

Survival of the Unfittest: The Relationship between Generation Time and Organismal Complexity.

Chrisantha Fernando

July 7, 2004

Abstract

1 Introduction

The notion of complexity is multifaceted. To a first approximation at least, organismal complexity is proportional to the time it takes for an organism to complete development, (i.e. from being conceived to conceiving, the generation time, or the inverse of intrinsic growth rate, $1/r$). We call this notion r -complexity for brevity. In many cases this is consistent with our intuitive notions of complexity,¹ but in other cases it seems to contradict out intuitive notions, e.g. clams replicate more slowly than frogs [insert graph of replication rate v. size/population size here and discuss]. However, our intuitive notions of some sort of progress up a complexity ladder are absolutely not to be trusted as several scientific fau pas have shown, [ref], and we are best sticking to measurable variables where possible. We may restate the question without referring to complexity for the moment; Under what circumstances can more slowly replicating organisms originate and be maintained?

If an organism takes longer to develop (measured in generation time), then it seems at first glance that it is at a disadvantage compared with organisms that develop more rapidly, i.e. with organisms having higher intrinsic growth rates. This seems to be evident in the two examples below. Tom Ray's Tierra [ref], is an artificial evolutionary system in a computer in which machine code programs undergo interspecific and intraspecific competition for a single 'renewable' resource, the CPU. Small programs replicate faster than long ones and so end up using more CPU time. Parasites and hyperparasites evolve that can replicate

¹Intrinsic rates of increase (per day) for several species, *E. coli* 60, *Paramecium aurelia* 1.24, *P. caudatum* .94, *Tribolium confusum* .12, *Calandra oryzae* .11, *Eurostis hilleri* .01, *Rattus norvegicus* .015, *Canis domesticus* .009, *Homo sapiens* .0003

extremely rapidly. These out compete the longer programs. The second example is Spiegelman's experiment in which he evolved RNA strands with access to a single resource, an RNA replicase [check this is true!]. Shorter RNA strands were selected for because they could replicate faster and out-competed the longer RNA strands. In both these circumstances distinct species of replicator are in competition for a single resource, the CPU, and the replicase, respectively.

Lotka-Volterra equations can be used to describe interactions between a fixed number of s species.

$$\frac{dN_1}{dt} = \frac{r_1 N_1 (K_1 - \alpha_{11} N_1 - \alpha_{12} N_2)}{K_1} \quad (1)$$

$$\frac{dN_2}{dt} = \frac{r_2 N_2 (K_2 - \alpha_{22} N_2 - \alpha_{21} N_1)}{K_2} \quad (2)$$

N_1 and N_2 represent the population sizes of the different species, r values are the intrinsic growth rates of each species, K values represent the carrying capacity of each species, and α values represent the matrix of influences on growth rates between and within species. We wish to know the positive values of N_1 and N_2 where the rates of change of both species is zero, i.e. where both can co-exist. This is done by solving both equations above to obtain the equilibrium equations below. We assume that intraspecific competition in both species α_{11} and α_{22} is unity.

$$N_{1eq} = K_1 - a_{12} N_2 \quad (3)$$

$$N_{2eq} = K_2 - a_{21} N_1 \quad (4)$$

Substituting $K_1 - a_{12} N_2$ for N_1 , and similarly for N_2 we obtain...

$$N_{1eq} = \frac{K_1 - a_{12} K_2}{1 - a_{12} a_{21}} \quad (5)$$

$$N_{2eq} = \frac{K_2 - a_{21} K_1}{1 - a_{12} a_{21}} \quad (6)$$

For these equilibrium values of population size to be both positive, it is necessary that $a_{12} a_{21} < 1$ and that both $K_1 > a_{12} K_2$ and $K_2 > a_{21} K_1$. So, for coexistence of two species, their competition coefficients must be less than self-inhibition, i.e. both species must inhibit themselves more than they inhibit the other. But also, the carrying capacity of each species must exceed the product of the competition coefficient and the carrying capacity of the competing species. Interestingly, it is the "relative potential sizes of the populations, rather than the actual population sizes per se, that determine whether there will be coexistence." given that $a_{12} a_{21} < 1$ [ref p 410 Ecology Ricklefs and Miller]. Also,

the intrinsic rate of replication r does not feature in the equilibrium equation so it does not effect the outcome of competition, only its time course, according to these equations. This result suggests that species with very low relative replication rates can coexist as long as the above inequalities hold. In Ray and Spiegelman’s experiment, these inequalities do not hold, and there is exponential growth. It has been demonstrated that with exponential growth, intrinsic replication rate does determine survival, “survival of the fittest”, [Szathmary], and that where there is sub-exponential growth (in particular parabolic growth), there can be “survival of everybody”.

