The Paradox of the Plankton: Oscillations and Chaos in Multispecies Evolution

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Abstract. Two theoretical ecologists have recently discovered that even under the simplest models of competition, three species are sufficient to generate permanent oscillations, and five species can generate chaos (Huisman & Weissing, 2001). We can show that these results carry over into genetic algorithm (GA) resource sharing after making one minor change in the "usual" sharing methods. We also bring together previous, scattered results showing oscillatory and chaotic behavior in the "usual" GA sharing methods themselves. Thus one could argue that oscillations and chaos are fairly easy to generate once individuals are allowed to influence each other, even if such interactions are extremely simple, natural, and indirect, as they are under resource sharing. We suggest that great care be taken before assuming that any particular implementation of resource sharing leads to a unique and stable equilibrium.

1 Introduction and Background

Population biologists have long known about oscillations and chaotic behavior in multispecies competition models. But in the much simpler and more abstract models of evolution employed in genetic algorithms, we usually assume smooth convergence to stable equilibria (especially under selection alone). In particular, the simple and natural method of niching via the sharing of common resources has been shown to induce stable, long-term equilibria with multiple species coexisting (e.g., Horn, 1997). Yet even under the widely-used technique of simply dividing up finite resources among competing individuals, we can find evidence of oscillatory behavior and non-monotonic approaches to equilibrium.

1.1 Resource Sharing

A natural niching effect is implicitly induced by competition for limited resources (i.e., finite rewards). The sharing procedure we discuss here is common to the models of theoretical ecologists as well as to those of GA practitioners. The fundamental steps of resource sharing are intuitive:

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1. For each of the finite resources r_i, divide it up among all individuals contending for it, in proportion to the strengths of their claims. (Thus two equally deserving individuals should be allocated equal amounts of the resource.)
2. For each individual, add all rewards/credits earned in the first step, and use this amount (perhaps scaled) as the fitness for GA selection.
3. After a new generation is produced, replenish/renew the resources and start over at the first step above.

The notions of competition and niche overlap are easy to visualize in the case of resource sharing. In Figure 1, the circle represents the resources *covered* by the corresponding species. In a learning classifier system, for example, the circles would represent the subset of examples that are correctly classified by individuals of that species[1]. The resources in the overlapped niches are covered by multiple species, and must be shared among the individuals of *all* such species. (The resources covered by only one species must also be shared, but only among members of that one species.)

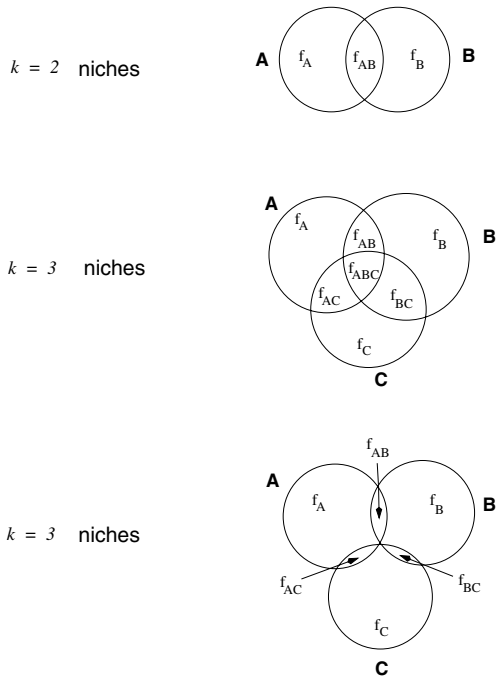

Fig. 1. Different situations of overlapping resource coverage.

[1] For the purposes of this paper, we will use the term "niche" to refer to such a subset of resources covered by a species.

