

Evolutionary design vs. optimal design: some observations

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The population dynamics of biological systems are defined in terms of fitness. Fitness is a function of strategies used by the organisms. When these strategies are chosen so as to maximize fitness then this is referred to as optimal design. When the strategies are determined by means of an evolutionary process, then this is referred to as evolutionary design. Evolutionary design may lead to an evolutionarily stable strategy (ESS). These two methods for determining strategies will generally yield different results. Organisms using optimal design are usually unable coexist with an organisms employing an ESS. However there are some interesting situations in which optimal design may have a role to play. Two such situations are examined here. The first situation is one in which both optimal design and evolutionary design lead to the same results. This situation becomes interesting when an ESS does not exist. The second situation is when an ESS strategy exists, but where it is possible for optimal design to mimic the ESS.

1 Introduction

Consider a population of n_s different species. The scalar x_i represents the number or density or biomass¹ of individuals of species i and the vector \mathbf{x} to represent the population densities of the n_s different species.

$$\mathbf{x} = [x_1 \quad \cdots \quad x_{n_s}] .$$

All individuals in the population are identified by the heritable phenotypes or strategies which characterize that individual as belonging to a particular species. In order to simplify analysis scalar strategies are assumed in this presentation. The notation u_i is used to denote the strategy (e.g. bill length) of individuals of species i . The vector of all strategies used by all the species in the population is given by

$$\mathbf{u} = [u_1 \quad \cdots \quad u_{n_s}] .$$

¹Since populations may be measured in terms of number, density, or biomass, all of these terms are used interchangeably.

Population dynamics equations of the form

$$\dot{x}_i = x_i H_i(\mathbf{u}, \mathbf{x}) \quad (1)$$

where, by definition, $H_i(\mathbf{u}, \mathbf{x})$ is the fitness of individuals of species i . In general, the fitness of an individual is a function of the density and strategy used by all individuals in the population.

Evolutionary design may be determined using evolutionary game theory (Vincent & Brown 2005). The fitness generating function concept plays an important role in this theory. A function $G(v, \mathbf{u}, \mathbf{x})$ is said to be a fitness generating function (G -function) for the population dynamics if and only if

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_i} = H_i(\mathbf{u}, \mathbf{x}) \quad i = 1, \dots, n_s \quad (2)$$

where \mathbf{u} and \mathbf{x} in G are exactly the same vectors as in H_i . In terms of the G -function, the population dynamic equations are written as

$$\dot{x}_i = x_i G(v, \mathbf{u}, \mathbf{x})|_{v=u_i} \quad (3)$$

The theory predicts that strategies evolve according to a strategy dynamic given by

$$\dot{u}_i = \sigma^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v} \Big|_{v=u_i} \quad (4)$$

Equations (3) and (4) solved together (Darwinian dynamics) will often result in an equilibrium solution for \mathbf{x} and \mathbf{u} . Such a solution is an evolutionary design. The non-zero solutions for x_i and their associated u_i form a coalition of strategies. If these strategies are able to resist invasion by other species with other (mutant) strategies, they are called evolutionarily stable strategies² (ESS). A necessary condition for an ESS is that the G -function takes on a maximum with respect to v . The ESS represents evolutionary design

We will also find it informative to compare evolutionary design with optimal design. That is a design process that maximizes fitness. There are a lot of options for strategy dynamics under optimal design. However, the trajectory following gradient algorithm (Vincent 2000), (Vincent & Grantham 2002) of the form

$$\dot{u}_i = \frac{\partial H_i(\mathbf{u}, \mathbf{x})}{\partial u_i} \quad (5)$$

provides an optimizing algorithm that resembles (4). This latter equation will generally result in a different dynamic for u_i with a different equilibrium solution. Equations (1) and (5) solved together (optimal dynamics) will generally result in a solution for \mathbf{x} and \mathbf{u} that maximizes the H_i functions. These optimal solutions represents optimal design.

There are three different dynamic outcomes of interest. Starting with a given number of species n_s with given starting densities $x_i(0)$ and strategies $u_i(0)$ $i = 1, \dots, n_s$ we will be interested in the equilibrium conditions obtained under:

²The formal definition as given in (Vincent & Brown 2005) requires, in addition, that an ESS be convergent stable

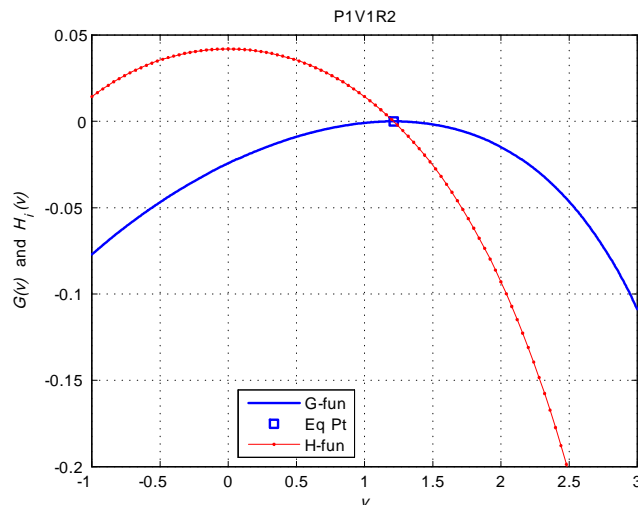


Figure 1: The adaptive landscape and the fitness landscape are generally different.

1. Population dynamics: Solutions obtained using (3) with fixed strategies $\mathbf{u} = \mathbf{u}(\mathbf{0})$.
2. Darwinian dynamics: Solutions obtained using (3) and (4).
3. Optimal dynamics. Solutions obtained using (1) and (5).

