

Introduction

Geometric approaches to the study of evolution are among us since Wright's adaptive landscape metaphor was posed. Adaptive landscapes are a tool frequently used in evolutionary thinking. Selection processes are studied traditionally as regression problems (Li 1967; Price 1970), or more recently as invasion processes, using adaptive landscapes dimensionally reduced (Geritz et al. 1998). Geometrical metaphors of evolution pervades the literature. In despite of such a success, it has been recently argued that such a metaphor lacks empirical support (Coyne et al. 1997). Therefore we need formulations of adaptive landscapes useful to deepen the current problems that a empiricist evolutionary biologist deals with.

In the early eighties, the pioneering work of E. Akin (Akin 1979) posed a vector field formulation of population genetics. His formulation predicted by first time fluctuating evolutionary dynamics without fluctuating selection, increasing the number of observed patterns accounted by theory. Nevertheless, Akin's work let interaction among different traits unaccounted. Life history theory starts considering interactions among traits relevant to fitness. Henceforth, a geometrical study of trait interactions is a desirable extension of Akin's work. Moreover, the last two decades brought new tools into the theoretical study of selection, as the adaptive dynamics framework. Their articulation into Akin's framework is desirable.

In the present note I attempt a formulation of selection on many interacting traits using a vector field as a main tool. Using a simplified version of the Price equation I will construct the two metric forms of a space in which three traits interact under selection. This section establishes links among the curl of a vector field and patterns arising from selection experiments. The gaussian curvature defines a measure of selection strength. In the next section of the paper I redefine the theoretical space in which selection takes place. Then I show how the gaussian curvature measures the success of an invading mutant, definition of fitness in the adaptive dynamics framework (Metz et al. 1992). This paper brings two points about selection on interacting traits, namely: a) It is possible to account for turbulent responses to selection with the curl of a vector field and b) Evolvability and invasibility are shown to be the same, using a vector field. An underlying theme runs through this note. Interacting traits and selection produce curvature in the space in which evolution takes place.

Price equation and metrics

The standard equations for evolutionary change under selection seems to have been formulated independently by Robertson, Li and Price in the sixties and early seventies. Price's work is the clearest derivation, allowing the incorporation of genetics effects in a straight way (Frank 1997). I will use the simplest expression of Price result, considering meiosis and recombination random in respect to the genes that are modeled. This keeps the model simple and by no means prevents other formulations of the genetics. A brief account of Price reasoning follows:

Consider two populations, parental and descendent. Individuals in each generation are indexed. In each individual there is a measurable trait z . The value of such a character in each individual comes from the dose g of a gene A in each individual. So the frequency of the gene A in one individual will be $q = g / n_z$, where n_z , stands for the zygotic ploidy of gene A . Correspondingly, the frequency of gene A in the population will be $Q_T = \Sigma g / n_z N$, being N the population size. A gamete from an individual i belonging to parental generation that contribute genes to the descendent generation will be considered as a successful gamete. Defining n_G as the gametic ploidy for gene A , z_i the number of successful gametes produced by individual i , g_i' the number of A genes in the set of successful gametes and q_i' the frequency of gene A in this set of gametes; the following holds:

$$\begin{aligned}
 Q_2 &= (\sum g_i') / \sum z_i n_G \\
 Q_2 &= \sum z_i q_i / N\bar{z} + \sum z_i \Delta q_i / N\bar{z} \\
 Q_2 &= \bar{q} + Cov(z, q) + \sum z_i \Delta q_i / N\bar{z}
 \end{aligned}$$

Equation 1,2 and 3

Being Q_2 the frequency of gene A in the descendent generation, and a roof – denoting the population average of the corresponding variable, the final equation for change in the frequency of a gene from parental to descendent generations becomes

$$\Delta Q = Cov(z, q)$$

Equation 4

if meiosis and recombination are random with respect to gene A (Price 1970). I recall here this well known relation to sustain my following definition of change in the frequencies of trait states under selection. I will use the first term of equation 2, leaving open the possibility of future use of the full equation in the determination of the metric form. This will be needed to incorporate genetic phenomena such as non randomness of meiosis or recombination in the transmission of each trait,.

Consider a trait X in a parental population and the frequencies of its n states as the set $\{x_1, \dots, x_i, \dots, x_n\}$. Using the previous reasoning, the frequencies of the states of X in the descendent generation (X') becomes

$$[x_i'] = [x_i f(x_i)]$$

Equation 5

and the change in average value of X correspond to

$$\Delta \bar{X} = \sum x_i' f(x_i) - \sum x_i$$

Equation 6

Here $f(x_i)$ stands for a arbitrary fitness function. If we take the infinitesimal model of quantitative genetics [Bulmer, 1980 #1669], we can think in the states of a trait as belonging to a continuous interval. In this case we consider $f(X)$ continuous and differentiable and along a differential of time it is true that

$$\Delta X = Xf'(X) - X$$

In the following it is assumed that f will remain fixed over evolutionary time, modeling density independent selection. Ways to include density-dependent selection are discussed later.