To be explicit about the actual sharing mechanism, we calculate the shared fitness for the members of a species **A** in the situation shown in Figure 1, bottom (i.e., only pairwise niche overlaps, with $f_{ABC} = 0$). Let f_A, f_B, and f_C be the *objective* (i.e., unshared) fitnesses for rules **A**, **B**, and **C** respectively[2]. Let f_{AB} be the amount of resources in the overlapping coverage of species **A** and **B**. That is, f_{AB} is the amount of resources shared by **A** and **B**. Let n_A, n_B, n_C be the number of members of each of the three species, in our population of size N (thus $N = n_A + n_B + n_C$). We calculate the shared fitness of **A**:

$$f_{sh,A} = \frac{f_A - f_{AB} - f_{AC}}{n_A} + \frac{f_{AB}}{n_A + n_B} + \frac{f_{AC}}{n_A + n_C}. \tag{1}$$

Similarly for $f_{sh,B}$ and $f_{sh,C}$.

To simulate an actual experiment (i.e., a run of a GA), we use the well-known method of *expected proportion equations*. We assume a generational GA with proportionate selection and no crossover or mutation:

$$P_{A,t+1} = \frac{n_{A,t} f_{sh,A,t}}{\sum_{\forall species X}(n_{X,t} f_{sh,X,t})} \quad = \quad \frac{P_{A,t} f_{sh,A,t}}{\sum_{\forall species X}(P_{X,t} f_{sh,X,t})}, \tag{2}$$

where $P_{A,t}$ means the proportion of the population taken up by copies of species **A** at time (generation) t (i.e., $n_{A,t+1}/N$), and $f_{sh,A,t}$ is the shared fitness (e.g., Equation 1) of **A** at time t.

Resource sharing is often incorporated in adaptive, or simulated, systems, including: learning classifier systems (LCS) (Booker, 1982; Wilson, 1994; Horn, Goldberg, & Deb, 1994), immune system models (Smith, Forrest, & Perelson, 1993), evolving cellular automata (Werfel, Mitchell, & Crutchfield, 2000; Juillé & Pollack, 1998), and ecological simulations (Huberman, 1988). It is known by other names, such as *example sharing* (McCallum & Spackman, 1990) and *shared sampling* (Rosin & Belew, 1997).

2 Oscillations in Traditional Models of Resource Sharing

2.1 Two-Species Oscillations

Oei, Goldberg, and Chang (1991) showed how the "naïve" combination of fitness sharing and tournament selection leads to oscillations and chaos. In their model, the population consisted solely of two species with no niche overlap[3]. If tournament selection is applied to the shared fitness values calculated at generation t, then the species with the lower shared fitness will lose every competition in which it is paired with the other species. This will result in an overcompensation by selection, in which the more crowded (and therefore less fit) species will

[2] In this paper we use the term *objective fitness* to mean the credit or reward earned by an individual for covering each resource, summed over all covered resources, **before** any sharing method is applied.

[3] Since resource sharing and fitness sharing are equivalent methods when there is no niche overlap (Horn, 1997), the following result applies to resource sharing as well.

suddenly become the under-represented and more highly fit species in the next generation.

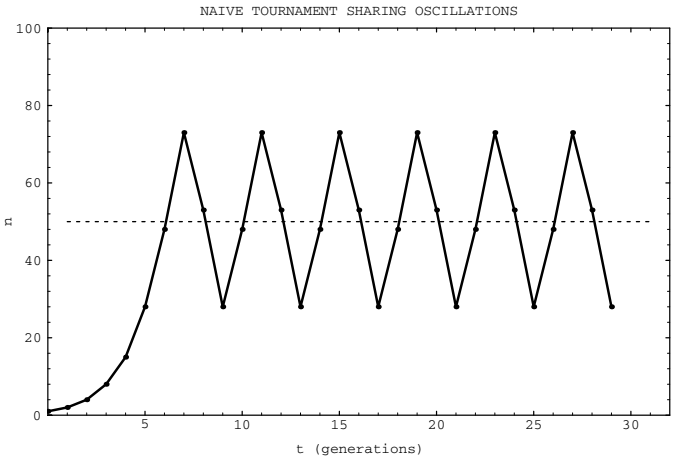

Fig. 2. Lotka-Volterra predator-prey oscillations under *naïve tournament sharing.*

These predicted swings in population are borne out in the plot of expected proportions shown in Figure 2. We trace the expected proportion of **A**s in a size $N = 100$ population under naive tournament sharing with two species of equal objective fitness: $f_A = f_B$. We start with one copy of **A** at $t = 0$, the initial generation. We observe a rapid convergence toward equilibrium, followed by an overshooting, then an undershooting, and so on; an apparently periodic oscillation. This seems reminiscent of predator-prey oscillations generated by Lotka-Volterra growth equations.

Although the oscillations in Figure 2 seem periodic, we note that this is an artifact of the model. By looking only at expected values, we are averaging out the randomness of an individual run. An actual run would involve the stochastic nature of tournament selection (in the random selection of tournament competitors). Oei, et. al. (1991) predict chaotic behavior, calculating a Lyapunov exponent of approximately 0.21, even with only two niches. In the case of $k > 2$ niches, we can imagine that the oscillations would be so coupled as to always result in chaotic behavior.

2.2 Non-monotonic Convergence with Three Species

Horn (1997) analyzed the behavior and stability of resource sharing under proportionate selection. He looked at the existence and stability of equilibrium for all situations of overlap, but most of this analysis was limited to the case of only

two species. Horn did take a brief look at three overlapping niches, and found the following interesting result.

If all three pairwise niche overlaps are present (as in Figure 1), then it is possible to have non-monotic convergence to equilibrium. That is, one or more species can "overshoot" its equilibrium proportion, as in Figure 3. This overshoot is *expected*, and is not due to stochastic effects of selection during a single run. We speculate that this "error" in expected convergence is related to the increased complexity of the niching equilibrium equations. For three mutually overlapped niches, the equilibrium condition yields a system of cubic equations to solve. Furthermore, the complexity of such equations for k mutually overlapping niches can be shown to be bounded from below: the equations must be polynomials of degree $2k - 3$ or greater (Horn, 1997).

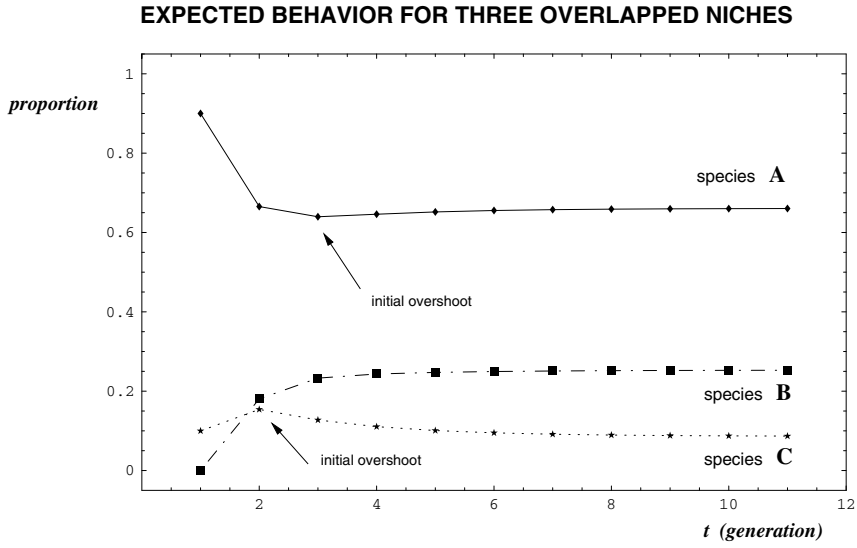

Fig. 3. Small, initial oscillations even under traditional "summed fitness".

3 Phytoplankton Models of Resource Sharing

Recent work by two theoretical ecologists (Huisman & Weissing, 1999; 2001), has shown that competition for resources by as few as three species can result in long-term oscillations, even in the traditionally convergent models of plankton species growth. For as few as five species, apparently chaotic behavior can emerge. Huisman and Weissing propose these phenomena as one possible new explanation of the *paradox of the plankton*, in which the number of co-existing plankton species far exceeds the number of limiting resources, in direct contradiction of theoretical predictions. Continuously fluctuating species levels can

support more species than a steady, stable equilibrium distribution. Their results show that external factors are not necessary to maintain non-equilibrium conditions; the inherent complexity of the "simple" model itself can be sufficient.

Here we attempt to extract the essential aspects of their models and duplicate some of their results in our models of resource sharing in GAs. We note that there are major differences between our model of resource sharing in a GA and their "well-known resource competition model that has been tested and verified extensively using competition experiments with phytoplankton species" (Huisman & Weissing, 1999). For example, where we assume a fixed population size, their population size varies and is constrained only by the finite resources themselves. Still, there are many similarities, such as the sharing of resources.

3.1 Differential Competition

First we try to induce oscillations among multiple species by noting that Huisman and Weissing's models allow *differential competition* for overlapped resources. That is, one species **I** might be better than another species **J** when competing for the resources in their overlap f_{IJ}. Thus species **I** would obtain a greater share of f_{IJ} than would **J**. In contrast, our models described above all assume equal competitiveness for overlapped resources, and so we have always divided the contested resources evenly among species.

Now we try to add this differential competition to our model. In the phytoplankton model, c_{ij} denotes the *content* of resource i in species j. In our model we will let $c_{I,IJ}$ denote the competitive advantage of species **I** over species **J** in obtaining the resource f_{IJ}. Thus $c_{A,AB} = 2.0$ means that **A** is twice as good as **B** at obtaining resources from the overlap f_{AB}, and so **A** will receive twice the share that **B** gets from this overlap:

$$f_{sh,A} = \frac{f_A - f_{AB}}{n_A} + \frac{c_{A,AB} * f_{AB}}{c_{A,AB} * n_A + n_B} \qquad f_{sh,B} = \frac{f_B - f_{AB}}{n_B} + \frac{f_{AB}}{c_{A,AB} * n_A + n_B}. \tag{3}$$

This generalization[4] seems natural. What can it add to the complexity of multispecies competition? We looked at the expected evolution of five species, with pairwise niche overlaps and different competitive resource ratios. After some experimentation, the most complex behavior we were able to generate is a "double overshoot" of equilibrium by a species, similar to Figure 3. This is a further step away from the usual monotonic approach to equilibrium, but does not seem a promising way to show long-term oscillations and non-equilibrium dynamics.

3.2 The Law of the Minimum

Differential competition does not seem to be enough to induce long-term oscillations in our GA model of resource sharing. We note another major difference

[4] Note that we get back our original shared fitness formulae by setting all competitive factors $c_{I,IJ}$ to one.

between our model and the Plankton model. Huisman and Weissing (2000) "assume that the specific growth rates follow the Monod equation, and are determined by the resource that is the most limiting according to Liebig's 'law of the minimum':

$$\mu_i(R_1, ..., R_k) = min\left(\frac{r_i R_1}{K_{1i} + R_1}, ..., \frac{r_i R_{1k}}{K_{ki} + R_k}\right)" \tag{4}$$

where R_i are the k resources being shared.

Since a *min* function can sometimes introduce "switching" behavior, we attempt to incorporate it in our model of resource sharing. Whereas we simply summed the different components of the shared fitness expression (Equation 1), we might instead take the minimum of the components:

$$f_{sh,A} = min\left(\frac{f_A - f_{AB} - f_{AC}}{n_A}, \frac{c_{A,AB} * f_{AB}}{c_{A,AB} * n_A + n_B}, \frac{c_{A,AC} * f_{AC}}{c_{A,AC} * n_A + n_C}\right). \tag{5}$$

Note that we have added the competitive factors introduced in Equation 3 above. We want to use differential competition to induce a *rock-paper-scissors* relationship among the three overlapping species, as in (Huisman & Weissing, 1999). To do so, we set our competitive factors as follows: $c_{A,AB} = 2$, $c_{B,BC} = 2$, and $c_{C,AC} = 2$, with all other $c_{I,IJ} = 1$. Thus **A** "beats" **B**, **B** beats **C**, and **C** beats **A**. These settings are meant to induce a cyclical behavior, in which an increase in the proportion of species **A** causes a decline in species **B** which causes an increase in **C** which causes a decline in **A**, and so on.

Plugging the shared fitness of Equation 5 into the expected proportions of Equation 2, we plot the time evolution of expected proportions in Figure 4, assuming starting proportions of $P_{A,0} = 0.2$, $P_{B,0} = 0.5$, $P_{C,0} = 0.3$. Finally, we see the "non-transient" oscillations that Huisman and Weissing were able to find. These follow the rock-paper-scissors behavior of sequential ascendency of each species in the cycle.

3.3 Five Species and Chaos

Huisman and Weissing were able to induce apparently chaotic behavior with as few as five species (in contrast to the seemingly periodic oscillations for three species). Here we attempt to duplicate this effect in our modified model of GA resource sharing.

In (Huisman & Weissing, 2001), the authors set up two rock-paper-scissors "trios" of species, with one species common to both trios. This combination produced chaotic oscillations. We attempt to follow their lead by adding two new species **D** and **E** in a rock-scissors-paper relationship with **A**. In Figure 5 we can see apparently chaotic oscillations that eventually lead to the demise of one species, **C**. The loss of a species seems to break the chaotic cycling, and it appears that immediately a stable equilibrium distribution of the four remaining species is reached.

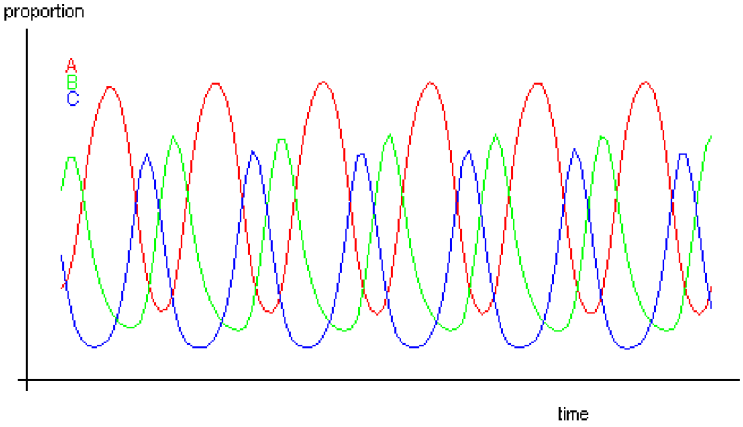

Fig. 4. Permanent oscillations.

We consider the extinction of a member species to signify the end of a trio. We can then ask which trio will win, given a particular initial population distribution. Huisman and Weissing found in their model that the survival of each species, and hence the success of the trios, was highly dependent on the initial conditions, such as the initial species counts. They proceeded to generate fractal-like images in graphs in which the independent variables are the initial species counts and the dependent variable, dictating the color at that coordinate, is the identity of the winning (surviving) trio.

Here we investigate whether our model can generate a fractal-like image based on the apparently chaotic behavior exhibited in Figure 5. We choose to vary the initial proportions of species **B** (x-axis), and **D** (y-axis). Since we assume a fixed population size (unlike Huisman and Weissing), we must decrease other species' proportions as we increase another's. We choose to set $P_{C,0} = 0.4 - P_{B,0}$ and $P_{E,0} = 0.4 - P_{D,0}$, leaving $P_{A,0} = 0.2$. Thus we are simply varying the ratio of two members of each trio, on each axis. Only the initial proportions vary. All other parameters, such as the competitive factors and all of the fitnesses, are constant.

Since our use of proportions implies an infinite population, we arbitrarily choose a threshold of 0.000001 to indicate the extinction of a species, thus simulating a population size of one million. If $P_{X,t}$ falls below $\frac{1}{N} = 0.000001$, then species **X** is considered to have gone extinct, and its corresponding trio(s) is considered to have lost. In Figure 6 we plot the entire range of feasible values of $P_{B,0}$ and $P_{C,0}$. The resolution of our grid is 400 by 400 "pixels". We color each of the 160,000 pixels by iterating the expected proportions equations (as in Equation 5) until a species is eliminated or until a maximum of 300 generations is reached. We then color the pixel as shown in the legend of Figure 6: red for

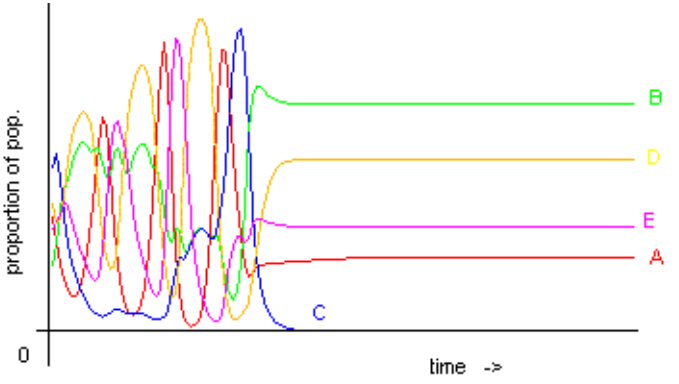

Fig. 5. Chaotic, transient oscillations leading to extinction.

a win by trio ABC, blue for an ADE win, and yellow if neither trio has been eliminated by the maximum number of generations[5].

Figure 6 exhibits fractal characteristics, although further analysis is needed before we can call it a fractal. But we can gain additional confidence by plotting a much narrower range of initial proportion values and finding similar complexity. In Figure 7 we look at a region from Figure 6 that is one one hundredth the range along both axes, thus making the area one ten thousandth the size of the plot in Figure 6. We still plot 400 by 400 pixels, and at such resolution we see no less complexity.

3.4 Discussion

How relevant are these results? The most significant change we made to GA resource sharing was the substitution of the *min* function for the usual Σ (sum) function in combining the components of shared fitness. How realistic is this change?

For theoretical ecologists, Liebig's *law of the minimum* is widely accepted as modeling the needs of organisms to reproduce under competition for a few limited resources. In the case of phytoplankton, resources such as nitrogen, iron, phosphorus, silicon, and sunlight are all critical for growth, so that the least available becomes the primary limiting factor of the moment. We could imagine a similar situation for simulations of life, and for artificial life models. Instances from other fields of applied EC seem plausible. For example, one could imagine the evolution of robots (or robot strategies) whose ultimate goal is to assemble "widgets" by obtaining various widget parts from a complex environment (e.g.,

[5] We also use green to signify that species **A**, a member of both trios, was the first to go. But that situation did not arise in our plots.

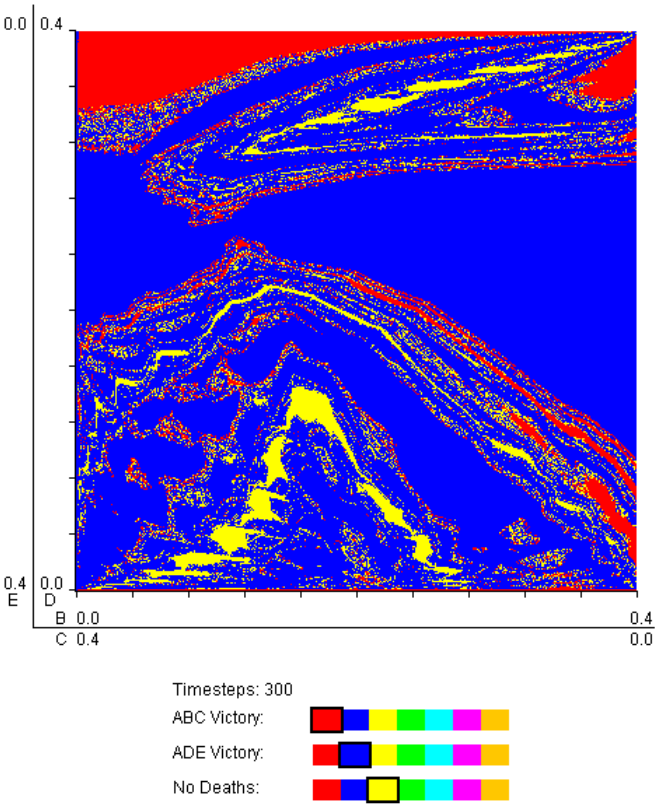

Fig. 6. An apparently fractal pattern.

a junkyard). The number of widgets that a robot can assemble is limited by the part which is hardest for the robot to obtain. If the stockpile of parts are "shared" among the competing robots, then indeed the law of the minimum applies.

4 Conclusions and Future Work

There seem to be many ways to implement resource sharing with oscillatory and even chaotic behavior. Yet resource (and fitness) sharing are generally associated with unique, stable, steady-state populations of multiple species. Indeed, the oscillations and chaos we have seen under sharing are better known and studied in the field of *evolutionary game theory* (EGT), in which species compete pairwise according to a payoff matrix, and selection is performed based on each individual's total payoff.

For example, Ficici, et. al. (2000) found oscillatory and chaotic behavior similar to that induced by *naïve tournament sharing*, but for other selection

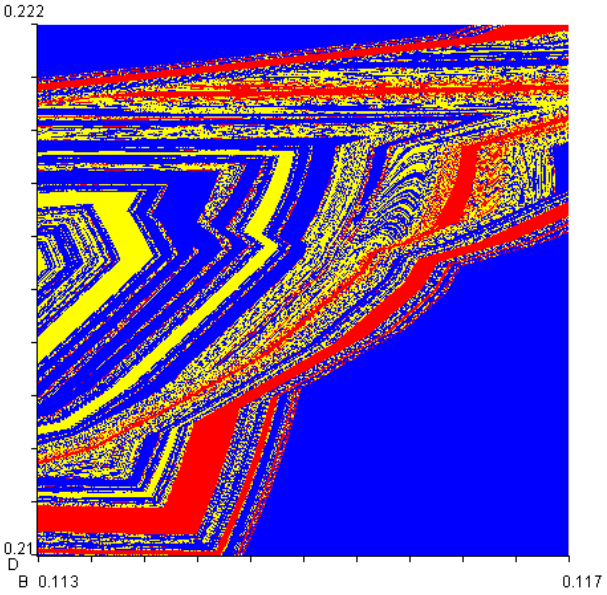

Fig. 7. Zooming in on $\frac{1}{10{,}000}^{th}$ of the previous plot.

schemes (e.g., truncation, linear-rank, Boltzmann), when the selection pressure was high. Although they did not analyze fitness or resource sharing specifically, their domain, the *Hawk-Dove* game, induces a similar coupling (Lotka-Volterra) between two species.

Another example of a tie-in with EGT is the comparison of our rock-paper-scissors, five-species results with the work of Watson and Pollack (2001). They investigate similar dynamics arising from "intransitive superiority", in which a species **A** beats species **B** which beats species **C** which beats **A**, according to the payoff matrix.

Clearly there is a relationship between the interspecies dynamics introduced by resource sharing and those induced by pairwise games. There are also clear differences, however. While resource sharing adheres to the principal of conservation of resources, EGT in general involves non-zero-sum games. Still, it seems that a very promising extension of our findings here would be mapping resource sharing to EGT payoff matrices.

It appears then that some of the unstable dynamics recently analyzed in theoretical ecology and in EGT can find their way into our GA runs via resource sharing, once considered a rather weak, passive, and predictable form of species interaction. In future, we as practitioners must be careful not to assume the existence of a unique, stable equilibrium under every regime of resource sharing.

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