In general, the first will lead to results that are neither evolutionarily stable or are at maximum fitness. The second yields an evolutionary design that may or may not be evolutionarily stable and may or may not be at maximum fitness. The third yields an optimal design that is at maximum fitness but need not be evolutionarily stable.

A plot of $G(v, \mathbf{u}, \mathbf{x})$ vs. v for fixed \mathbf{u} and \mathbf{x} is called an **adaptive landscape**. Such a plot gives graphic information about the evolutionary stability of a particular strategy. Briefly, when \mathbf{u} and \mathbf{x} are at equilibrium, an evolutionarily stable strategy (ESS) must correspond to a global maximum on the adaptive landscape. This is known as the ESS maximum principle (Vincent & Brown 2005). In a somewhat similar fashion, a plot of $H_i(\mathbf{u}, \mathbf{x})$ vs. u_i for fixed \mathbf{x} and all strategies in \mathbf{u} fixed except for u_i , called a **fitness landscape**, graphically illustrates how the fitness of cells of type i will change with strategy under the given conditions. We can plot both of these functions together by designating the adaptive landscape plot by $G(v)$ and the fitness plot by $H_i(v) = G(u_i, \mathbf{u}, \mathbf{x})|_{u_i=v}$ (replacing u_i by v provides a fitness function definition that can be plotted vs. v). In general, a plot of the adaptive landscape and a plot of a given fitness function do not coincide as illustrated in Figure 1. In summary

1. A plot of $G(v, \mathbf{u}, \mathbf{x})$ vs. v for fixed \mathbf{u} and \mathbf{x} is called an adaptive landscape.
2. A plot of $H_i(\mathbf{u}, \mathbf{x})$ vs. u_i for fixed \mathbf{x} and all strategies in \mathbf{u} fixed except for u_i , called a fitness landscape.

3. Both can be plotted together by designating the adaptive landscape plot by $G(v)$ and the fitness plot by $H_i(v) = G(v, \mathbf{u}|_{u_i=v}, \mathbf{x})$

It is usually easier to work in terms of just G -functions rather than both the G -functions and H -functions when doing simulations. By definition (1) and (3) are identical and by making note that

$$\frac{\partial H_i(\mathbf{u}, \mathbf{x})}{\partial u_i} = \frac{\partial G(v, \mathbf{u}|_{u_i=v}, \mathbf{x})}{\partial v} \Big|_{v=u_i} \quad (6)$$

(5) may be replaced by

$$\dot{u}_i = \frac{\partial G(v, \mathbf{u}|_{u_i=v}, \mathbf{x})}{\partial v} \Big|_{v=u_i} .$$

2 The first situation

The first situation occurs when Darwinian dynamics and optimal dynamics lead to the same equilibrium solutions. This will happen whenever there is either no frequency dependence in the model or when frequency dependence fortuitously drops out (Brown & Vincent 1987). The term frequency dependence implies that the fitness of any individual depends on the strategies used by all other individuals in the population. If there is no frequency dependence then

$$G(v, \mathbf{x})|_{v=u_i} = H_i(u_i, \mathbf{x}) \quad i = 1, \dots, n_s.$$

Consider equilibrium under unbounded strategies. Under Darwinian dynamics equilibrium requires

$$\begin{aligned} G(v, \mathbf{x}^*)|_{v=u_i} &= 0 \\ \frac{\partial G(v, \mathbf{x}^*)}{\partial v} \Big|_{v=u_i} &= 0 \end{aligned}$$

and under optimal dynamics, we obtain the same equilibrium requirement is obtained

$$\begin{aligned} H_i(u_i, \mathbf{x}^*) &= G(v, \mathbf{x}^*)|_{v=u_i} = 0 \\ \frac{\partial H_i(u_i, \mathbf{x}^*)}{\partial u_i} &= \frac{\partial G(v, \mathbf{x}^*)}{\partial v} \Big|_{v=u_i} = 0. \end{aligned}$$

However it is also possible, when fitness is a function of all other strategies, for frequency dependence to "drop out" at equilibrium. This will happen when the equilibrium conditions for Darwinian dynamics and optimal dynamics give the same results, that is

Darwinian		Optimal
$G(v, \mathbf{u}, \mathbf{x}^*) _{v=u_i}$	=	$H_i(\mathbf{u}, \mathbf{x}^*)$
$\frac{\partial G(v, \mathbf{u}, \mathbf{x}^*)}{\partial v} \Big _{v=u_i}$	=	$\frac{\partial H_i(\mathbf{u}, \mathbf{x}^*)}{\partial u_i}$

The first condition is true by definition. From (6) it follows that the second condition will be true when

$$\left. \frac{\partial G(v, \mathbf{u}, \mathbf{x}^*)}{\partial v} \right|_{v=u_i} = \left. \frac{\partial G(v, \mathbf{u}|_{u_i=v}, \mathbf{x}^*)}{\partial v} \right|_{v=u_i} \quad (7)$$

Note that (7) is trivially satisfied when there is no frequency dependence.