Now consider two characters more in the picture, namely X^2 and X^3 (so I rename X as X^1). Accordingly, lets define f , g and h as their fitness functions. Furthermore, lets define a trait space of average values, T , in which each dimension correspond to the average value of a trait. It is easy to see that if selection on X^1 , X^2 and X^3 is independent, namely that each fitness function only depends on the state of the same trait in the past generation, the available displacement on trait space along time is a n-dimensional ball, a sphere in the case of three traits. The expression for T follows and the displacement of averages values is depicted in Fig. 1a.

$$T = X^1 f(X^1) \hat{i} + X^2 g(X^2) \hat{j} + X^3 h(X^3) \hat{k} \quad \text{Equation 7}$$

This expression corresponds to the case in which the evolution of each trait is independent of each other. But I am interested in the evolution of traits that

constrain each other. Lets introduce relations connecting the traits under study. First suppose that one trait is a composite of the two others. Namely $x^3=C(x^1,x^2)$. C stands for any function that goes from the pair (x^1,x^2) to the corresponding x^3 . If this is the case, the space of interest in which the average values of the population will change is not anymore a sphere, but a generalized surface. Accordingly, the subset of T that interests me now is a space totally determined by the evolution of the traits X^1 and X^2 . The graphical representation of this new subset of the whole space is depicted in Fig. 1b.

$$T = X^1 f(X^1) \hat{i} + X^2 g(X^2) \hat{j} + C(X^1, X^2) h(C(X^1, X^2)) \hat{k} \quad \text{Equation 8}$$

8

The analysis of an average displacement in a sphere now becomes the analysis of the displacement on a surface. A mere composition of traits is far too short for exhausting the possibilities of trait interaction. Another way of traits to interact comes when the fitness function of a trait does depend on the fitness function of other interacting trait. In such a case, for the second trait of our example we have a composite fitness function $f \circ g$ (instead of the independent fitness function g) that will map from (x^1, x^2) to a fitness value, *sensu* Price. The new function $f \circ g$ constrains more the space of interest. Instead of having a surface, we have a line on this surface, represented by

$$T = X^1 f(X^1) \hat{i} + (X^2) f \circ g(X^1, X^2) \hat{j} + C(X^1, X^2) h(C(X^1, X^2)) \hat{k}$$

Equation 9

In Equation 9 $f \circ g$ stands for the particular form of fitness interaction in between X^1 and X^2 . The projection of the composite function $f \circ g$ into the previous surface is what results in our final line. From here on, I am interested in describe the resulting line, depicted in Fig. 1c. The fundamental theorem of differential geometry states that such a line is completely described with its curvature and torsion. These two values describe a line due to the surface in which it lies (torsion) and due to its intrinsic evolution, independent from its embedding surface (curvature). The torsion and curvature partition is particularly interesting in biological cases, because it provides a new analysis for the components of evolutionary displacement. **The partition of evolutionary displacement into curvature and torsion reflects the different interactions that constraint the evolution of average trait values.** I have provided an embedding surface due to trait composition, and a peculiar line into this surface, due to fitness interaction. Notice that even though my example is with three traits (in order to present graphs in the “familiar” geometry of a three dimensional space, R^3) the analysis of curvature and torsion is well defined for multidimensional spaces, which allows the extension to an arbitrary number of interacting traits. To calculate curvatures and torsions of a curve, I will introduce expressions for the first and second fundamental metric forms of a space.

For a generalized curve α on a surface S lying in R^3 , $\alpha(p) = S(x^1(p), x^2(p))$, (being p the parameter of α) its first metric forms is:

$$dl_\alpha^2 = g_{11}(dx^1)^2 + 2g_{12}dx^1dx^2 + g_{22}(dx^2)^2 \quad \text{Equation 10}$$

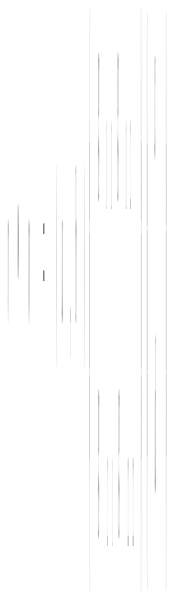
Here g_{11} is twice the derivative of S respect to x^1 , g_{12} is the derivative of S respect x^1 times the derivative of S respect x^2 and g_{22} corresponds to twice the derivative of S respect to x^2 . Equation 10 calculates lengths of α , being l_α the length of an arch of α . Using Einstein convention, summations signs can be omitted from any sum in which each index of summation appears both as a subscript and as a superscript. Equation 10 then becomes

$$dl_\alpha^2 = g_{ij} dx^i dx^j \quad \text{Equation 11}$$

The first metric form yields the intrinsic curvature of α , independent of the space in which α is embedded. To see that, consider:

$$\begin{aligned} v &= ax^1 + bx^2 \\ w &= cx^1 + dx^2 \end{aligned}$$

as two tangent vectors in a point of the surface $S(x^1, x^2)$ (a, b, c and d natural numbers). Their dot product can be written as:



Then the first fundamental form (the g_{ij} matrix) determines dot product of tangent vectors, so determines the angle of a curve at a given point.