So have we answered our question already. All we need to ensure is sub-exponential growth, in order for generation time to be irrelevant to selection. But how can this be ensured in a situation in which species are in competition for several distinct resources?

We investigate the distributions of replication rate that we could expect in a more realistic setting where species can exploit multiple resources so altering their carrying capacities and replication rates. We use a Lotka-Volterra model to represent N species competing for up to M resources. A resource is defined as something which increases the carrying capacity of a species that can utilize it, and which may contribute to an increase in intrinsic replication rate. However, we also assume a cost for being able to exploit a wide range of resources by stating that intrinsic growth rate decreases as a function of the number of resources used. The assumption underlying this cost is that developmental time is linearly related to the number of resources utilized [Present evidence for this]. The net effect of both these influences on intrinsic growth rate is represented by an constant, C , added to the intrinsic replication rate per resource utilized. Thus in this model we assume that C implicitly represents the summed contribution of both increased intrinsic replication rate due to the extra resources and the complexity cost due to the time needed to exploit these extra resources. Although we do not represent these two values separately we can investigate the outcomes for both positive and negative C values, thus investigating both the cases where utilization of resources provides net increase and net decrease of r . If multiple species exploit the same resource we assume there is competition for that resource.

2 Methods.

A C program was written to simulate the Lotka-Volterra equations for s species. In addition to the Lotka-Volterra equations described above we constructed a model of resource use by this fixed number s of species that was used to determine values of r_s , K_s and properties of the $s * s$ interaction matrix. This model is represented using the resource matrix of Figure 1. S species are represented on the x-axis and M resources on the y-axis.

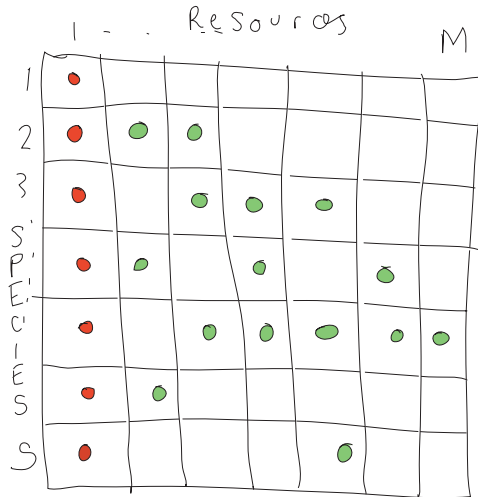


Figure 1:

For a given species, s , we assume that r_s changes by a fixed amount for each resource exploited by that species, so that $r_s = R_{s-initial} - CN$, where C is the change in intrinsic growth rate accrued per resource, which is implicitly the gain replication rate gain due to the resource minus the complexity cost of exploiting multiple resources. N is the number of resources exploited and R_s is the initial growth rate². For each resource that is available to a species we assume that the carrying capacity of that species, K_s increases by a fixed amount b , so $K_s = bM$, where b represents the benefit to that species of being able to exploit a new resource. If multiple species are using the same resource, then we assume there is competition between species for that resource. So for example if species q and p are both using the same resource we assign a small negative value w to α_{pq} and α_{qp} . Thus we establish a correspondence between the distribution of resource use and the Lotka-Volterra equations of growth on the basis of the definition of a resource as something that increases the carrying capacity of a

²We also experiment with negative values of C , i.e. where resources actually produce a net increase in intrinsic growth rate.

species, requires a developmental cost which may manifest as decreased intrinsic growth rate if it outweighs the benefits that the resource confers to growth rate, and results in competition if multiple species use it. In the course of this investigation we implement a wide range of assumptions regarding ecosystem structure (the α matrix), self-inhibition of growth (α_{qq} values), variable resource benefits (non-uniform b distributions across resources) and resource costs (non-uniform C distributions across resources).

Finally we make a further explicit assumption about the nature of variation of the capacity to utilize different numbers of resources. We assume that the rate of utilization of a new resource and the rate of loss of the capacity to utilize an existing resource are described by rates U and L respectively. These are modeled stochastically by assuming that $\text{Prob}(\text{Loss}) = 1 - \exp^{-dtL}$ and $\text{Prob}(\text{Gain}) = 1 - \exp^{-dtU}$. At each time-step (dt) in the simulation, for each species, we test whether a random number is less than $\text{P}(\text{Loss})$ or $\text{P}(\text{Gain})$, and if it is we abolish a current resource for that species, or we randomly assign a novel resource for that species.