The first case will be examined using the Lotka-Volterra competition model that has been extensively studied in an evolutionary setting (Case 1982), (Rummel & Roughgarden 1983), (Vincent, Cohen & Brown 1993). In this basic model the strategies are scalars and the fitness function for a given species i , is given by

$$H_i(\mathbf{u}, \mathbf{x}) = r - \frac{r}{K(u_i)} \sum_{j=1}^{n_s} \alpha(u_i, u_j) x_j,$$

where n_s is the total number of different species currently in the community, r is the intrinsic growth rate common to all species, $K(u_i)$ is the carrying capacity of species i , and $\alpha(u_i, u_j)$ is the competitive effect of species j using strategy u_j on the fitness of individuals of species i using strategy u_i . Provided that all species possess the same set of evolutionarily feasible strategies and experience the same fitness consequences of possessing a given strategy within a given environment, the fitness function for any species may be obtained from the following G -function (Vincent & Brown 2005)

$$G(v, \mathbf{u}, \mathbf{x}) = r - \frac{r}{K(v)} \sum_{j=1}^{n_s} \alpha(v, u_j) x_j. \quad (8)$$

Evolving populations using scalar strategies with fitness determined from a single G -function with dynamics that lead to equilibrium solutions is the simplest case possible for the study of evolving populations. However, as with numerous other studies based on the simplest problem, one can gain useful insight without having to add complexity (multiple G functions, vector strategies, non-equilibrium dynamics, etc.).

We will make use of the K and α functions used in (Roughgarden 1983). That is,

$$K(v) = K_m \exp \left[-\frac{v^2}{2\sigma_k^2} \right] \quad (9)$$

and

$$\alpha(v, u_j) = \exp \left[-\frac{(v - u_j)^2}{2\sigma_a^2} \right]. \quad (10)$$

A nominal set of parameters are provided by

$$\begin{aligned} r &= 0.25 \\ K_m &= 100 \\ \sigma_\alpha^2 &= 4 \\ \sigma_k^2 &= 4 \end{aligned}$$

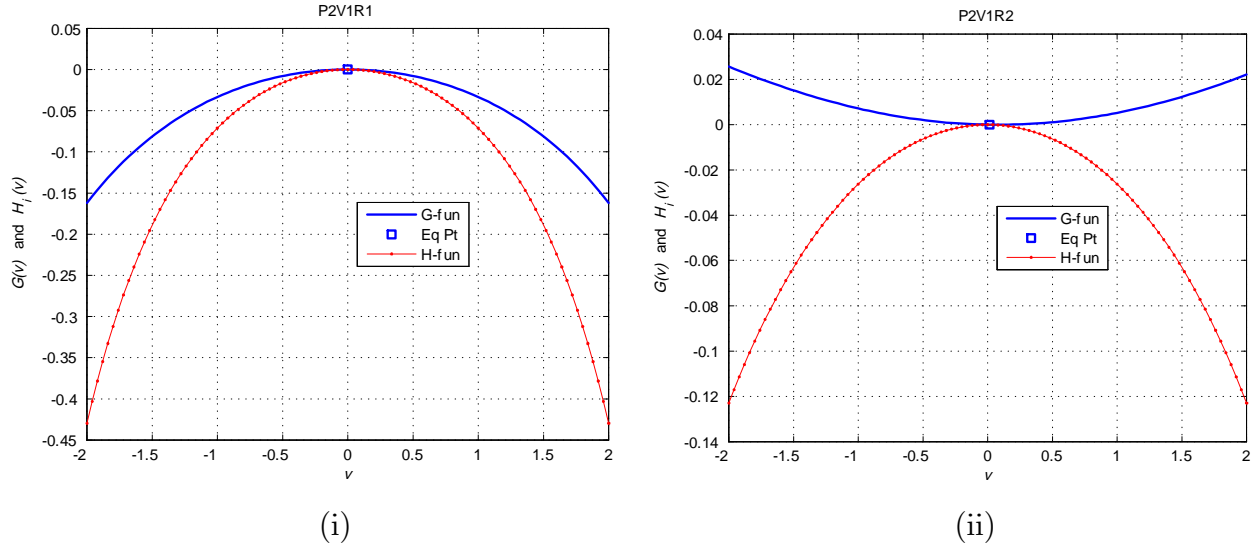


Figure 2: (i) When $\sigma_k < \sigma_\alpha$ there exists an ESS coalition of one. Optimal design and evolutionary design produce the same result. (ii) When $\sigma_k > \sigma_\alpha$ there is no ESS solution. However optimal design and evolutionary design produce the same results.

For this particular model (7) is satisfied so that both Darwinian dynamics and optimal dynamics yield the same results. However only when $\sigma_k < \sigma_\alpha$ does there exist an ESS solution. In this case resources are limited in the sense that for all values of v other than the ESS at \mathbf{x}^*

$$\sum_{j=1}^{n_x} \exp \left[-\frac{(v - u_j)^2}{2\sigma_a^2} \right] x_j^* > K_m \exp \left[-\frac{v^2}{2\sigma_k^2} \right].$$

These expressions are equal at equilibrium. Figure 3(i) illustrates this situation by changing the nominal value of σ_k^2 to $\sigma_k^2 = 2$. The strategy $u_1 = 0$ both maximizes the fitness function and the G -function. As such it is both an ESS and provides the maximum possible equilibrium population size of $x_1 = 100$. When $\sigma_k > \sigma_\alpha$ an ESS no longer exists (under an unbounded strategy set) as illustrated in Figure 3(ii) with $\sigma_k^2 = 5$. In this case resources are unlimited in the sense that for all values of v other than the optimal value at \mathbf{x}^*

$$\sum_{j=1}^{n_x} \exp \left[-\frac{(v - u_j)^2}{2\sigma_a^2} \right] x_j^* < K_m \exp \left[-\frac{v^2}{2\sigma_k^2} \right].$$

The strategy $u_1 = 0$ results in maximizing fitness (with a population size of $x_1^* = 100$), however this strategy is easily invaded as illustrated in Figure 3(i). After the system reaches equilibrium neither strategy is at maximum fitness, however if the system is allowed to evolve by means of either evolutionary or optimal design a new equilibrium is obtained as illustrated in Figure 3(ii)

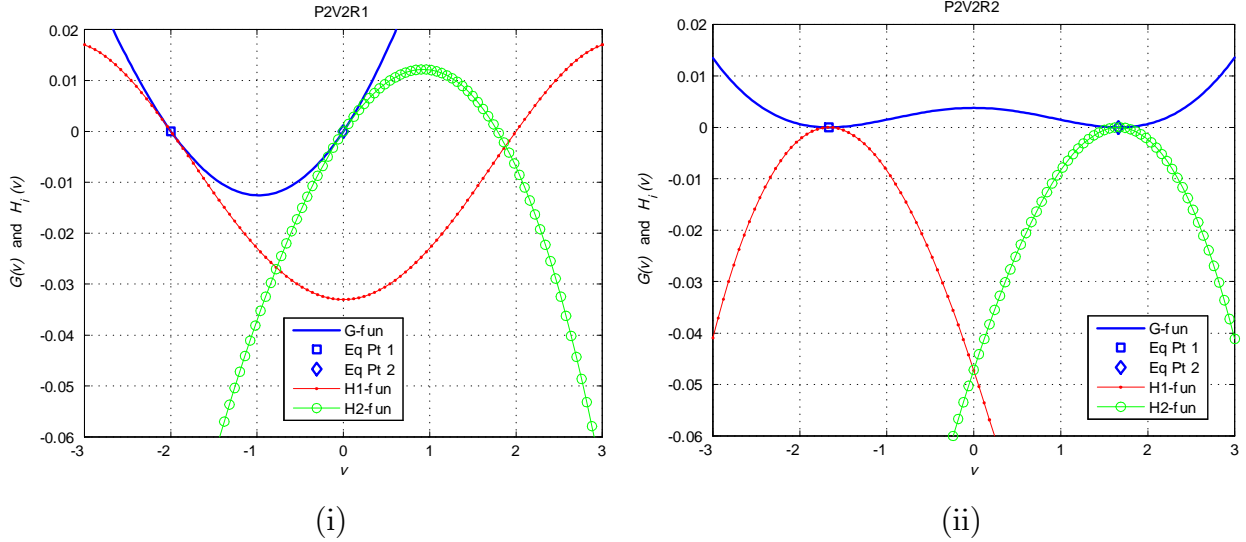


Figure 3: (i) An invading strategy can coexist with the strategy $u = 0$. When $\mathbf{u} = [-2 \ 0]$, the equilibrium population is $\mathbf{x} = [33.5695 \ 79.6388]$. (ii) Both evolutionary and optimal design result in maximum fitness coexistence. The equilibrium solution is symmetric with $\mathbf{u} = [-1.6651 \ 1.6651]$ and $\mathbf{x} = [69.6439 \ 69.6439]$.

For example in Figure 4(i) the two invading strategies $u_2 = -1$, $u_3 = 1$ drives the species using $u_1 = 0$ to extinction ($x_1^* = 0, x_2^* = x_3^* = 59.21$). The first species is now at a fitness minimum. This result is obtained assuming fixed strategies using population dynamics (3) only. Note that the two invading fixed strategies are not at maximum fitness. Invasion results are not predictable. For example when $u_2 = -2$, $u_3 = 2$, all three strategies can coexist under fixed strategies ($x_1^* = 35.58, x_2^* = x_3^* = 53.11$). Again the invading strategies are not at maximum fitness as illustrated in in Figure 4(ii). If we use either Darwinian dynamics or optimal dynamics starting with these three strategies, the first strategy remains unchanged ($u_1 = 0$) but the second two evolve ($u_2 = -u_3 = 2.924$) and are driven to fitness maxima ($x_1^* = 72.76, x_2^* = x_3^* = 39.68$) as illustrated in Figure 5(i). Note that when all three strategies are at fitness maxima, the total biomass is greater than in the previous case. Figure 5(ii) illustrate coexistence of four optimal design strategies. Additional strategies can coexist maintaining this symmetric arrangement. For example, adding the strategy $u = 0$ to this case and then rerunning the Darwinian dynamics or optimal dynamics redistributes the four strategies so that there are now five strategies at fitness maxima. It is apparent that coexistence of any number of strategies is possible when there is no ESS but when Darwinian dynamics and under optimal design.

Interestingly, as the number of optimal coexisting strategies increase, the strategies together provide some resistance to invasion by mutant strategies. This is illustrated in Table 1 where optimal design coalitions of 1 to 4 are played against a mutant strategy and the

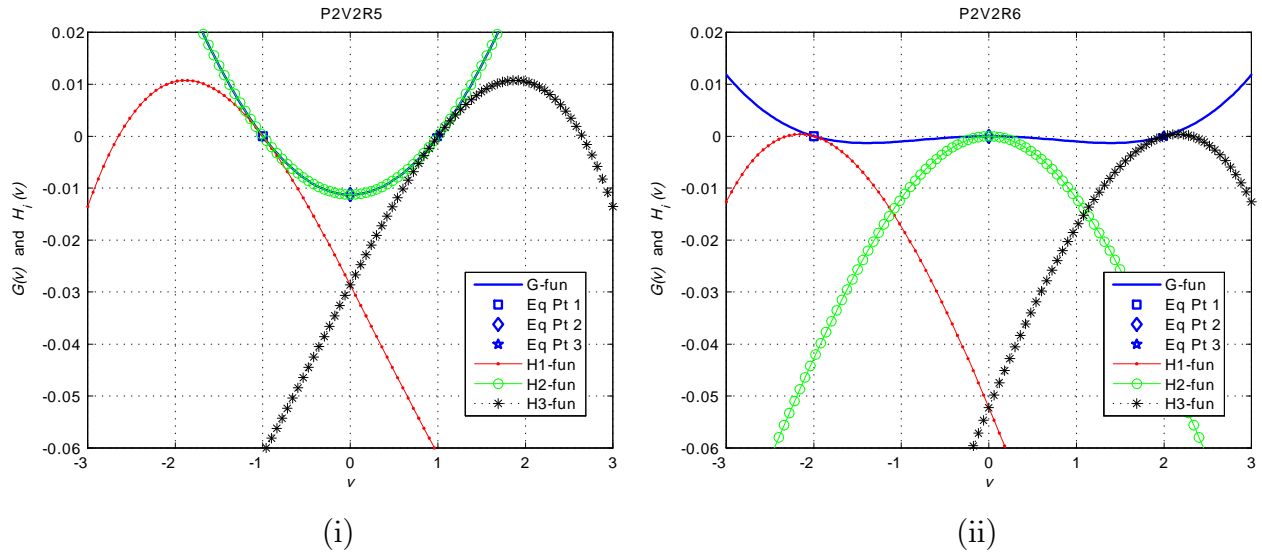


Figure 4: (i) Two symmetric strategies invade driving the species with the optimal strategy to extinction. (ii) Two invading strategies can also result in coexistence of three strategies.

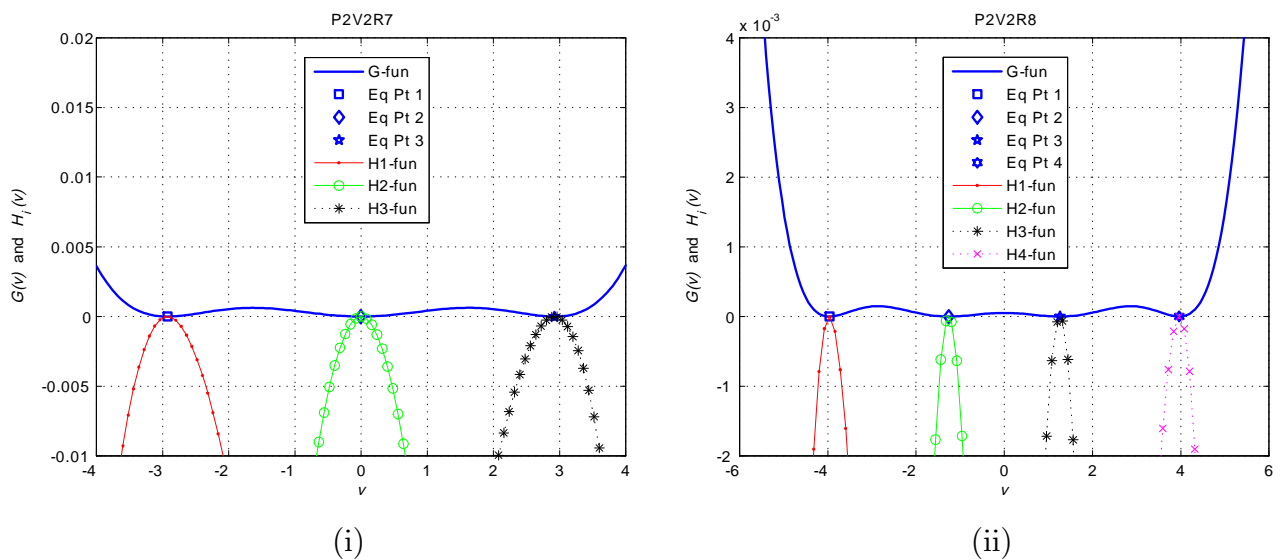


Figure 5: (i) Three strategies using optimal design. (ii) An optimal design coalition of four provides protection for invasion of mutant strategies.

simulation run until equilibrium is obtained. The first column gives the optimal strategy coalition and the equilibrium populations associated with the coalition. After a mutant strategy of $u = 2$ is added to this mix at a population of $x = 50$, this population will die back with time as it competes with the species using the other fixed strategies. This result is given in column two where the last entry in the vector \mathbf{x} is the equilibrium value of the mutant. The other elements of the vector give the equilibrium values for the other species and may be compared with equilibrium values before the mutant is added. Note that some rearrangement in population equilibrium values (strategy values are fixed) is obtained. With a large enough optimal coalition, the coalition population remains unchanged and the mutant population approaches zero.

Optimal design coalition + Mutant ($u_i = 2, x_i(0) = 50$) = new equilibrium					(depends somewhat on u_i)					
$u_1 = [0], x_1 = [100]$					$\mathbf{x} =$	79.6	33.6			
$\mathbf{u} =$	-1.67	1.67	$, \mathbf{x} =$ 69.64 69.64		$\mathbf{x} =$	70.2	60.9	8.7		
$\mathbf{u} =$	-2.93	0	2.93	$, \mathbf{x} =$ 39.6 72.6 39.6	$\mathbf{x} =$	39.8	72.0	38.2	1.9	
$\mathbf{u} =$	-3.97	-1.27	1.27	3.97	$, \mathbf{x} =$ 20.6 57.56 57.56 20.6	$\mathbf{x} =$	20.5	57.6	56.9	20.4 0.7

Table 1. Adding the same mutant to an increasing number of optimal strategies decreases its ability to invade.

This result has some interesting implications. In a biological situation where Darwinian dynamics and optimal design lead to the same results, but were there is no ESS, the introduction of new species is simple and natural. This could have paved the way for a rapid increase in the number of species in early life. Cellular structure may operate in such an environment where the requirement of many coexisting cellular types must be derived from a common stem cell. The resistance to invasion of non-evolving mutant type provides stability for the system and may account for the "social" constraints present in cells that strives for perfect clonal reproduction. When this structure breaks down a mutant can avoid extinction by evolving to a strategy that allows coexistence.

When the strategy set is unbounded and if (7) is satisfied then:

1. Darwinian dynamics and optimal dynamics yield the same results
2. When an ESS exists, it is also at maximum fitness.
3. When there is no ESS, a large optimal-coalition of fixed strategies can resist invasion by a mutant strategy.

3 The second situation

If the ESS is frequency dependent, then the optimal solution and the ESS solution are no longer equal. For example, modifying the model given by (8) - (10) by replacing (10) with

$$\alpha(v, u_j) = 1 + \exp \left[-\frac{(v - u_j + \beta)^2}{2\sigma_a^2} \right] - \exp \left[-\frac{\beta^2}{2\sigma_a^2} \right]$$

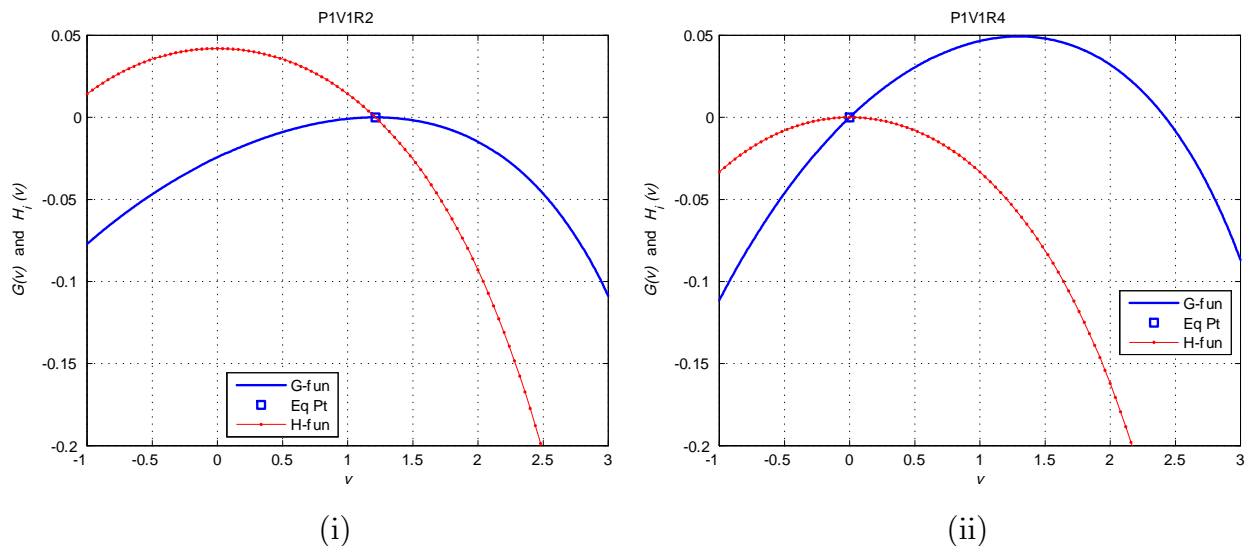


Figure 6: (i) With frequency dependence an ESS coalition of one does not maximize fitness. (ii) A single strategy optimal solution.

introduces a non-symmetric competition coefficients that, in turn, results in a frequency dependent solution for the ESS. Figure 6(i) is generated using

$$\begin{aligned}
 r &= 0.25 \\
 K_m &= 100 \\
 \sigma_\alpha^2 &= 4 \\
 \sigma_k^2 &= 4 \\
 \beta &= 2
 \end{aligned}$$

and it illustrates both the G -function and H -function for this case. The G -function takes on a maximum at an ESS solution of $u_1 = 1.2131$ at an equilibrium density of $x^* = 83.196$. This solution is clearly does not optimize H that has a maximum value to the left of the ESS.

The optimal solution for H with $u_1 = 0$ and $x^* = 100$ is illustrated in Figure 6(ii). The optimal solution maximizes the equilibrium population size, however it is not evolutionarily stable. This is easily tested by playing the ESS strategy and the optimal solution together. Regardless of the non-zero initial conditions provided, the population using the ESS solution always becomes dominate driving the optimal solution to extinction.

However when two or more optimal solutions are played together, the situation changes. Consider starting with two populations at non-zero population numbers at two different strategies. Using the trajectory following gradient algorithm, the H functions for each of these populations are maximized. The result is both populations coevolve to the same

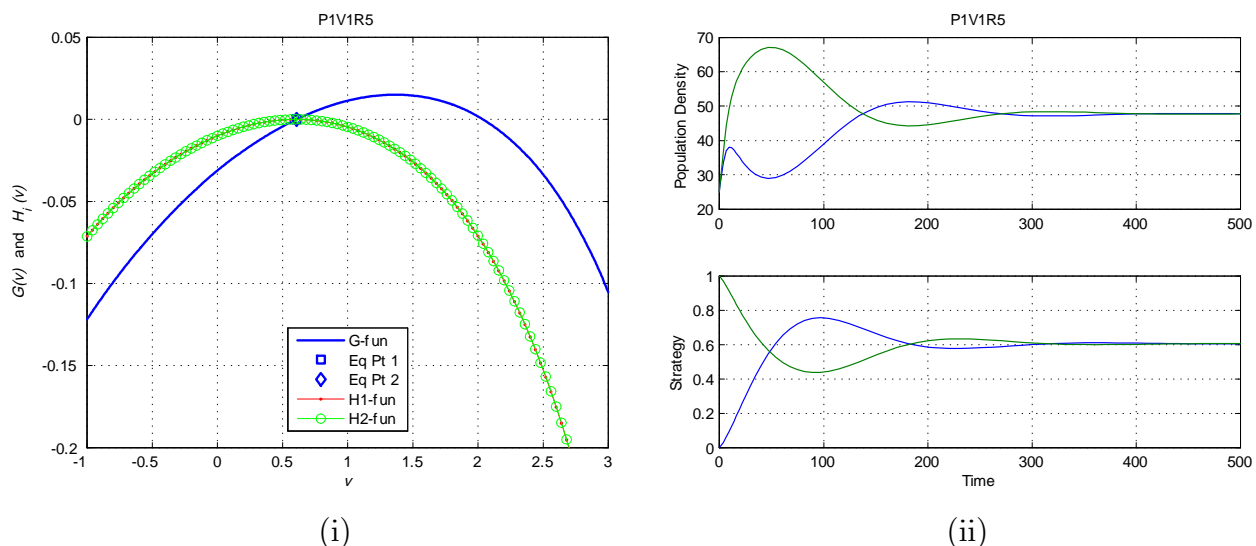


Figure 7: (i) The optimal solution for two strategies is the same and is closer to the ESS solution than with the single strategy case. (ii) Strategies and density oscillate before reaching equilibrium.

solution $u_1 = u_2 = 0.6065$ at $x_1^* = x_2^* = 47.75$. The two populations are distinct, but indistinguishable from each other in terms of this strategy (they may differ in other respects that do not influence their fitness functions, but never-the-less keep the two species from breeding with one another). Note that in going from optimizing a single strategy ($u_1 = 0$) to optimizing two strategies ($u_1 = u_2 = 0.6065$) the resultant strategy moves toward the ESS strategy. Also the sum of the two equilibrium populations is less than the value obtained for the single population. The two H functions lie on top of one another as illustrated in Figure 7(i).

This process can be continued. Starting with four different populations, the trajectory following gradient algorithm results in the optimal solution $u_i = 0.9098$ and $x_i^* = 22.54$ (sum = 90.16). This result is even closer to the ESS solution of $u_1 = 1.2131$, $x_1^* = 83.198$. Figure 8(i) with all four H functions on top of one another illustrates this result. Even though their common strategy is not an ESS, as a coalition, they behave somewhat like an ESS. For example, if these four fixed strategies are played against a fifth mutant strategy that is not near the ESS, they will continue to coexist and drive the mutant toward extinction. It is observed that optimizing a very large number of different populations will result in the situation where the H functions lie on top of the G -function. This result is constant with our previous observation that a very large number of optimizers (with very small equilibrium population sizes) will have a strategy very close to the ESS as may be easily demonstrated through simulation by increasing the number of species to 10 and beyond.

A comparison can be made the other way around by examining coexistence under Dar-

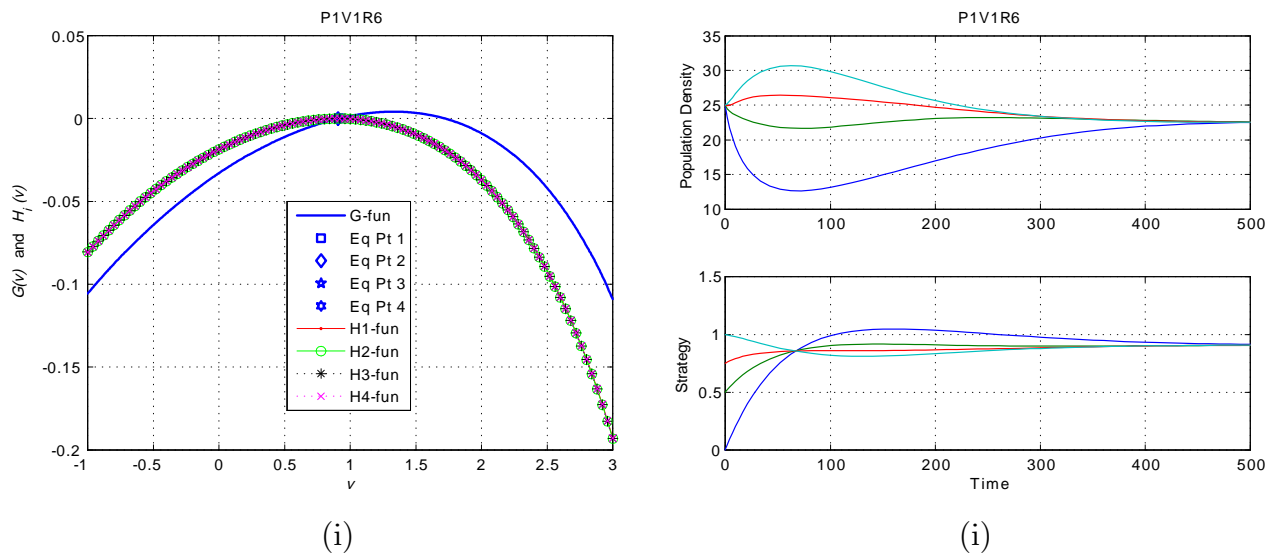


Figure 8: (i) Four optimal strategies more closely approximate the ESS solution. (ii) As more species are added, the equilibrium population for each is less.

winian dynamics. For example starting with the same four population with the same initial conditions that were used to produce Figure 8, but now used Darwinian dynamics to drive the system to equilibrium we obtain the result $u_i = 1.2131 \mathbf{x} = [2.16 \ 35.06 \ 33.11 \ 12.86]$ (sum = 83.198). This result illustrated in Figure 9(i) shows that none of the species (each using the ESS strategy) optimize their individual fitness functions. However the species with the smallest equilibrium number (H_1 designated with dots) is very close to having optimal fitness. As the number of species is further increased, density of each species decreases (sum remains at 83.198) with the individual H functions again lying on top of the G -function.

It appears that a single strategy ESS can be viewed in three different ways:

1. It is a single species that has evolved via Darwinian dynamics to a global maximum point on the adaptive landscape.
2. It is one or more distinct species that have coevolved via Darwinian dynamics to a global maximum point on the adaptive landscape. When the number of species is large, their densities will be small, but each of them will be at or near maximum fitness.
3. It is a large population of species that through optimal design are all playing the same strategy. They are all at maximum fitness and as a group will have the ESS property of being resistant to invasion from a mutant strategy.

It is not clear at this point what conclusions can be made for coalitions of two or more.

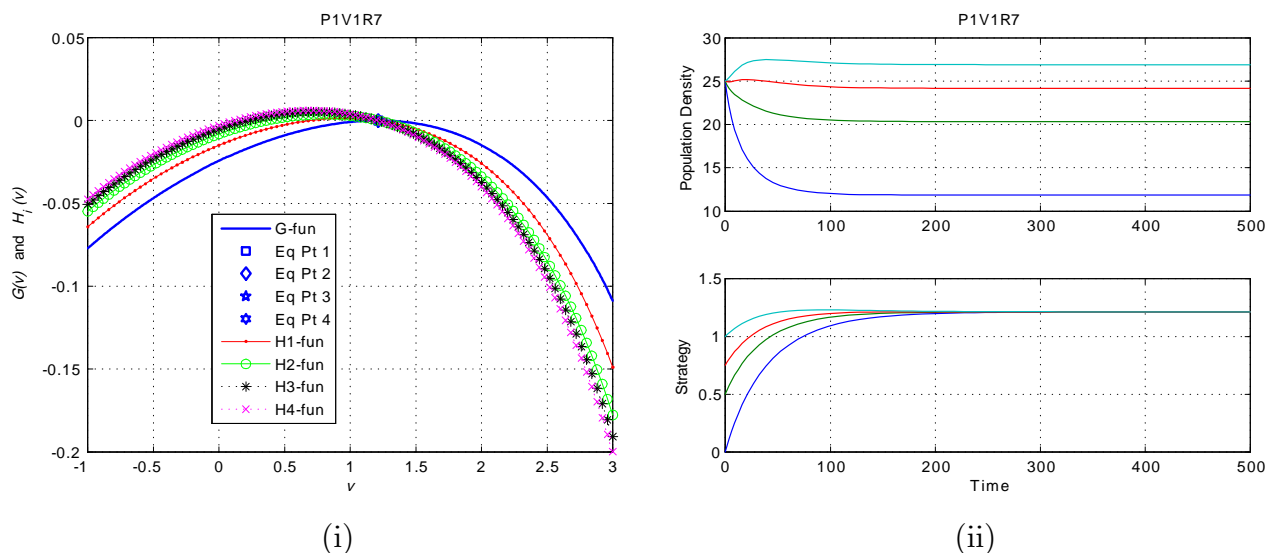


Figure 9: Under Darwinian dynamics, four species coevolve to the ESS. The sum of their densities is the same as the density of an ESS coalition of one.

4 Discussion

By replacing the words "optimal design" with "intelligent design" one could easily be lead down a philosophical path that we do not intend to take here. Never-the-less, it is curious that under the proper circumstance that optimization and evolution can lead to the same result.

Coexistence, adaptation, and speciation remain fundamental research topics in biology. All three topics are important in understanding the nature of life itself. The development of cells within the body in many ways mimics the development of early life forms. In the modeling of cell growth using evolutionary game methods, Gatenby & Vincent (2003) discovered an underlying reason why the strategies used by cells are "cooperative." In short, there are situation in which Darwinian evolution (under competition) and optimization (under cooperation) yield the same resultant strategy. It has become clear that the cooperative nature of cells plays a key role in allowing for the coexistence of a large number of similar, but different functioning cell types. This in turn allows for complex organisms composed of skin, blood, liver, etc. Unfortunately, unless carefully controlled (e.g. via DNA) a cooperative optimal strategy is always subject to cheating. The onset of cancer appears to not only be a breakdown in this control structure allowing for the coexistence in mutant cells, but the mutant cells themselves change the local environment so that Darwinian evolution for the mutant cells no longer results in a cooperative strategy. The mutant cells evolve to an evolutionarily stable state that defines the cancer.

In the first situation when there is no ESS and when Darwinian dynamics and optimal

design yields the same result, it is easy to see that this could be advantages to the early formation of complex organism where many different coexisting cell types are required. Later the situation could change with the introduction of frequency dependence. This would require the situation we have today where cells are under strict genetic code to reproduce as perfect clones.

The second situation could also follow from the first. That is initially Darwinian dynamics leads to a cooperative solutions involving many different types of closely related species. But then it turns out that when faced with a changing environment that evolves frequency dependence, they are using a strategy that allows them to continue to coexist.

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