Now, the generalized curvature of α is the length of α'' , a vector normal to α . Through the first metric form we can calculate an intrinsic component of this curvature, independent of the surface in which it lies. To relate α'' with the surface in which α lies, α'' can be decomposed in unitary vectors normal (torsion) and tangent (curvature) to the surface in which it lies, so we can state $\alpha'' = \alpha''_{\text{tan}} + \alpha''_{\text{nor}}$. It can be said that the curvature measures the speed with which the curve depart from being a straight line, and the torsion measures the speed with which the curve departs from being flat. To achieve such decomposition we begin with the unit tangent vector:

$$\alpha' = x^{i'} \frac{\partial T}{\partial x^i} \quad \text{Equation 12}$$

and the second derivative of α :

$$\alpha'' = x^{i''} \frac{\partial T}{\partial x^i} + x^{i'} \frac{\partial}{\partial s} \frac{\partial T}{\partial x^i} \quad \text{Equation 13}$$

To achieve the decomposition in normal and tangent components, the second term to the right is explicitly calculated and reordered. The second derivative of α then becomes

$$\alpha'' = \left(x^{r''} + \Gamma_{ij}^r x^{i'} x^{j'} \right) X_r + \left(L_{ij} x^{i'} x^{j'} \right) U \quad \text{Equation 14}$$

The coefficient of U (unit normal vector) is called the second fundamental form and describes how the curve deviates from being in a flat surface. Γ_{ij}^r and L_{ij} are functions of (x^i, x^j) , known as Gauss' formulas. The coefficient of interest for us, L_{ij} , is computed from the relation $L_{ij} = X_{ij} \cdot U$. As the fundamental theorem of geometry says, a curve is completely defined with its curvature and torsion. Notice that we had described a curve separating its generalized curvature in a component intrinsic to the curve and another component intrinsic to the surface in which the curve lies. Now let's find the first and second fundamental forms for the three interacting traits described above.

The first fundamental form is the matrix g_{ij} . The explicit expression of the matrix component is due to Gauss:

$$\begin{aligned} g_{11} &= \left(\frac{\partial T}{\partial x^1}\right)^2 \\ g_{22} &= \left(\frac{\partial T}{\partial x^2}\right)^2 \\ g_{12} = g_{21} &= \frac{\partial T}{\partial x^1} * \frac{\partial T}{\partial x^2} \end{aligned} \quad \text{Equation 15 (a), (b) and (c)}$$

carefull!! Is this delta T or is it delta S??

The partial derivatives are:

$$\begin{aligned} \frac{\partial T}{\partial x^1} &= \partial \frac{f(x_i^1)}{\partial x_i^1} \hat{i} + \partial \frac{C(x_i^1, x_i^2)}{\partial x_i^1} \hat{k} \\ \frac{\partial T}{\partial x^2} &= \left(\partial \frac{f \circ g(x_i^2)}{\partial x_i^2} \hat{j} + \partial \frac{C(x_i^1, x_i^2)}{\partial x_i^2} \hat{k} \right) \end{aligned} \quad \text{Equation 16 (a) and (b)}$$

CORREGIDO HASTA AQUI.

The coefficients of U in equation 14 comes from the expression $L_{ij} = X^{ij}U$. Because the second form is related to second derivatives, here X^{ij} stand for the second derivatives, using the summation convention: $\delta^2 T / \delta x^i \delta x^j$. For the sake of future applications, instead of use the summation convention, I write the full equations.

$$\frac{\partial^2 T}{\partial^2 x^1} = \left(\begin{aligned} & \left(\sum_i 2 \left(\frac{\partial f g(x_i^1, x_i^2)}{\partial x_i^1} \right) + x_i^1 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial^2 x_i^1} \right) \hat{i} + \left(\sum_i x_i^2 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial^2 x_i^1} \right) \hat{j} + \\ & + \left(\sum_k \frac{\partial^2 C(x_i^1 f g(x_i^1, x_i^2); x_i^2 f g(x_i^1, x_i^2))}{\partial^2 x_i^1} + \sum_k \frac{\partial^2 C(x_i^1; x_i^2)}{\partial^2 x_i^1} \right) \hat{k} \end{aligned} \right)$$

$$\frac{\partial^2 T}{\partial x^1 \partial x^2} = \left(\begin{aligned} & \left(\sum_i \frac{\partial f g(x_i^1, x_i^2)}{\partial x_i^2} + x_i^1 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial x_i^1 \partial x_i^2} \right) \hat{i} + \left(\sum_i \frac{\partial f g(x_i^1, x_i^2)}{\partial x_i^1} + x_i^2 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial x_i^1 \partial x_i^2} \right) \hat{j} + \\ & + \left(\sum_k \frac{\partial^2 C(x_i^1 f g(x_i^1, x_i^2); x_i^2 f g(x_i^1, x_i^2))}{\partial x_i^1 \partial x_i^2} + \sum_k \frac{\partial^2 C(x_i^1; x_i^2)}{\partial x_i^1 \partial x_i^2} \right) \hat{k} \end{aligned} \right)$$

$$\frac{\partial^2 T}{\partial^2 x^2} = \left(\begin{aligned} & \left(\sum_i x_i^1 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial^2 x_i^2} \right) \hat{i} + \left(2 \left(\frac{\partial f g(x_i^1, x_i^2)}{\partial x_i^2} \right) + x_i^2 \frac{\partial^2 f g(x_i^1, x_i^2)}{\partial^2 x_i^2} \right) \hat{j} + \\ & + \left(\sum_k \frac{\partial^2 C(x_i^1 f g(x_i^1, x_i^2); x_i^2 f g(x_i^1, x_i^2))}{\partial^2 x_i^2} + \sum_k \frac{\partial^2 C(x_i^1; x_i^2)}{\partial^2 x_i^2} \right) \hat{k} \end{aligned} \right)$$

Equation 17 (a), (b) and (c).