So, a timestep in the algorithm consists in running the LV equations, recalculating the values of r_s , K_s and α 's on the basis of the current resource matrix, and then stochastically changing the resource matrix.

3 Results

The C implementation of the deterministic logistic equation produces the expected results given a single resource, single species model, with $K_1 = B = 10$, $\alpha_{11} = 1$ and $r = 4.95$ (because $R = 5$ and $C = 0.05$), and a time-step of 0.01. See figure. 2. The species drifts to its carrying capacity. Decreasing r reduces growth rate and decreasing K decreases the equilibrium population size. Figure. 3 part a. shows the results of a run with 10 species with the same value of r , all exploiting the same resource, where self-inhibition is unity, and competition is also unity, i.e. $\alpha_{pq} = 1$ for all species pairs. Species are initialized with random population sizes ranging from 0 to 5. Figure. 3 part b. shows the same experiment, except here with self-inhibition (1.0) is greater than competition (0.5). Figure. 3 part c. shows the same experiment but with self-inhibition (0.5) being less than competition (1.0).

3.1 Under what circumstances can agents with long generation times persist when there is access to multiple resources?

We examined the distribution of no of resources utilized at equilibrium, of species in an ecosystem, where each species was capable of evolving to exploit

more or less resources at random, determined by rates $U = 0.1$ and $L = 0.1$. Intraspecies competition was set to unity and interspecies competition was set to 0.5 for the 100 species investigated. Species could exploit up to 100 different resources, and initially used the same resource. Initially we assumed a net cost C per resource of 0.05, with an initial r value for all species set to 5.0. K values per resource were uniformly 10. We see that only a few species exist at levels greater than zero. Most species are driven to very low levels by competition which would most likely cause extinction. Of the 3 species that do exist at high levels at the end of the experiment, each exploits about 60 resources. Figure. 4

Compare this to an identical experiment except where the cross-competition coefficient is reduced from 0.5 to 0.01. We see that in this case many more species can exist at moderate frequencies simultaneously. Diversity is far greater than before. Species evolve to use a greater number of resources despite the decrement in reproduction time that results. Figure. 5

What about where there is a very high cost for utilizing novel resources, e.g. 0.5 per resource decrement in intrinsic replication rate. Species still evolve to decrease cross-competition by exploiting a novel resource and tend to exploit as many resources as possible, even though this means very low replication rates. Figure. 6

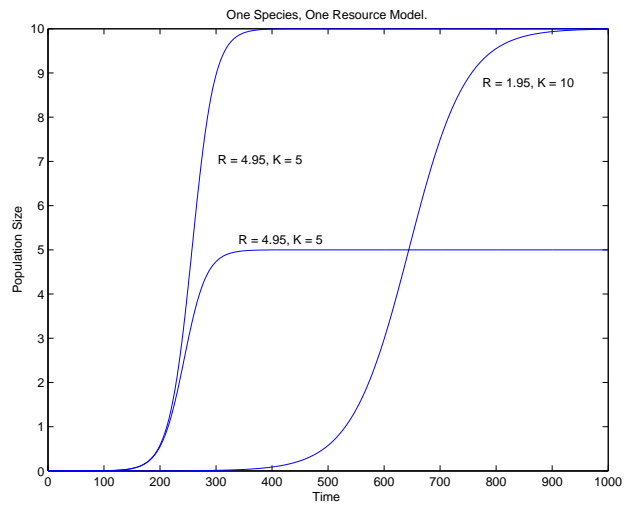


Figure 2:

