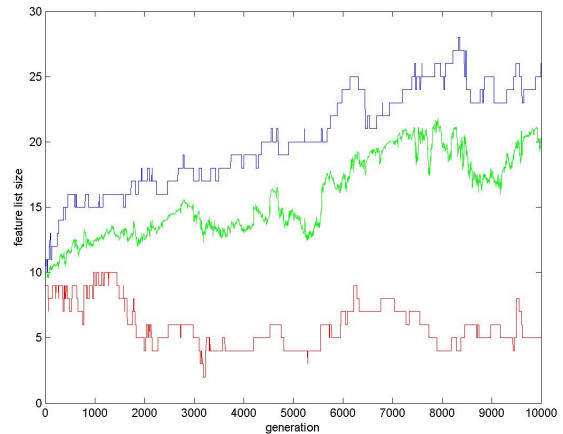


Figure 1: Average, largest, and smallest feature length vector plotted against time, for 10,000 mutation events] green (mean), blue (maximum), and red (minimum) feature length vector plotted against time, for 10,000 mutation events. Number of species as a function of time in a typical run, showing 10,000 speciation events. Mean and maximum feature length increases, but minimum feature length remains approximately constant.

and deletions always sums to 40%. Runs from each of 30 ratios tested are performed 6 times. Each run consists of 2,000 speciation events, see figure 2. Remarkably, feature length increases even when deletion occurs twice as often as addition of features. However, below an addition-to-deletion ratio of 0.5, feature lengths decrease. Superimposed on this graph are the results of two control cases used to identify the possible causes of feature length increase. In the first control, (bottom line, green), only the first 10 features of any species are used to calculate the S_{ij} values, even though $P(\text{addition})$ and $P(\text{deletion})$ are as before. In the second control, (top line, red), again only the first 10 features are used to calculate S_{ij} values, but in addition, the scaling of S_{ij} does not include the coefficient $1/\sqrt{L_i * L_j}$; rather, $1/L = 0.1$ irrespective of the feature vector lengths of the i,j pair. The fact that there is a greater increase in feature length when all features are used in the calculation of

S_{ij} compared to the first control suggests that feature length increase is not merely passive, but is affected by ecosystem level interactions.

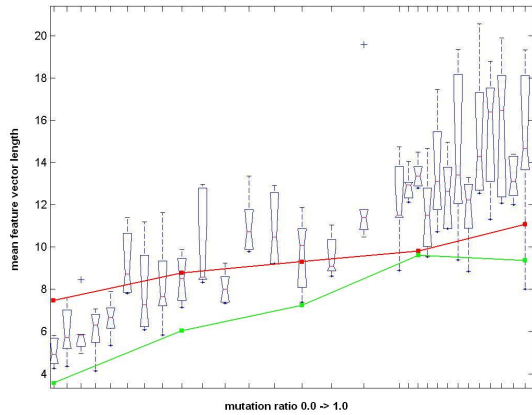


Figure 2: Box plot of final mean feature vector length for different values of $P(\text{addition})/P(\text{deletion})$.

The number of species increases with increasing $P(\text{addition})/P(\text{removal})$ ratio, see figure 3 (top). Why is this? As Standish has shown, ?? species diversity relates inversely to connectedness. Figure 4 (Bottom) shows that indeed, increasing feature length is related to decreased connectedness. However, figure ?? shows that connectivity decreases even in the control cases, where only the first 10 features contribute to S_{ij} . Therefore, we can demonstrate no clear link between increased feature length per-se and the decrease of connectivity in this system.

Why does ‘complexity’ increase?

The first hypothesis that increasing complexity is due to passive diffusion is less likely given figure 2 which shows that increased feature length is greater than control cases with equal $P(\text{addition})/P(\text{deletion})$ ratios, but where extra features are not used to calculate S_{ij} . However, no attempt was made to control for the effect of feature length on competition dynamics α_{ij} .

The second hypothesis is that more ‘complex’ species are often disconnected species (i.e. have no predators) at the time of origin, such that they are more likely to survive and further speciate. A partial confirmation of this hypothesis came from six more runs in which after a speciation event, the new species was examined to see if it was disconnected; in other words, basal with no active predator. If it was a disconnected species, it was discarded and another speciation event occurred, until a predator or a basal species with a predator developed. The resulting webs had little change in species complexity from the initial size of 10, to a final average feature list size of 10.7. Examining a few samples from

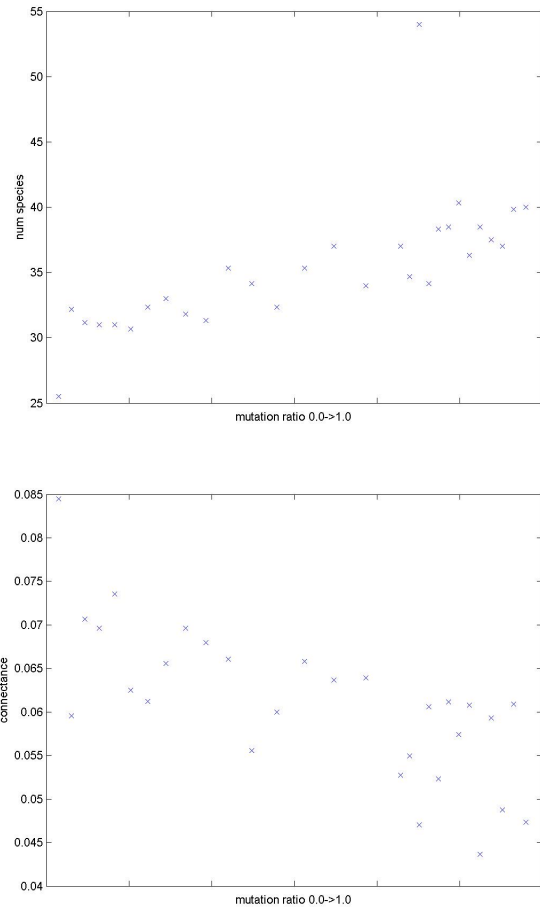


Figure 3: Top: Mean number of species in response to variations in addition/deletion mutation ratio Bottom: Mean connectance in response to variations in addition/deletion mutation ratio

previous runs, disconnected species were usually the first to evolve longer features lists and persist. Further experiments are required to confirm this hypothesis.

The third concern was that because of the scaling of S_{ij} by $1/\sqrt{L_i * L_j}$, there may have been an unfair advantage for longer feature length species, i.e. there is a tendency for the mean and variance of S_{ij} to be lower. This would mean that ecosystems consisting of more complex species have weaker interactions and lower connectedness. However, in a control case where $1/L = 0.1$ the increase in feature length was even greater. Thus, feature length increases even when this possible advantage due to scaling of S_{ij} values is removed. Of course, an extra new advantage is had by more complex organisms in the second case since the mean S_{ij} values increase by this scaling method.

A fourth hypothesis is that speciation events are less disruptive in longer species. Longer species are less likely to

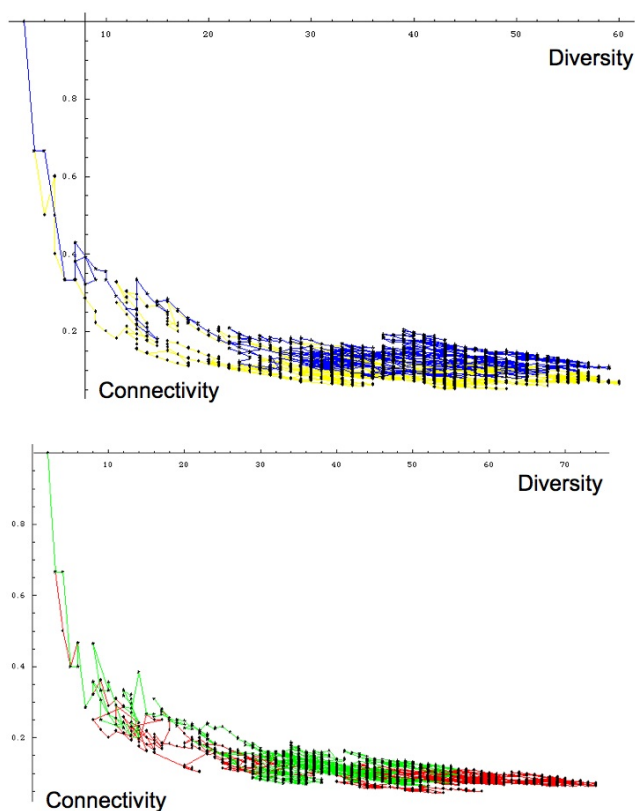


Figure 4: Top: Connectance is inversely related to diversity (number of species) in both the active and passive controls. Co-efficient for calculating S_{ij} is variable. Yellow = (Active) All features used to calculate S_{ij} , Blue = (Passive) Only first 10 features used to calculate S_{ij} . Bottom: As above, except co-efficient for calculating S_{ij} is fixed. Red = Active, Green = Passive. Active ecosystems obtain higher diversities for the same connectance value.

produce species that immediately go extinct since a longer feature vector means that a single change to a feature will have less of an effect on the overall S_{ij} value. In biological terms, a small change to a more complex organism is less disruptive ecologically than a small change to a simple organism. However, we found that there was no significant tendency for longer species to produce off-spring species that were less likely to go extinct. Nevertheless it would be useful to compare the mean life-time of children compared to the mean life-time of parent species, as a function of feature length.

Discussion

After considerable further analysis it is still not clear why complexity or feature vector length in this model increases. Passive diffusion is tentatively ruled out, and the ecological benefit of increased feature length is not confirmed. More work is required to completely rule out passive diffusion, since competition differences as a function of length are still present in the control cases. Presumably it is also difficult

to rule out subtle ecological interactions in biological systems, in order to confirm the existence of passive diffusion, rather than adaptive benefits to complexity. Further investigation is required to explore the benefits of increased feature length, e.g. do more complex species have more stable speciation events, do more complex species benefit from weaker interactions and fewer predators. Is it reasonable to model organismal complexity as increased feature length? In addition, no cost has been imposed on complexity, and there undoubtedly is one. The main contribution of this paper is to highlight the fact that ecological interactions are likely to influence the evolution of complexity in subtle ways. We have only succeeded in hinting at a range of ecological factors that may influence this process.

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References

- Bonner, J. (1988). *Evolution of Complexity, by Means of Natural Selection*. Princeton University Press.
- Drossel, B., Higgs, P., and McKane, A. (2001). The influence of predator-prey population dynamics on the long-term evolution of food web structure. *Journal of Theoretical Biology*, 208:91–107.
- Drossel, B. and McKane, A. (2003). *Modelling Food Webs*. Berlin: Wiley-VCH.
- Drossel, B., McKane, A., and Quince, C. (2004). The impact of non-linear functional responses on the long-term evolution of food web structure. *Journal of Theoretical Biology*, 229:539–548.
- Dunne, J., Brose, U., Williams, R., and Martinez, N. (2004). Modelling food-web structure and dynamics: implications for complexity-stability. Technical Report 04-07-021.
- Dunne, J., Williams, R., and Martinez, N. (2002). Food-web structure and network theory: The role of connectance and size. *PNAS*, 99:20.
- Fernando, C. (2005). The good symbiont. *ECAL*, Advances in Artificial Life, 8th European Conference, ECAL 2005, Canterbury, UK, September 5-9, 2005, Proceedings. Lecture Notes in Computer Science.
- Gould, S. (1996). *Full House*. Harmony Books, New York.
- Lenski, R.E. Ofria, C., Collier, T., and Adami, C. (1999). Genome complexity, robustness, and genetic interactions in digital organisms. *Nature*, 661-664.

- Maron, M. (2004). An ecological approach to the evolution of organism complexity. Master's thesis, University of Sussex, Evolutionary and Adaptive Systems.
- Maynard Smith, J. S. and Szathmary, E. (1995). *The Major Transitions in Evolution*. Oxford University Press.
- McKane, A. (2004). Evolving complex food webs. *Eur. Phys. J. B*, 38:287–295.
- McShea, D. (1994). Mechanisms of large-scale evolutionary trends. *Evolution*, 48:1747–1762.
- McShea, D. (1996). Metazoan complexity and evolution: is there a trend? *Evolution*, 50:477–492.
- Morin, P. (1999). *Community Ecology*. Blackwell Science, Inc.
- Quince, C., H. P. and McKane, A. (2004a). Deleting species from model food webs. *Oikos*, 110:283–296.
- Quince, C., H. P. and McKane, A. (2004b). Topological structure and interaction strengths in model food webs. *Ecological Modelling*, 187:389–412.
- Williams, R. and Frausto da Silva, J. (2005). *The Chemistry of Evolution - The Development of our Ecosystem*. Elsevier.
- Wilson, E. (1992). *The Diversity of Life*. Harvard University.