With the precedent set of equations, given well-defined interactions among traits, the trajectory of the average values of the traits under selection are described. It is worth to note, in despite of the size of the last equations, their simplicity and symmetries. If the second term of Price equation is incorporated (in case of departures from randomness of meiosis and recombination) the resulting equations might be more complicated.

The description of a curve through its curvature and torsion yields a relevant partition of effects of interacting traits. Recalling Fig. 1 we can note that the evolutionary space is constrained from a ball (Fig. 1a) to a surface (Fig. 1b) to a line on the surface (Fig. 1c). Now we can describe this line in terms of a component due to the surface and another component intrinsic to the curve. So we are considering a component due to the first level of interaction I mention (compound traits) and another component due to the second level of interaction (compound fitness functions). Then, the partition of the curve followed by a lineage along its evolutionary history can be analyzed in terms of compound traits (torsion) and interacting fitness functions (curvature).

It is worth to note that the above formulation consider the displacement in trait space described by a vector field. A generalized vector field can be characterized by three quantities, its gradient, its divergence and its curl. The gradient is a quantity that appears also in a scalar field, been the traditional selection strength (Lande 1982).

A vectorial field formulation adds multidimensionality. In a scalar field view, we have a set of traits defining an organism that maps to a fitness value. In my view fitness is not added as another dimension, but arises as curved displacements into the space. The augmented dimensionality opens the possibility of interpret the curl of the vector field in biological terms. This magnitude has not been explored before in the context of evolutionary biology, -to the best of my knowledge-. Its explicit definition for a three dimensional vector field:

$$\text{curl } \vec{A} = \begin{vmatrix} \hat{i} & \hat{j} & \hat{k} \\ \frac{\partial}{\partial x_1} & \frac{\partial}{\partial x_2} & \frac{\partial}{\partial x_3} \\ f & g & h \end{vmatrix}$$

Equation 18

The curl is in itself a vectorial magnitude, and intuitively it represents eddies in a turbulent flux. As can be seen from the definition, its terms involve differences among components in a vector field, measuring its irregularity. My interest in recall it here is that it might prove to be a useful concept, since it measures irregularities in displacement due to intrinsic interactions among the components of the flux. A laminar fluid has a curl equal to zero. This means that a flux without interactions among its dimensional component is very smooth, without irregularities. Particles moving along such a flux will move without eddies. The evolution under selection of sets of correlated traits has

not been proved as a very smooth displacement in trait space, but the contrary. Selection on one trait release a cascade of effects in other correlated traits. The curl is a candidate to measure such effects, if we are able to define the vector field of interacting fitness functions for a particular example. Using the notation in this paper, the mnemotechnical matrix of the previous equation reads:

$$\text{curl}T = \left(\frac{\partial x^3}{\partial x^2} - \frac{\partial x^2}{\partial x^3}\right)\hat{i} + \left(\frac{\partial x^1}{\partial x^3} - \frac{\partial x^3}{\partial x^1}\right)\hat{j} + \left(\frac{\partial x^2}{\partial x^1} - \frac{\partial x^1}{\partial x^2}\right)\hat{k} \quad \text{Equation 19}$$

Is important to note that this equation applies for a vector field in which each of its dimensions is a function of itself and the other ones. The way in which I choose the constrained space of selection here reduced each dimension to a function of two variables, assuming that one of the traits is a composition of the other two. Henceforth, the curl of T here does not yield a vector field. However, in a case with more complicated interactions, in which each fitness function is a function of the three traits, there will appear the eddies that the curl represent, from the interactions of fitness functions. Complex sets of traits under selection reacts in a non linear way to it, and the curl of the resulting evolutionary vector field measures such deviations from linearity. For reasons of space I will not construct such a case, leaving it for future applications. It is interesting to note in this formulation that turbulent responses to selection are expected after certain degree of complexity in the interactions among the traits under selection. Conversely, several interacting traits are needed to have turbulent responses to non-fluctuating selection.

When the concept of turbulence arises and it is considered as measurable by a mathematical construct as the curl of a vector field, for the empiricist the relevant question becomes “What am I able to say when I do not know the fitness functions (and their interactions) of the traits I am selecting?”. The first step to answer this question is to obtain an estimate of the number of meaningful dimensions. It is important to know how many traits are interacting.

From the theoretical study of turbulence, re-constructions of attractors in phase space are useful in similar circumstances. The basic idea is that different variables interacting and defining the observed trajectory of a flux acts with different time delays. So it is possible to take the trajectory of an observed variable, construct dimensions with time delays and analyze the resulting attractor, if any. In low dimensional systems meaningful reconstructions have been achieved from data that seems to be completely random at first look. I will not construct any example here to avoid diversions from the main geometrical argumentation, but the interested reader is referred to Eckmann & Ruelle (1985) and Casdagli (1992).

Curvature and adaptive dynamics

There is an alternative way to calculate the curvature of a surface in a particular point belonging to it. It is more intuitive, directly linking to the notion of a curved surface.

Imagine a point p in our surface T . Now define a neighborhood around p and ask that the surface is continuous in the neighborhood. Consider the unitary normal vectors to the surface in the neighborhood. If the surface is flat (there is no curvature in p), all those vectors will be the same. Meanwhile more curved the surface is around p , the normal vectors will be pointing to more different directions. To evaluate this difference, we can take the normal vectors, translate them to the center of a sphere and compare the area of the neighborhood of p with the area covered in the sphere. It has been demonstrated that at the limit in which the neighborhood tends to p , the ratio among the two areas is the gaussian curvature of the surface in p . A graphical representation of the verbal argument is depicted in Fig. 2 and the analytical expression follows.

$$Curvature(p) = \lim_{\Omega \rightarrow (x_0^1, x_0^2)} \frac{AreaU(\Omega)}{AreaX(\Omega)}$$

Equation 20

Here Ω is the neighborhood, (x_0^1, x_0^2) is the position of p , $Area X(\Omega)$ is the area of the neighborhood in the surface and $Area U(\Omega)$ is the area in the sphere after map the normal vectors to Ω in a sphere. I will use this concept of curvature to characterize the fate of a mutant in a resident population.

The adaptive dynamics framework sets its concept of fitness in the success of an invading mutant. In order to consider this scenario I will rephrase the space I used before. Consider then the trait space in which are depicted not

averages but all the states of the traits and its frequencies. I will consider the vector field of difference of frequencies from one generation to the next one. This two changes are aimed to introduce dynamics in the geometry that the curvature is describing.

In the previous section, a population was defined as a point in the evolutive space, and my description concerned the displacement of this point. Now a population is defined as a set of vectors. Each vector has as many elements as traits are modeled. So we will have as many vectors as many combinations of traits are possible. Each vector will have the frequency of its traits' combination as an extra dimension. Fig. 3 exemplified this reformulation, adding some graphical simplifications and showing a mutant in a resident population.

Last and not the least, we will follow the space of differences among two times as the vector field that we are interested in. Differences are taken to be able to follow changes in the structure of frequencies throughout generations.

A mutant can be considered as a state that change its frequency from zero to another value. It will be called x_m^i , meaning that the state m in the trait i has become present. Now we can consider a neighborhood Ω around the new point of interest in the space. This neighborhood will be the states $\{x_{m+\delta}^i, x_{m-\delta}^i\}$, where δ stands for an arbitrary small value. If the mutant is successful the differences in frequencies of states in such a neighborhood will increment in time, because their frequencies will change. If this is not the case and the

mutant went extinct in the next generation, the frequencies of neighboring states will recover stable values, even though not necessarily the previous ones. In both cases the vector space of frequencies' differences (from one generation to the other) will not be a flat surface as far as the mutant keeps on altering neighboring frequencies. At the moment in which an equilibrium is attained, the vector of differences becomes the plane zero, which indeed is a flat surface. The graphics corresponding to this verbal argument are depicted in Fig. 4 and Fig. 5. Fig. 4 shows a population in which a mutant arises and get established. Four moments of this process are depicted. Fig. 5 depict the case of a mutant that arises but is not able to invade. In the figures I did not took differences, to exemplify the dynamics of a mutant as simple as possible.

The relevance of analyze the curvature of such a space in order to understand invasion processes is that the invasibility is understood as a highly contingent process. The information provided by the curvature is relevant in each generation, and the detailed evolutionary dynamic must be followed to asses the outcome of a selective scenario. One of the shortcomings of define mutant fitness as its long term growth rate is that the details of a beginning invasions are missed. Examples have been built in the literature (Diekmann et al. (1999) and references therein) to show that might exist attractors of low frequencies in which residents or displaced population lies. When such attractors are present, displaced residents can recover their original frequencies, even in despite of having mutants with positive growth rate in early stages of invasion. Since my analysis follows a curvature that occurs from one generation to the

next, no assumptions about the fate of mutants with positive growth rate are made.

Relations with other research lines

Selection in density-dependent scenarios implies the inclusion of another variable into the definition of the fitness function. From a geometrical point of view it adds dimensions to the space in which evolution is conceived, but the basic framework remains similar. One of the most appealing propositions of the adaptive dynamics framework is their analyses of density dependent selection scenarios. I have shown that the concept of curvature is useful to describe the invasion of a mutant, to incorporate the scenario of adaptive dynamics into my geometric approach. Work to incorporate density-dependent scenarios is needed to make full comparisons meaningful. Moreover, density-dependent scenarios have arisen traditionally in ecological quarters, related to the study of life history evolution. It is important to establish connections with such a broad field of research.

My formulation of mutation processes conceive the occurrence of mutation as a single point event. In this conceptualization, the random walk of evolution fueled by mutation (as the streetcar-car of adaptive selection pose it, see Hammerstein 1996) is a process in which one new option is posed each time by mutants. As much mutation is a source of variation, traditionally recombination has been considered another one. Akin's approach developed

selection, mutation and recombination vector fields to integrate them into the population genetics vector field. The intrinsic difficulty of introducing recombination into this framework is that we need to consider a two-entities process. Recombination implies the mixing of two parental genotypes into one.

An attempt to model recombination conceptually linked with mine uses graph-theory approaches (reviewed in Stadler & Wagner 1997). They propose algebraic structures able to incorporate the combination of parental genotypes into the descendent one. Their solution introduced the so called hyper-graphs, structures in which parents are represented as vertex of a graph and recombinants are edges among vertexes. Into this space is imposed a "landscape", a function from each configuration of the graph to a real value. The work of Stadler & Wagner (1997) uses a Fourier expansion of the landscape to incorporate interactions among the components of the graph. Expressions for the local geometry of the landscape are derived through the concept of correlation and ruggedness of the landscape. I will not go into the details of such a derivation, but here is important to point that the landscape geometry is analyzed using the Laplace equation to decompose the landscape into elementary components. Such a decomposition is related to the geometrical decomposition that I attempt into the vector field of selection. Further work should establish the full connection among recombination modeled using graph theory and my description of evolutionary sequences characterized by the curvature and torsion of the selective space. It is important to note that geometrical characterization of landscapes of

interacting elements is a topic frequently arising in molecular biology. In this quarter of biology, is common the view of traits as the combinatorial arrays used by the graph approach. Links from my work with this also populated research of evolutionary biology are as desirable as connections with density-dependent scenarios.

To describe the evolution of a lineage under selection, I phrased the relevant space as the space in which the average values of a set of traits moves. In this formulation each lineage is reduced to a point, the average value of the sets of traits. Later on, to describe the fate of a mutant in terms of geometrical attributes of an adaptive landscape, I rephrased the relevant space and introduce the full vector field of frequencies of traits-states' combination. Previous work (a. o. Frank & Slatkin (1992); Coyne et al. (1997)) has repeatedly pointed out that two interpretations of Wright's adaptive landscape were possible. One of a phenotypic space and another of a frequency space. I have used one of them in each case. But a third possible phrasing has been recently discussed (Rice 1990, 1998). This is the so called phenotypic landscape, in which a dimension correspond to a trait and all the others correspond to contributing attributes of an organism to the focusing trait. This is an alternative way to model interaction among traits. Rice (1998) shows how such epistatic interactions introduce curvature into the space. In my work I have shown how curvature induced by similar interactions determines the outcome of selection. Further work to establish the conceptual linkage among mine and Rice conclusions is desirable.

The work of Rice is aimed to provide conceptual background to developmental evolutionary biology. Considering that selection is fueled by variation (mutation and recombination), we must agree that the expression of variation is an equally important topic. This is the main goal of developmental biology. So here are also relevant links needed to the third important quarter of evolutionary biology, the so called evo-devo realm.

Concluding remarks

The primeval objective of this paper was to establish a meaningful geometrical approach to evolution under natural selection. This goal was pursued analyzing: a) the geometry of an adaptive landscape in which many traits interacts and b) the geometry of a landscape in which a mutant arises. In both cases the curvature of the space is the parameter that describes evolutionary displacement.

In the case of interacting traits, the well known description of a curve using its curvature and torsion yield an interesting and -to the best of my knowledge- non explored way to separate the effects of interacting traits in an evolutionary trajectory. Moreover, a magnitude is proposed to measure the effects of interacting fitness functions, the curl of a vector field.

A reformulation of the evolutive space allows to say that the Gaussian curvature also measures the fate of an invading mutant. This new

interpretation of curvature allows to establish relevant links with the established dynamic view of selection, the adaptive dynamics framework. The way in which the curvature is measured avoid the overlooking of processes such as “the resident strikes back”, underlying the highly contingency of any evolutionary process.

Bibliography

- Akin, E. (1979). *The geometry of population genetics*. Berlin, Springer Verlag.
- Casdagli, M. (1992) Chaos and Deterministic Versus Stochastic Nonlinear Modeling. *Jour. Roy. Stat. Soc. B- Meth.* **54**,303-328.
- Coyne, J. A., Barton, N. H.& Turelli, M. (1997) A critique of Sewall Wright's shifting balance theory of evolution. *Evolution* **51**, 643-671.
- Diekmann, O., Mylius, S. D.& ten Donkelaar, J. R. (1999) Saumon a la Kaitala et Getz, sauce hollandaise. *Evol. Ecol. Res.* **1**,261-275.
- Eckmann, J. P.& Ruelle, D. (1985) Ergodic-Theory of Chaos and Strange Attractors. *Rev. Mod. Phys.* **57**,617-656.
- Frank, S. A. (1997) "The Price equation, fisher fundamental theorem kin selection and causal analysis". *Evolution* **51**, 1712-1729.
- Frank, S. A.& M., S. (1992) Fisher's fundamental theorem of natural selection. *TREE* **7**, 92-95.
- Geritz, S. A. H., Kisdi, E., Meszema, G.& Metz, J. A. J. (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**,35-57.
- Hammerstein, P. (1996) Darwinian adaptation, population genetics and the streetcar theory of evolution. *Jour. Math. Biol.* **34**,511-532.
- Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* **63**, 607-615.
- Li, C. C. (1967) Fundamental theorem of natural selection. *Nature* **214**, 505-506.

Metz, J. A. J., Nisbet, R. M. & Geritz, S. A. H. (1992) How should we define fitness for general ecological scenarios. *TREE* **7**, 198-202.

Price, G. R. (1970) Selection and covariance. *Nature* **227**, 520-521.

Rice, S. H. (1990) A geometric model for the evolution of development. *J. theor Biol.* **143**, 319-342.

Rice, S. H. (1998) The evolution of canalization and the breaking of von Baer's law: Modeling the evolution of development with epistasis. *Evolution* **52**, 647-656.

Figure Legends

Figure 1

In this figure the phenotypic space is depicted. Each coordinate correspond to the states of a trait. The evolutionary displacement in which I am interested is the displacement of the average value of each trait. Figure 1a depicts the space reachable for the average if evolution is independent in each trait. Figure 1b depicts the same space for the case in which one of the traits is a composition of the other two. Figure 1c depicts the further complication in which two traits have a fitness function with interacting terms.

Figure 2

This figure represent the so called Gauss mapping, an alternative way to measure curvature. It is done in two points of a surface T . The point Q lays in a less curved area of t than the point P . Accordingly the surface covered in a unitarian sphere by vectors normal to the surface T in the Ω neighborhood of each point is different.

Figure 3

This figure introduce the following two figures. Figure 3a depicts a population in which five combinations of traits $T1$ and $T2$ are possible. Each of the combination has a frequency, depicted in the "z" ax. Figure 3b paints a imaginary surface in which the frequencies lie. The "x" in figure 3c represent a mutant, arising in a low frequency. Figure 3d paints another imaginary surface surrounding the mutant, for the sake of visualization of the whole surface in which the frequencies lie as the combination of two leaves (the resident one and the mutant one). In the following figures, the changes in the frequency of the mutant are depicted as changing the relation of the two leaves, henceforth changing the curvature of the surface in a neighborhood of the mutant state.

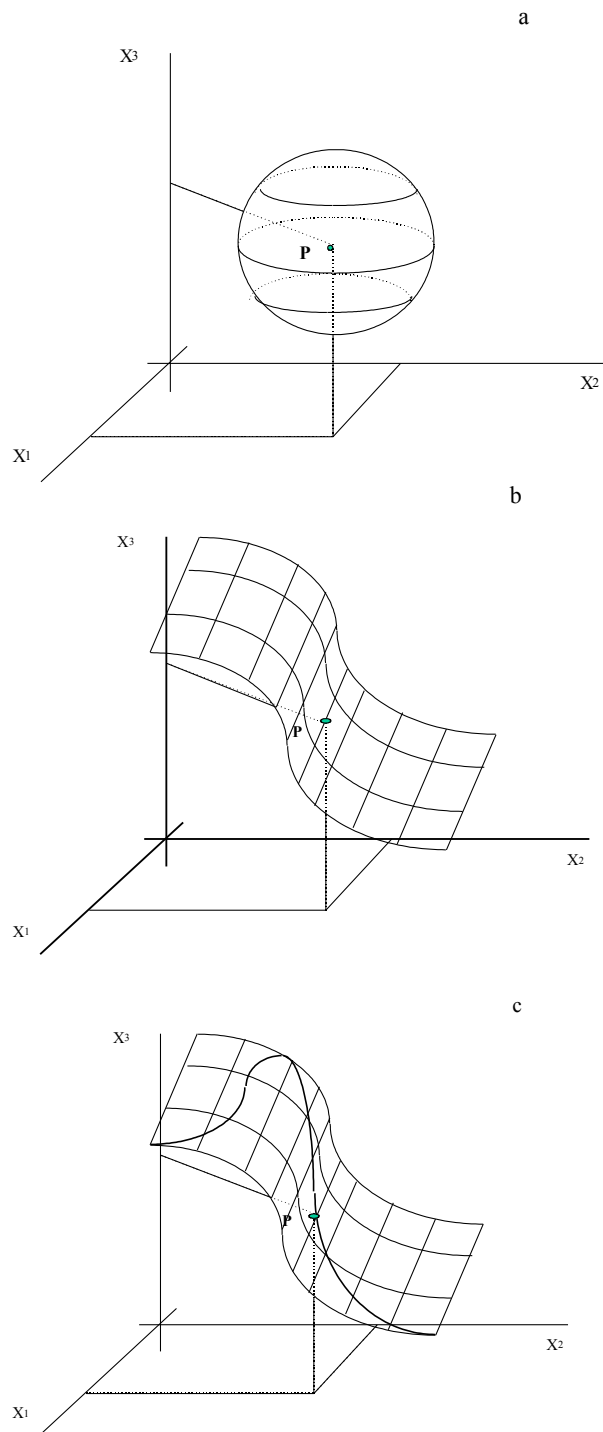
Figure 4

This figure uses the metaphor of figure 3. Here it is depicted the case in which a mutant arises in a low frequency (4a), increase its frequency (4b), reaches its higher frequency value (4c) and stays stable (4d). It is important to note that if the differences among this sequence are considered, we will find curvature (measurable as the figure 2 indicates) from a to b, from b to c, but not from c to d. The increase of curvature when a mutant increase frequency is a positive one.

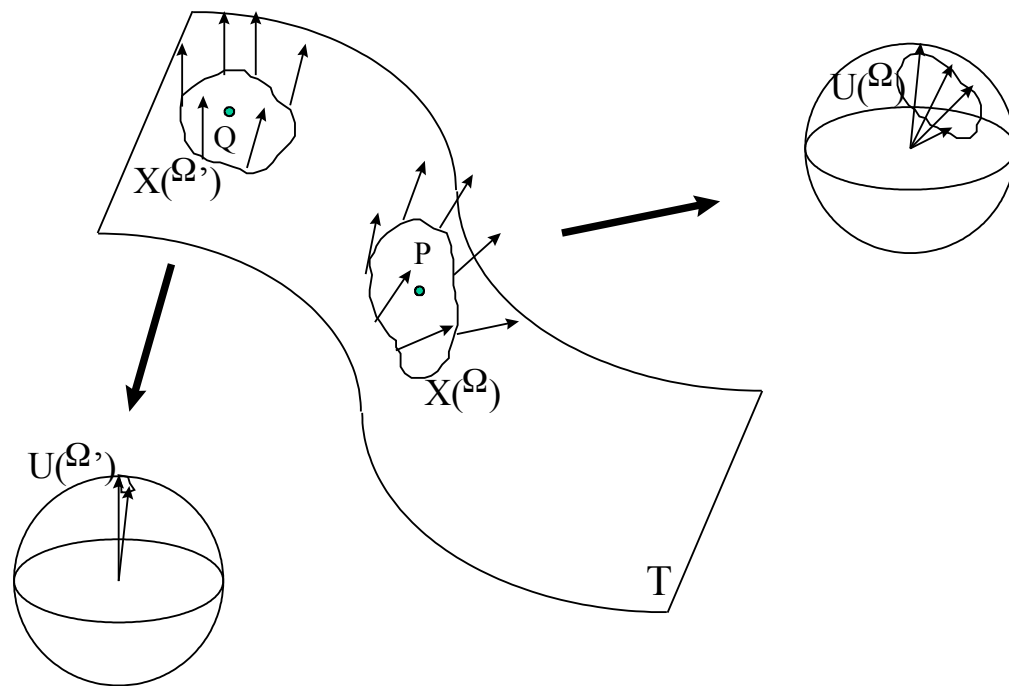
Figure 5

The case depicted here is the arise (5a), increase (5b), decrease (5c) and disappearance (5d) of a mutant. Considering the vector field of differences among these "snapshots", we will have curvature appearing in all the differences. But the curvature due to the decrease of mutant frequency is of negative value, making a useful difference with the case in which the mutant increase its frequency.

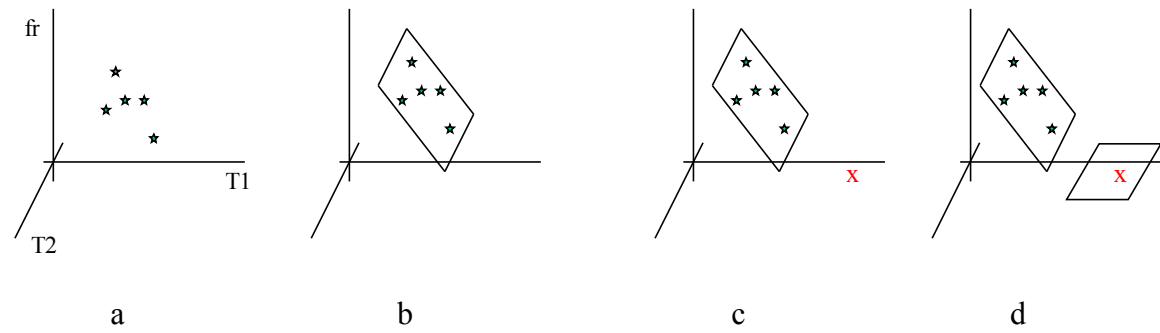
Suarez, Figure 1



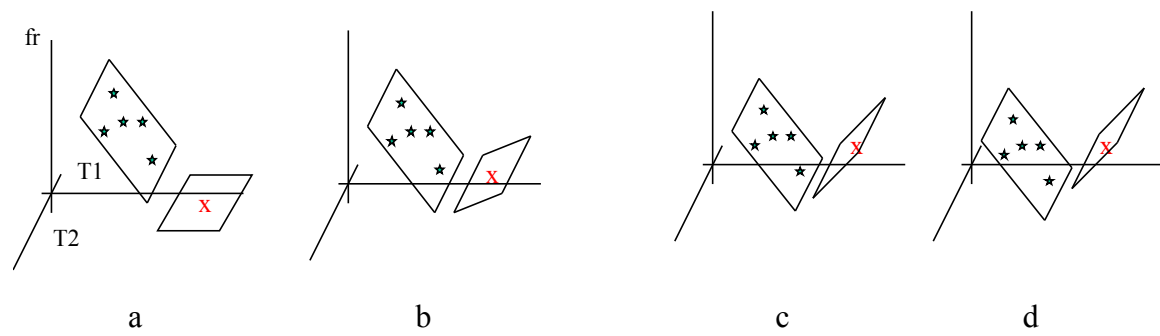
Suarez, Figure 2



Suarez, Figure 3



Suarez, Figure 4



Suarez, Figure 5