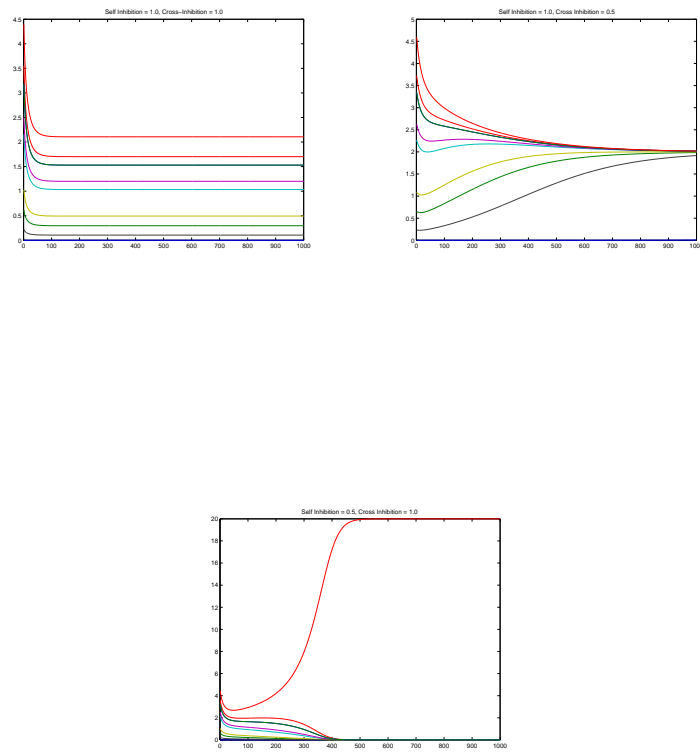


Figure 3:

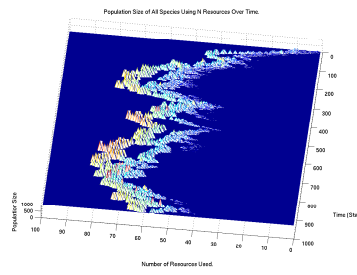
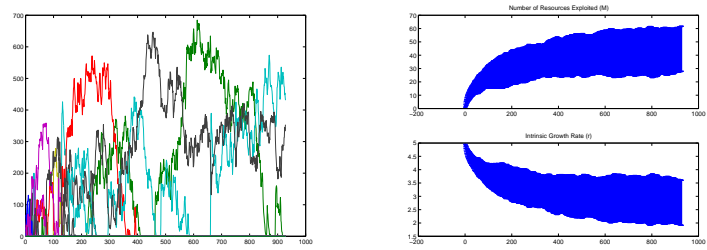


Figure 4:

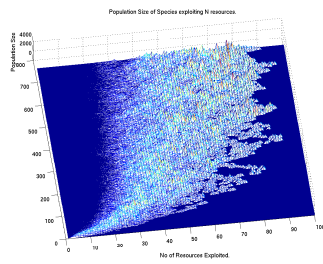
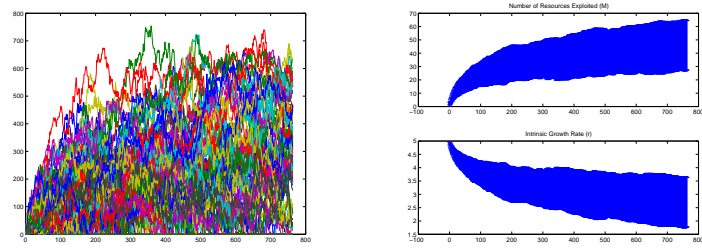


Figure 5:

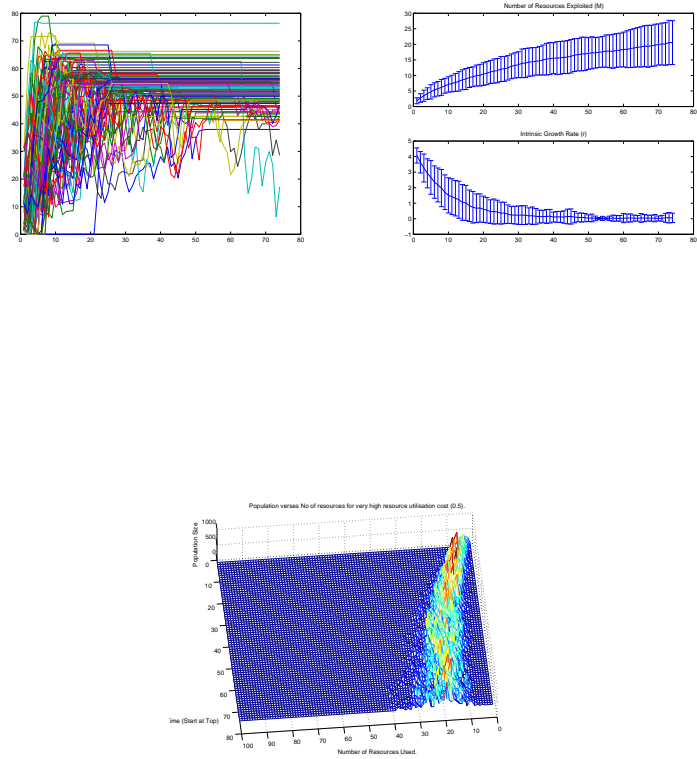


Figure 6: