Evolutionary Ecology Research, 2009, **11**: 589–610

Life: optimality, evolutionary, and intelligent design?

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ABSTRACT

Questions: What constitutes design in a natural system? In what ways are the three design concepts involving optimality, evolutionary, and intelligent design similar, and under what conditions do they diverge?

Mathematical method: Adaptive landscapes are generated by using fitness-generating functions from evolutionary game theory.

Key assumptions: Natural selection, which may be frequency dependent, occurs on adaptive landscapes. Gradient-following algorithms find optima on fitness landscapes. Darwinian dynamics find evolutionary equilibrium points on adaptive landscapes and irreducible complexity from intelligent design manifests itself as a discontinuous adaptive landscape.

Conclusions: In the absence of frequency-dependent evolution, optimality design (OD) and evolutionary design (ED) may produce the same landscapes and yield equivalent solutions resulting in maximum population size for the species. However, in the presence of frequency-dependent selection, the landscapes for OD and ED differ and solutions need not agree. Solutions generated by ED can produce species, which, as a group, can always invade species produced by OD. The model also highlights three claims of intelligent design (ID) irreducible complexity and finds them false: that Darwinian dynamics used by ED must entirely account for evolutionary change; that such dynamics cannot navigate a discontinuous evolutionary landscape; and that the extent of zero-slope regions on landscapes are too vast to be traversed by biological processes in finite time.

Keywords: evolutionary design, intelligent design, irreducible complexity, landscapes, optimality design.

OVERVIEW

We present three different world views on how design might take place in a biological system. For many, if not most individuals, evolutionary design (ED) as proposed by Darwin is the most favoured and prevailing scientific explanation. However, there are individuals at recognized scientific institutions who do not dismiss evolutionary design outright, but hold the view that there are 'gaps' that cannot be explained using Darwin's theory alone, in

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which case intelligent design (ID) must be required to complete the design process. The writings of Behe (2007) perhaps express this view best. Because this view of ID potentially has some scientific merit and has a recognized spokesperson, with an academic background, we will focus on this view of ID. This relieves us of the burden of having to deal with other ID proposals that are entirely faith based. Optimality design (OD) potentially includes faith-based ID (e.g. God prefers perfection and hence designs in an optimal way). However, we do not use OD in this context. Rather, we examine OD in the context of horizontal gene transfer as described by Woese (2004). Our conclusions on how OD may represent a world view are speculative and should be regarded as such. Perhaps more important are some of the interesting relationships we examine between OD and ED. Finally it should be noted that we use the terminology 'optimality design' rather than 'optimal design' for two reasons. First, when dealing with multiple species, the interaction between species is that of an n player game (Vincent and Grantham, 1981) that has many different solution concepts. In a game setting, optimal design is not applicable unless there is only one player. Second, we want to make clear that we are not referring to other optimal design concepts such as the optimization research program proposed by Mitchell and Valone (1990).

For individuals that operate within the framework of ID, this paper provides a detailed account of how modellers might integrate different perspectives. It challenges proponents of ID to imagine what is optimized, what models would be appropriate, and why irreducible complexity may not be an issue for ED. This approach also provides an appraisal of ID from the viewpoint of an evolutionary biologist. This allows ID proponents the opportunity to respond and rebut.

Our approach employs mathematical models to simulate population dynamics. This allows us to compare different design concepts of OD, ED, and ID using the same model and mathematics. Our objective is to compare design concepts rather than any specific population dynamic model.

DESIGN

Historically, three design concepts – OD, ED, and ID – have been used collectively to address questions related to the origins of design in biological system. These three offer explanations for design in organisms and artifacts through both naturalistic mechanisms and through the agency of a non-naturalistic Designer. We will examine why these processes differ and how they may lead to different outcomes.

Design is defined as 'the general arrangement or layout' of a thing (*Oxford Dictionary*), or more specifically, 'a thing planned for an outcome' (*Webster's Dictionary*). The contrast between the two definitions (Oxford's definition is passive, whereas Webster's is active – planning 'for' implies a planner) reflects current differences in thinking about biological design. For the biologist, it is but a small step to expand the passive Oxford definition to 'the general arrangement or layout provided by artificial or natural selection'. In contrast, with Webster's active definition it is not possible to have a planned outcome without an intelligent agent providing the plan.

Design may also be thought of as a process or outcome of a process that orders existing things to produce new things that serve a purpose. This parallels Mayr's (1963) definition of evolutionary novelty as 'any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone'. Indeed, design questions have featured in debates about the evolutionary history of life, including whether theories other than Darwinian gradualism are necessary to explain the nature of early prokaryotic evolution (Woese, 2004), multicellularity, or the Cambrian explosion of metazoan life (Wills *et al.*, 1994; Gould, 2002).

Evolutionary, optimality, and intelligent design are not necessarily mutually exclusive or opposing alternatives: ED is explicit in what purpose is served (maximizing individual fitness) and how it is attained (via natural selection); neither OD nor ID make assertions about both purpose and mechanism. OD asserts a purpose (maximize group fitness) while remaining open to all methods of optimization. In contrast, ID is vague about purpose, but the method is Divine Fiat. In all cases, the design is apparent because the outcome notably serves a purpose (flagella beat, whether that suits God or an Euglena).

Much of Darwin's *Origin of Species* (Darwin, 1859) is organized to contrast his theory of natural selection with the 'Argument from Design' (e.g. Paley, 1826). The design argument, by analogy with artifacts designed by humans, uses the fit of form and function (FF&F) that characterizes living organisms to argue for the existence of God. Although Darwin did not specifically use the term 'design', he opens his 'long argument' by analogy with artificial selection by man for the purposes of husbandry to the FF&F via natural selection in the struggle for existence. More recently, Dennett (1995) argued explicitly that the adaptations of organisms consist of the accumulation of design via natural selection. In his classic critique, Williams (1966, pp. 4–5) categorizes adaptation as the end result of the design process provided by natural selection. In contrast, Behe *et al.* (2000) assert that design cannot be an accumulation of natural processes, but that a given design implicates an intelligent designer: all design is intelligent design.

Except for the mechanism by which it is attained, our understanding of design as an outcome that serves a purpose is similar when considered by either Paley or Darwin. Evolutionary design and intelligent design are neither opposite nor opposing concepts in this regard, although they are often discussed as such (Gould, 2002, p. 124) because they have frequently been interpreted to have opposite moral implications [incorrectly so: see Dennett (1995) and Haught (2003) for discussion] and opposite levels of action (at the level of the individual vs. that of God).

The notion of function and purpose is inherent in the concept of design and adaptation, yet has confounded laymen and philosophers of evolutionary theory alike. How are these concepts linked? Dennett (1991) recognizes that function and purpose arise together in elementary form literally at the boundaries of life. Life exists as individuals: either an individual cell, or groups of cells functioning as a single unit. Individuals have boundaries, from which arises a point-of-view: inside vs. outside, 'me' vs. not me, and finally, good (for me) vs. not good (for me).

Function and purpose in biological design arise as an inevitable condition of individuality in life, and are those of the organism itself (and its genes). Functions serve the continuation of the underlying genes into succeeding generations, leading to the notorious concept of the 'selfish gene' (Dawkins, 1976). Other authors have postulated similarly selfish demes (Wilson, 1989), species or even clades (Gould, 2002) on which natural selection may act to yield evolutionary change. However, in this paper we will regard biological FF&F and purpose principally as properties of individuals. Optimality design asserts only that the purpose is served such that some suitable measure of performance (efficiency, for example) is maximized. Thus, under OD, the purpose may belong to a designer (e.g. an engineer, as a product of intelligent tinkering), to an individual (as a product of natural selection), to a group, or even to some combination. Intelligent design theorists, in contrast, have emphasized that the purpose of design (details and processes) is revealed by its 'irreducible complexity' (Behe *et al.*, 2000), and that from irreducible complexity one is logically compelled, based on the argument from design, to infer a designer. Intelligent design rejects natural selection as the sole explanation for design found in nature.

Irreducible complexity

Behe (2000) argues that irreducible complexity commonly exists in designed artifacts (his favourite example is a mousetrap) and in biological adaptation (molecular machines such as a cilium and a flagellum). Irreducible complexity has a specified function and complex information content comprised of numerous interacting parts, 'where the removal of any one of the parts causes the system to effectively cease functioning'. Behe argues that irreducible complexity cannot arise through Darwin's accumulation of 'numerous, successive, slight modifications' or 'slight, successive, favorable variations', because all intermediate steps towards the property yield no selective advantage until the final step.

Biologists, too, have confronted this dilemma over the history of evolutionary theory, seeking a naturalistic theory to account for the appearance of evolutionary novelty. By the time of the modern synthesis, the problem was framed as the inability of populations to cross valleys in a continuous evolutionary fitness landscape (Wright, 1931). However, models of evolutionary games have shown that the underlying evolutionary mechanism involves a flexible adaptive landscape (Vincent and Brown, 2005) in which valleys are fordable by natural selection as the landscape flexes in response to the evolving populations. At least one recent study (Whibley et al., 2006) indicates that selection also circumvents valleys along trajectories that follow adaptive ridge-lines.

If we are to compare optimality, evolutionary, and intelligent design, we must attempt to charitably translate Behe's critiques of natural selection (Behe, 2000, 2007) into a model on an adaptive landscape. Darwin's first postulate states that like begets like but there is heritable variation in traits associated with each type of organism. By more effective reproduction, fitter individuals in the heritable variation move the mean strategy up the adaptive landscape (Fig. 1a). Behe (2007) agrees that there is natural selection, but argues that 'the only way a plant or animal becomes fitter . . . is by sustaining a serendipitous mutation' and that 'random mutation is extremely limited' (Fig. 1b). Behe argues that the probability of random events leading to complex systems is astronomically small and cannot account for what is found in nature. Hence such complexity is irreducibly complex. In ED, heritable variation allows not only for relatively rapid evolution through small changes, and the gradual development of complexity, but also allows for speciation to take place (Vincent and Brown, 2005). Thus, in Behe's ID models, the processes of natural selection are similar (but far less efficient) than ED, but as we will see, the ID landscapes are argued to have a different geometry as well.

An adaptive landscape may be imagined with features such as isolated plateaus with vertical sides that cannot be accessed from nearby parts of the landscape. This is reminiscent of Sir Arthur Conan Doyle's fictional *Lost World*, an isolated plateau in the Amazon surrounded by unscalable cliffs where dinosaurs survived until modern times. Such lost world landscapes have the form advocated by ID for irreducible complexity, considered in its strict sense; where there is no pathway of 'slight, successive, favorable variation' by which one species may be transformed into varied and related forms. As irreducible complexity is described in ID theory, lost worlds have very small plateaus where species can

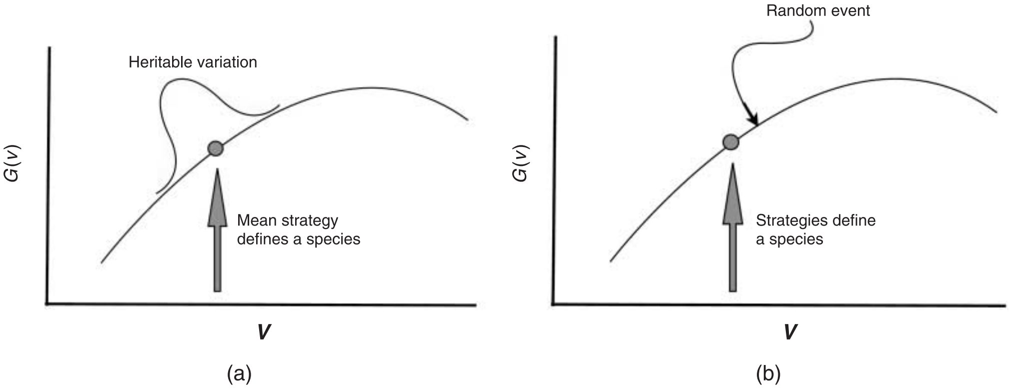

Fig. 1. (a) Darwin's mechanism for adaptation through heritable variation, depicted on an adaptive landscape. Variation exists around the mean strategy for a species. Variants higher on the adaptive landscape increase in relative frequency at the expense of those lower on the landscape. (b) Behe's view of Darwin's mechanism of evolution depicted on an adaptive landscape. Species are characterized by a strategy. Evolution occurs when a random event, of vanishingly small probability, gives rise to a species characterized by a different strategy higher on the landscape.

only vary slightly over a fixed phenotypic range. However, in principle, lost world plateaus might also be very broad, and have complex landscapes themselves. Large plateaus would be equivalent to bauplans, occupied by entire clades, domains or even biospheres. Regardless of size, lost world plateaus have the features of irreducible complexity (Behe *et al.*, 2000) – a functional trait comprised of a significant number of elements that individually do not improve fitness unless assembled into a correct and single complex unit.

We must take care in evolutionary theory when making comparisons with gravitational analogies such as landscapes. In gradient-following and Darwinian dynamics (see below), we speak of natural selection 'driving' populations up adaptive landscapes to adaptive peaks, while Dennett (1995) has emphasized the crane-like nature of natural selection doing the lifting in evolutionary R&D. By analogy with physics, the challenge and the work comes from the vertical dimensions travelled. In these analogies, height corresponds to the force doing work. However, on both these and other landscape analogies such as the lost world plateau, the design work (change in organization) is represented along the x-axis (movement across the landscape), and the vertical dimension (change in fitness) represents the strength of the force securing that movement.

Our models will show that lost world plateaus are accessible through natural selection. Indeed, it is not the unscalable cliff with which Darwinism has trouble. Rather, it is the perfectly flat featureless plain, at the base of cliffs, which presents a problem. Should such plains prove frequent and extensive on adaptive landscapes, this is the terrain that natural selection alone will have difficulty navigating.

Frequency-dependent selection

Importantly, is evolutionary design (resulting from natural selection) similar to, or different from, optimality design? Natural selection is capable of maximizing fitness (leading to optimality design), but it does not always do so in part because of the critical role of competing individuals. Fitness functions depend on the design variables (strategies/ phenotypes) used by all individuals in a population. Because of this, optimality design will generally differ from evolutionary design. The classic illustration of this is the Hawk–Dove game: in a world of Hawks, because of the costs of injury, no-one does as well as in a world of Doves. But in the world of Doves, any Hawk will do better than the Doves. This is a case of frequency dependence, where the fitness of one individual is dependent on the strategies used by all individuals, which means that individual selection under ED diverges from group selection under OD.

Frequency dependence is a common condition in living systems, but it is not universal: strict genic selection may lead to OD. One such case of genic selection is that of 'selfish DNA' like meiotic drives, genes that destroy competitor alleles in the gamete stage before they enter the next generation, ensuring only the selfish allele reaches the next generation [e.g. Medea, a genic element that produces a toxin to kill all egg cells except those containing the Medea element (Chen *et al.*, 2007)].

The group vs. individual selection is to be distinguished from the process of horizontal gene transfer (HGT), in which gene copies move across organismal lineages, disrupting organismal heritability as well as individual selection for adaptive advantage. An important contributor to HGT is the modularity of the gene involving how much of its function is independent of complex interactions with other aspects of organismal physiology. Woese (2004) argues that when high levels of HGT are prevalent, evolution will be largely communal among loosely connected and highly modular genes. With frequent HGT, evolution would no longer be characterized by reproductively isolated lineages of organisms (species), but instead be dominated by reticulated patterns of inheritance. He also argues that because selection at the individual level is of reduced importance, competition and frequency-dependent selection between any two lineages becomes disrupted, and natural selection is less likely to involve ED. Based on these arguments, we propose that under HGT selection, OD becomes a possibility and this strengthens the usefulness of OD as a viable world view. This will be true of any system of reticulated evolution, where lineages cannot only diverge, but also merge in whole or in part.

LANDSCAPES

To compare the three different design concepts, we need to define and understand the role that a landscape plays in our analysis.

The landscapes discussed are distinguished by either the functions used for the vertical (y-) axes or by their discontinuous geometry. We assume that the fitness of a species is a function of strategies used by them. A strategy (*sensu* game theory) is traditionally chosen by a player (e.g. economics and engineering) or inherited and passed on via natural selection (biology), and is deliberately agnostic regarding OD, ED, and ID. Fitness is determined from the particular mathematical model used to define the population dynamics.

Consider a population of n_s different species. The scalar x_i represents the density of individuals of species i and the vector $\mathbf{x}$ the population densities of the n_s different species. Individuals in the population are identified by the heritable strategies (i.e. phenotypes) that characterize those individuals as belonging to a particular species. Scalar strategies are assumed in this presentation; and the notation u_i is used to denote the strategy (e.g. bill length) of individuals of species i, while $\mathbf{u}$ is the vector of all strategies used by all species in the population. We will use population dynamics equations of the form

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

where, by definition, $H_i(\mathbf{u}, \mathbf{x})$ is the fitness of individuals of species i, and is generally a function of the density and strategies of all individuals in the population.

We are using a differential equation approach for convenience. Conclusions remain unchanged regardless of the particular equations (e.g. difference equations) used for modelling the population dynamics. Generally, we will be examining the different design processes that determine how maximum points are achieved on different landscapes.

Fitness landscape

If one chooses a strategy vector $\mathbf{u}$, and initial conditions for the densities $\mathbf{x}$, equation (1) may be integrated to produce a solution for $\mathbf{x}$ as a function of time, typically with an equilibrium solution $\mathbf{x}^*$ and at least one $x_i^* > 0$. It follows from the population dynamics that the fitness for those species with $x_i^* = 0$ must be negative and for those with $x_i^* > 0$ must be zero. For example, consider a population composed of species whose population dynamics are given by the Lotka-Volterra equations

$$\dot{x}_i = x_i \left[r - \frac{r}{K(u_i)} \sum_{j=1}^{n_s} a(u_i, u_j)\, x_j \right]$$

where n_s is the number of species; r is an intrinsic growth rate common to all species; $K(u_i)$ is the carrying capacity of species i whose value depends on the strategy used by species i; and $a(u_i, u_j)$ are interference coefficients that depend on both the strategy used by species i and the strategy used by species j. By definition, fitness for species i, designated by H_i, is the term in brackets and is a function of all strategies $\mathbf{u}$ and densities $\mathbf{x}$:

$$H_i(\mathbf{u}, \mathbf{x}) = \left[r - \frac{r}{K(u_i)} \sum_{j=1}^{n_s} a(u_i, u_j)\, x_j \right]. \tag{2}$$

Given the strategy vector $\mathbf{u}$, and the corresponding equilibrium solution $\mathbf{x}^*$, both $\mathbf{x}^*$ and every component of $\mathbf{u}$ except for u_i are held fixed in the following definition. A fitness landscape[1] for a surviving species i is defined as a plot of $H_i(w)$ vs. w. This function is obtained by replacing u_i in the function $H_i(\mathbf{u}, \mathbf{x}^*)$ by w holding all other strategies fixed. It follows that when $w = u_i$ equilibrium requires $H_i(w)|_{w=u_i} = 0$. By comparing the fitness landscapes of all surviving species, one will discover that, in general, none may be at maximum fitness. For a given strategy, u_i, if actual fitness (always zero at equilibrium) is below the maximum fitness on the fitness landscape for species i, then a greater equilibrium density could be obtained by using any different strategy displaced from u_i towards the strategy of maximum fitness, as illustrated in Fig. 2(a). However, as explained below, the strategy leading to the higher population density will not be evolutionarily stable if it is not at a maximum point on the adaptive landscape, as illustrated in Fig. 2(b).

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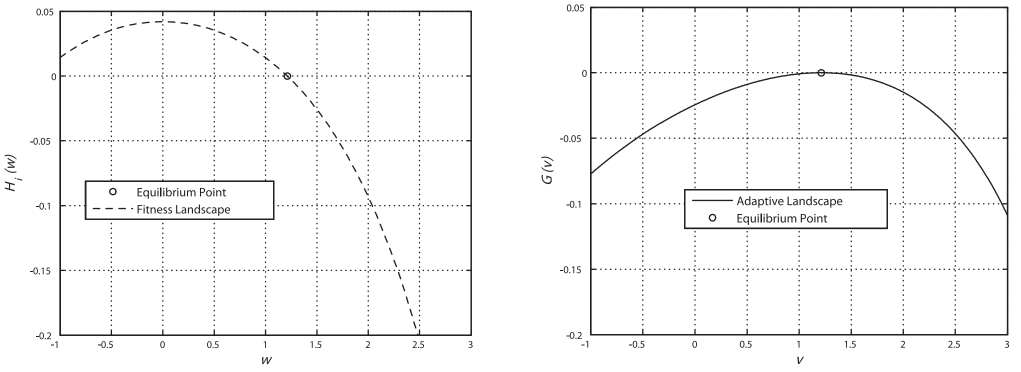
[1] We recognize that this term has been used to refer to other concepts in which the word 'landscape' is attached. By giving a specific definition of a fitness landscape, for our uses here, we hope any confusion in this regard has been avoided.



(a) (b)

Fig. 2. (a) The equilibrium solution ($u_1^* = 1.2126$) located by the circle on the fitness landscape is an evolutionarily stable strategy (ESS) as defined in the section on adaptive landscapes. This solution is at zero fitness with an equilibrium population of $x_1^* = 83.2124$. The higher fitness hump to the left implies that a larger equilibrium population density could be obtained by using a strategy such as $u_1 = 0$. However, if a species were to use this strategy, it could be invaded by a species of small population density using any strategy in the vicinity of the ESS. (b) The ESS strategy corresponds to a maximum on the adaptive landscape and is resistant to invasion by individuals using any other strategy.

Adaptive landscape

The adaptive landscape may be understood using the methods of evolutionary game theory (Vincent and Brown, 2005). The fitness-generating function 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

$$G(v, \mathbf{u}, \mathbf{x})|_{v=u_i} = H_i(\mathbf{u}, \mathbf{x}) \quad i = 1, \ldots, n_s \tag{3}$$

where $\mathbf{u}$ and $\mathbf{x}$ in G are the same as defined in H_i, and v is a virtual variable that has the property that replacing v in the G-function yields the fitness of any focal individual in a population of individuals defined by the same G-function. This possibility is not unusual and for the example cited above

$$G(v, \mathbf{u}, \mathbf{x}) = r - \frac{r}{K(v)} \sum_{j=1}^{n_x} a(v, u_j) x_j$$

The adaptive landscape differs from the fitness landscape in that only one landscape is needed to characterize the fitness for all species modelled by the G-function. Again for a given strategy vector $\mathbf{u}$, it is assumed that there exists an equilibrium solution $\mathbf{x}^*$ with at least one $x_i^* < 0$. The adaptive landscape corresponds to a plot of $G(v, \mathbf{u}, \mathbf{x}^*)$ vs. v where $\mathbf{u}$ and $\mathbf{x}^*$ are held fixed. The adaptive landscape may be thought of as a plot of the fitness of an individual using the strategy v near zero density when played against all other strategies at their respective equilibrium population densities, as was done to generate Fig. 2(b).

It can be shown that a necessary condition for a given strategy to be an evolutionarily stable strategy (ESS) is that it must correspond to a maximum point on the adaptive landscape (Vincent and Brown, 2005). Clearly, the OD solution $u_1 = 0$, as suggested by the fitness landscape of Fig. 2(a), does not satisfy this condition and hence it is not evolutionarily stable. In fact, the OD solution is a group fitness maximum. Any individual can benefit by not using the group optimal strategy and will increase its own fitness at the expense of others. This situation is best expressed in terms of the adaptive landscape of Fig. 2(b). The major property of an ESS is that if all individuals in a population are using ESS, then other individuals using a 'mutant' strategy cannot invade or even co-exist. The adaptive landscape provides a useful tool for determining the evolutionary stability of a given strategy.

Intelligent design landscape

An 'intelligent design landscape' is an adaptive landscape that contains lost world plateaus, isolated by cliffs and surrounded by featureless plains, and thereby discontinuous with the surrounding landscape (see above under Design). The literature on adaptive landscapes that we are aware of deals with a landscape that is continuous. Thus, we will refer to an adaptive landscape that is discontinuous as an ID landscape. The assertion inherent in the notion of irreducible complexity is that evolutionary processes used in ED can neither find the plateaus nor climb the cliffs. However, if there was only one plateau, then for life to exist, it must be on the plateau and the only design alternatives are OD and ED. For the moment, we will consider this to be the case, so that OD and ED can be compared and discussed in detail. After this discussion, we will return to the intelligent design landscape and discuss ID in detail.

OPTIMALITY DESIGN

Optimization is the foundation for many concepts such as least action, minimum potential, shortest path, and minimum cost; and has been and remains a prevalent concept in science, mathematics, and engineering. One might be tempted to say that OD is ID, arguing that an intelligent designer would seek to maximize species fitness. However, it is easy to show that, in general, an ED can invade an OD driving it to extinction. Nevertheless, there are some interesting features of OD that are applicable to both ED and ID.

In biology, fitness, $H_i(\mathbf{u}, \mathbf{x})$, determines the rate of growth as given by (1) and the problem in OD is to determine $\mathbf{u}$ such that, at equilibrium, this function takes on a maximum with respect to u_i for every species that has an equilibrium population greater than zero. At equilibrium for these species, this maximum value will be zero.

One numerical method for finding maximal points for the fitness function is to use a gradient-following algorithm for the strategy

$$\dot{u}_i = \frac{\partial H_i(\mathbf{u}, \mathbf{x})}{\partial u_i} \tag{4}$$

to be solved along with the population dynamics (1) until equilibrium is obtained. Although this method is not particularly efficient numerically, (4) will always converge to a maximum solution (Vincent and Grantham, 2002). We refer to (4) as a strategy dynamic because changes in strategy with time are determined from the solution of a differential equation. At equilibrium the gradient of the function approached zero, satisfying a necessary condition for a maximum. One advantage to using a gradient algorithm for solving an optimization problem is that it closely resembles the strategy dynamic used for evolutionary design on the adaptive landscape. The main difference is that while (4) is *ad hoc*, the strategy dynamics follows from the observation that a distribution of strategies (phenotypes) exists within the population of a given species of individuals (Darwin, 1859) (Fig. 1a).

Equilibrium solutions that maximize the H_i functions using equations (1) and (4) represent OD on a fitness landscape. Because OD maximizes group fitness within a given H_i function, it can always be invaded by an ESS when these two solutions differ (Brown and Vincent, 1987) (see below). Nevertheless, if there is a relationship between horizontal gene transfer and OD, optimality design may indeed play a role in nature in cases when there is no ESS. Indeed, this may be relatively common.

EVOLUTIONARY DESIGN

While both adaptive and fitness landscapes involve fitness, they are quite different concepts. If there are, say, three co-existing species, then there are three fitness landscapes, but only one adaptive landscape. A hill-climbing process takes place on the adaptive landscape, driven by a strategy dynamic that is determined from the population dynamics. The strategy dynamics are derived by placing a distribution of strategies (phenotypes) about the mean strategy for each species (as in Fig. 2a) and then determining the change in mean strategy for each species by integrating the population dynamics equations.

In terms of the G-function, the population dynamic equations are written as

$$\dot{x}_i = x_i\, G(v, \mathbf{u}, \mathbf{x})\big|_{v=u_i} \tag{5}$$

and first-order strategy dynamics derived from these equations are given by

$$\dot{u}_i = \sigma_i^2 \frac{\partial G(v, \mathbf{u}, \mathbf{x})}{\partial v}\bigg|_{v=u_i} \tag{6}$$

where σ_i^2 is related to the variance in the distribution of strategies about the mean. This dynamic results from Darwin's observation that there is heritable variation in traits associated with each type of organism rather than from the *ad hoc* algorithmic approach used with optimality design (Vincent and Brown, 2005).

Thinking in terms of an adaptive landscape leads to concepts of games and evolutionary design. Equations (5) and (6) when solved together are called Darwinian dynamics (Michod, 1999; Vincent and Brown, 2005). Darwinian dynamics will often result in an equilibrium solution for **x** and **u**. 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 using different (mutant) strategies, they are evolutionarily stable strategies (ESS) (Maynard-Smith, 1974). A necessary condition for an ESS is that the G-function takes on a maximum with respect to v at each strategy in the coalition. The ESS represents evolutionary design, and the equilibrium strategies are adapted in the robust sense of occurring as a result of natural selection.

COMPARING OD AND ED

The population dynamics of a biological system as defined by (1) or (5) are expressed in terms of fitness as a function of strategies used by the organisms. When these strategies are determined by maximizing a fitness H_i on a fitness landscape, this is referred to as OD.

When such strategies are determined by maximizing the *G*-function on an adaptive landscape, then this is referred to as ED. These two methods for determining strategies will generally yield different results when evolution is frequency dependent. In this case, OD organisms will usually be unable to co-exist with organisms resulting from ED. However, there are some interesting situations in which OD may have a role to play. Two such situations are examined below. The first situation is one in which both OD and ED 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 OD to mimic the ESS.

When OD and ED agree

The Lotka-Volterra competition model with fitness given by (2) has been studied extensively in an evolutionary setting (Case, 1982; Rummel and Roughgarden, 1983; Vincent *et al.*, 1993). Since this model is a useful paradigm for evolutionary processes, we will re-examine it here as a model for our design study. The fitness function for the *i*th species may be obtained from the following fitness-generating function (*G*-function) (Vincent and Brown, 2005),

$$G(v, \mathbf{u}, \mathbf{x}) = r - \frac{r}{K(v)} \sum_{j=1}^{n_s} a(v, u_j)\, x_j \tag{7}$$

by noting that (3) is satisfied by this choice. We will make use of the *K* and *a* functions used in Roughgarden (1983). That is,

$$K(v) = K_m \exp\left[-\frac{v^2}{2\sigma_k^2}\right] \tag{8}$$

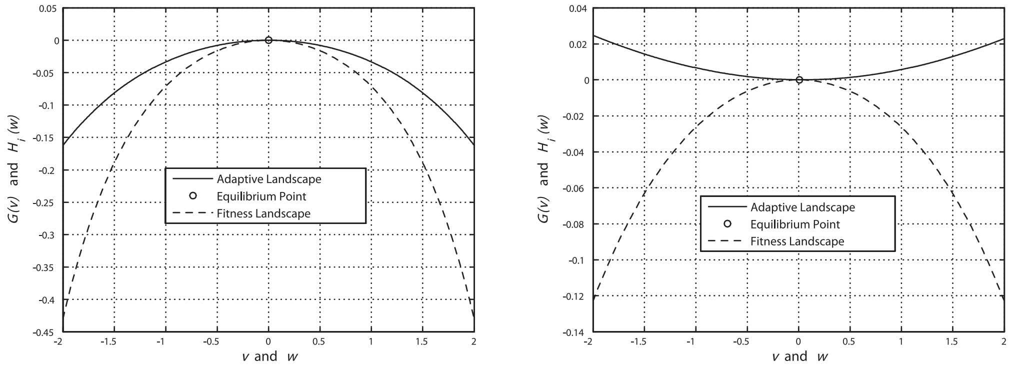
and

$$a(v, u_j) = \exp\left[-\frac{(v-u_j)^2}{2\sigma_a^2}\right]. \tag{9}$$

A nominal set of parameters is provided by $r = 0.25$, $K_m = 100$, $\sigma_a^2 = 4$, $\sigma_k^2 = 2$. Owing to the symmetry of this model, both Darwinian and optimality dynamics yield the same results. However, only when $\sigma_k^2 < \sigma_a^2$ does there exist an ESS solution. Figure 3(a) illustrates this situation using the nominal set of parameters. The strategy $u_1 = 0$ maximizes both the fitness function and the *G*-function. As such, it is both an ESS and provides the maximum possible equilibrium population size of $x_1 = 100$.

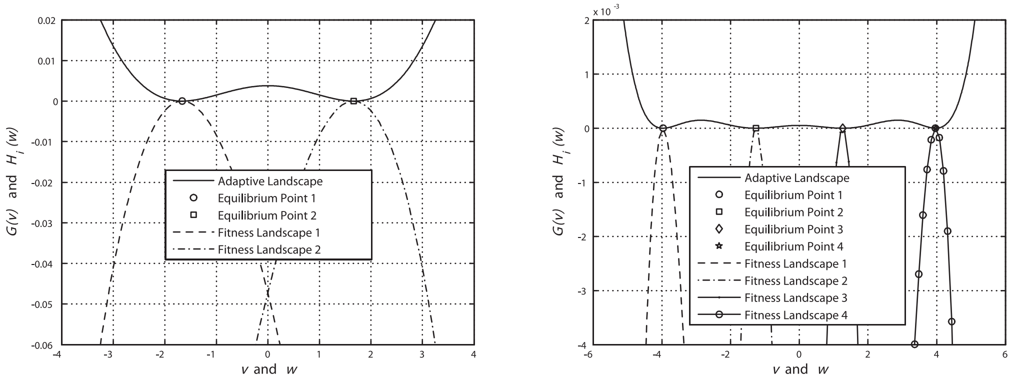
When $\sigma_k^2 > \sigma_a^2$, an ESS no longer exists (under an unbounded strategy set) as illustrated in Fig. 3(b), with $\sigma_k^2 = 5$. The strategy $u_1 = 0$ is at a maximum point on the fitness landscape, but is at a minimum point on the adaptive landscape. As a consequence, this strategy is easily invaded so that the co-existence of several strategies is possible. For example, using the nominal set of parameters except setting $\sigma_k^2 = 10$ and then using optimality (or Darwinian) dynamics, with two strategies to determine new equilibrium conditions, the two invading species evolve to $u_2^* = -u_3^* = 1.6651$ at an equilibrium population density of $x_2^* = x_3^* = 69.6440$, with both species at points of maximum fitness on the fitness landscapes (Fig. 4a).

It turns out that, for this example, any number of strategies may co-exist under OD. An example of four species is illustrated in Fig. 4(b) with equilibrium strategies and population



(a) (b)

Fig. 3. (a) When $\sigma_k < \sigma_a$ there exists an ESS coalition of one. OD and ED produce the same result. (b) When $\sigma_k > \sigma_a$ there is no ESS solution. However, OD and ED still produce the same results of $u_1 = 0$ with $x_1^* = 100$, although this result can be invaded by additional strategies (see text, Fig. 4).



(a) (b)

Fig. 4. (a) An OD coalition of two. (b) An OD coalition of four with equilibrium values given by $\mathbf{x}^* = [20.5987\ 57.4227\ 57.7652\ 19.6802]$ and $\mathbf{u}^* = [-3.9689\ -1.2635\ 1.2633\ 3.9687]$. If we fix these strategies and add a non-evolving mutant strategy, then under population dynamics, the coalition of four provides some protection from this invasion as noted in the text.

densities as noted in the figure caption. Additional co-existing strategies may be added and, as the number of co-existing strategies increases, the strategies together provide some resistance to invasion by non-evolving mutant strategies. For example, fixing the equilibrium values of Fig. 4(b), if one adds a single fixed mutant strategy of $u_5 = 5$ at an initial population density of $x_5 = 50$, this population will decrease with time until there is a population density less than one, as it competes with the species using the four remaining fixed strategies. However, if one relaxes the assumption of fixed strategies, then under either Darwinian or optimality dynamics, five strategies will be found to be able to co-exist at reasonable population densities. This result has some interesting implications. In a biological situation where Darwinian dynamics and OD lead to the same results, but where 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 simple cellular species in early life. Cellular structure may operate in such an environment where the requirement of many co-existing cellular types must be derived from a common stem cell. The resistance to invasion of several non-evolving mutant types located at evolutionary minimums provides some stability for the system, especially as it becomes saturated with greater diversity.

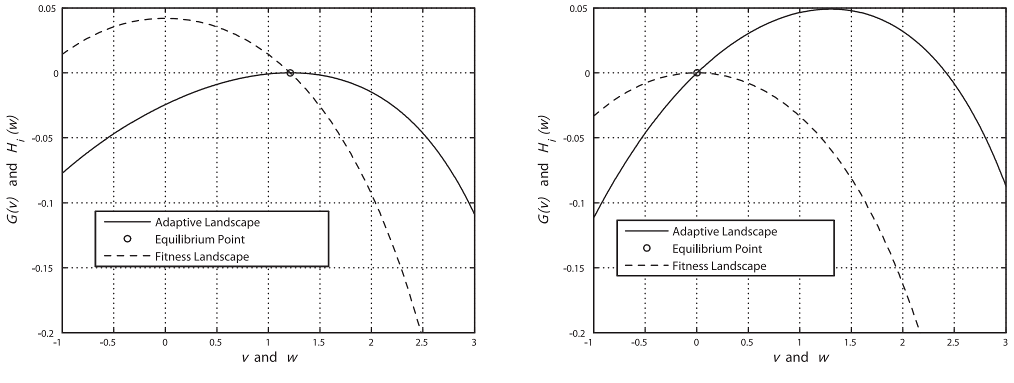
When OD and ED do not agree

When the ESS is frequency dependent, the optimality solution and the ESS solution will generally differ. For example, modifying model (7)–(9) by replacing (9) with

$$a(v, u_j) = 1 + \exp\left[-\frac{(v - u_j + \beta)^2}{2\sigma_a^2}\right] - \exp\left[-\frac{\beta^2}{2\sigma_a^2}\right] \tag{10}$$

introduces a non-symmetric competition coefficient that, in turn, results in a frequency-dependent solution for the ESS. Figures 5(a) and 5(b), generated using $r = 0.25$, $K_m = 100$, $\sigma_a^2 = 4$, $\sigma_k^2 = 4$, $\beta = 2$, illustrates the differences between the OD solution and the ED solution. Figure 5(a) shows an ESS at the maximal point on the adaptive landscape obtained as an equilibrium solution using ED [$u_1^* = 1.21$, $x_1^* = 83.20$]. Also shown is the fitness landscape indicating that higher fitness is possible by using a different strategy. Figure 5(b) shows the OD equilibrium solution [$u_1^* = 0$, $x_1^* = 100$] at a maximal point on the fitness landscape. This solution is clearly not an ESS because it is not at a maximal point on the adaptive landscape.

However, when two or more optimality solutions are played together, the situation changes. Starting with two non-zero populations with different strategies, and using the gradient-following algorithm, both populations arrive at the same equilibrium solution $x_i^* = 47.7529$, $u_i^* = 0.6065$ ($i = 1, 2$). The two H functions lie on top of one another (Fig. 6a). Both populations are distinct, but indistinguishable in terms of strategy (they may differ in other respects that do not influence their fitness functions but nevertheless keep the two species from interbreeding). Note that in going from optimizing a single strategy (Fig. 5b) to

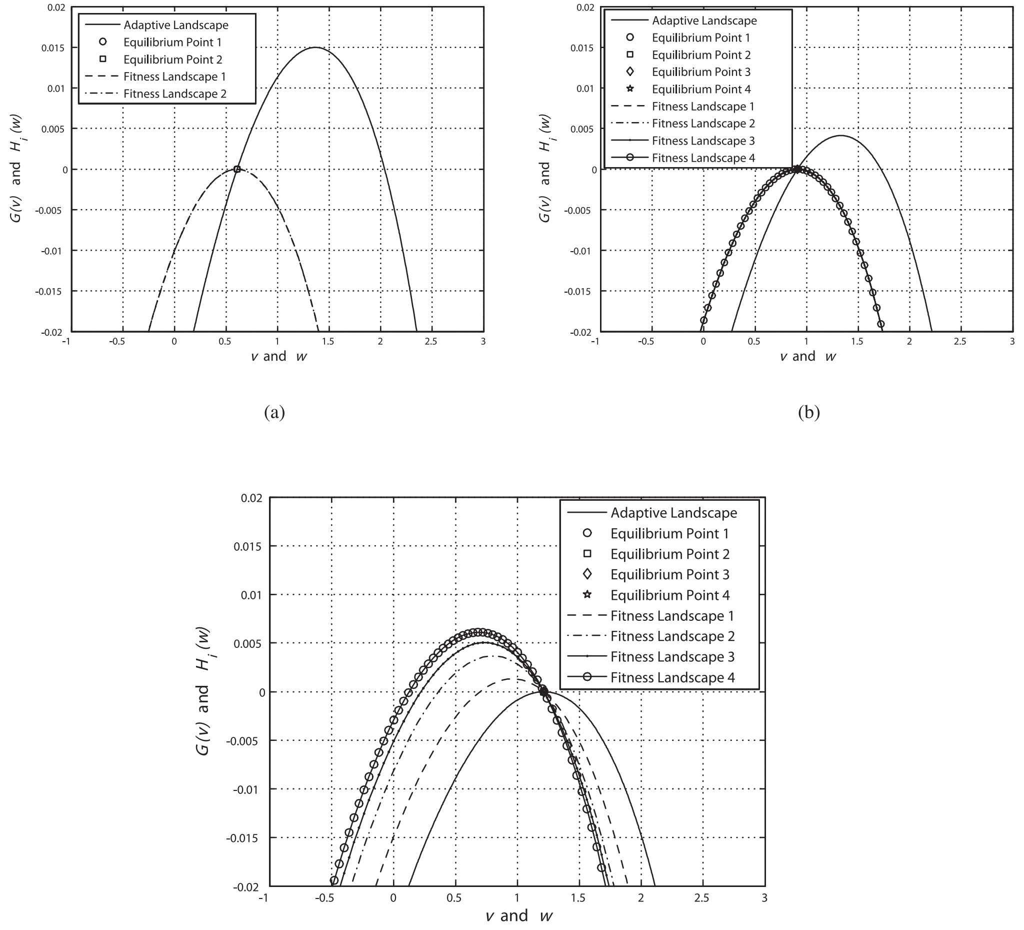


(a) (b)

Fig. 5. (a) With frequency dependence there is an ESS coalition of one at a maximum point on the adaptive landscape, but it does not maximize fitness. (b) A single strategy OD solution at a maximum point on the fitness landscape. If the ESS strategy of Fig. 5(a) is played with the OD solution of Fig. 5(b), it will drive the OD solution to extinction.

two strategies (Fig. 6a), the two strategies are closer in value to ESS strategy [0 → 0.6065]. Also, the sum of the two equilibrium populations is less than the value obtained for the single population.

This process can be continued. Four different populations results in the optimality solution $x_i^* = 22.5427$, $u_i^* = 0.9098$ $(i = 1, \ldots, 4)$. This strategy is even closer to the ESS solution $u = 1.21$. Consider playing these four against a fifth mutant strategy that is not



(a)

(b)

(c)

Fig. 6. (a) The OD solutions for two strategies that have the same equilibrium solutions and are closer to the ESS solution of Fig. 5(a) than the single strategy optimal equilibrium solution of Fig. 5(b). However, the sum of the population densities is less than the single strategy case $\mathrm{sum}(\mathbf{x}) = 95.50$. (b) Four OD strategies obtained using the gradient-following algorithm more closely approximate the ESS solution with a further drop in $\mathrm{sum}(\mathbf{x}) = 90.16$. The implication is as the number of OD solutions becomes large, not only will the common strategy approach the ESS, but the sum of the population numbers will approach the equilibrium population of a single strategy ESS. (c) Under Darwinian dynamics, four strategies will all co-evolve to the ESS, with $\mathrm{sum}(\mathbf{x}) = 83.20$. This result will hold for any number of strategies.

near the ESS, say $u_5 = 2$. The four will continue to co-exist while the mutant is driven to extinction. We conjecture that optimizing a very large number of different populations will result in the situation where all of the H functions will lie on top of the G-function and the common strategy will be ESS. It appears that a single strategy ESS can be viewed either as a guild of many distinct optimizers all playing the same strategy or as a population composed of identical individuals all playing the same strategy. It should be noted that the optimization procedure used here when more than one strategy is involved has the properties of a Nash solution (Vincent and Grantham, 1981).

Using the same populations and initial conditions used to produce Fig. 6(b), but now using Darwinian dynamics to drive the system to equilibrium, leads to an outcome in which none of the species (each using the ESS strategy) optimizes their individual fitness functions as illustrated in Fig. 6(c). In this case, all populations arrive at the ESS solution $u_i^* = 1.21$ $(i = 1, \ldots, 4)$, but at different equilibrium population densities $\mathbf{x}^* = [11.84\ 20.33\ 24.15\ 26.88]$, the sum of which adds up to the same density (83.20) as a single population obtains at the ESS. Note that the species with the smallest equilibrium density (H_1 designated by the dashed line) is very close to having a fitness close to the ESS in value. This result is consistent with our previous observation that a very large number of optimizers (with very small equilibrium population densities) will have a strategy very close to the ESS.

Multicellularity

When there is no frequency dependence, and there is no ESS, OD and ED will always agree and both Darwinian dynamics and the gradient-following algorithm used by OD will lead to the same results. However, in this case, there is no resistance to the invasion of additional strategies. It is easy to see that this could facilitate, from a single-celled ancestor, the formation of a multicellular, yet simple, organism, comprised of divergent cell types whose origins are allowed to co-exist in the absence of an ESS.

In the modelling of cell growth using evolutionary game methods, Gatenby and Vincent (2003) discovered an underlying reason why the strategies used by different cell types need not be ESS. In short, because there are situations in which OD and ED yield the same strategy solution at a minimum point on the adaptive landscape, the ecological co-existence of a cohort of cellular types is permitted. This cohort, as a group, may be thought of as cooperating in that they perform a function and do not allow other cells to join the cohort. The cooperative nature of such cells plays a key role in allowing for the co-existence of a large number of similar, but different, functioning cell types, which, in turn, may have allowed for complex organisms to have evolved composed of skin, blood, liver, etc. Unfortunately, unless carefully controlled (e.g. via DNA regulatory complexes), cooperation is always subject to cheating that can lead to the formation of cancer. In other words, the potential for carcinogenesis may be the consequence of a cellular landscape that permits the co-existence of different cell types that do not comprise an ESS.

With the introduction of frequency dependence, OD and ED no longer agree. However, Darwinian dynamics can still result in multiple cell types that can be ESS or non-ESS. Any non-ESS solutions (with or without frequency dependence) would require clonal reproduction to avoid further invasions once a complex organ has been established. Such restrictions are common in cells. As we have already noted, non-ESS coalitions do have some resistance to invasion and it may well be that a complex organ becomes defined when this grouping gets sufficiently large. Once established, two possibilities could maintain the organism. As previously mentioned, genetic constraints could require that cells reproduce as clones or, under changing environmental conditions, with the addition of frequency dependence, the adaptive landscape could change such that the cells in a complex organ evolve to an ESS.

INTELLIGENT DESIGN

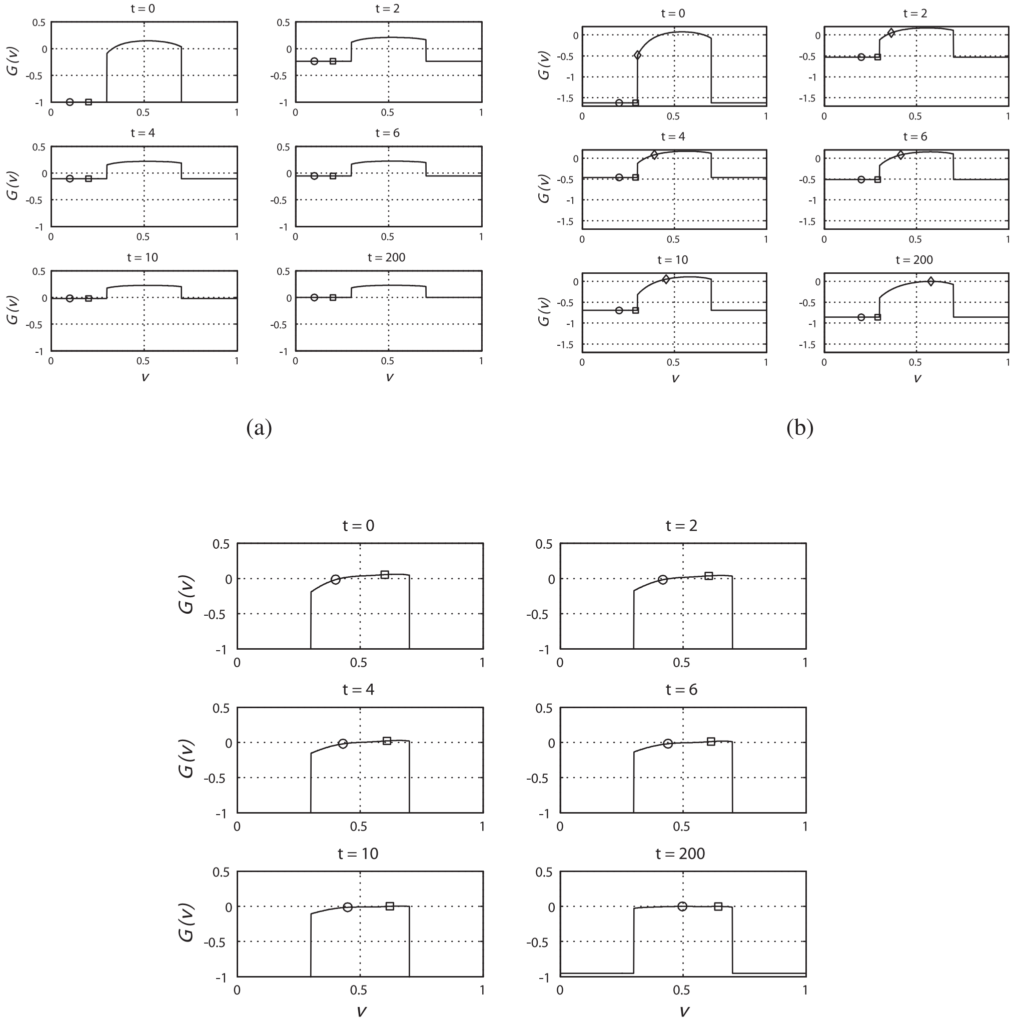
To examine claims regarding irreducible complexity, we model the same strategy dynamics on discontinuous ID adaptive landscapes. We use the same *G*-function modelling framework to test the assertion that Darwinian dynamics cannot find ESS solutions on a discontinuous landscape that entails all the defining characteristics of Behe's irreducible complexity, and to ask how strategy evolution will be different on a landscape where Darwinian processes operate, but are prevented (perhaps) from reaching the ESS because of problems of irreducible complexity. We first address the challenge of modelling discontinuous landscapes, and then explore the behaviour of evolving systems on such landscapes.

Overlooking arguments against the possibility that discontinuities exist in nature (see below), it is not difficult to create an ID landscape through the use of step functions. For example, Fig. 7(a) shows the *G*-function for the ID landscape given by (7), (8), and (10), except that both $K(v)$ and $a(v, u_i)$ are multiplied by step functions. Two species are introduced at non-equilibrium numbers and the only changes that can take place under Darwinian dynamics are for the densities of each species to reach equilibrium. This process is illustrated in the remaining panels of Fig. 7(a). The strategies cannot change because the slope of the landscape is flat and there is no selection. Hence no evolution occurs using Darwinian dynamics alone.

Darwinian dynamics in regions of zero slope

It follows from Fig. 7(a) that evolution, under Darwinian dynamics, in regions of zero slope, is not possible without some additional observation about natural processes. In fact, Darwin provided the needed observation with his argument 'Like tends to beget like and there is heritable variation in traits associated with each type of organism'. This observation was used in the development of the strategy dynamics as given in (6). The reason that equation (6) does not provide evolution on a flat landscape is that this expression is an approximation and does not capture some of the more subtle elements used by natural selection. One must go back to basic principles to understand how a distribution of strategies can move a species on the featureless plain of the flat landscape. The explanation involves the concept of drift.

Genetic drift is a well-known biological process. On the featureless plain, one strategy is as good as another, allowing any number of strategies to exist. One definition of a species is given in terms of a mean strategy with a cluster of strategies (phenotypes) distributed about this mean (Vincent and Brown, 2005). This cluster represents the 'heritable variation' referred to by Darwin. Because there is no advantage among strategies, the mean strategy carrying the distribution will exhibit random walk, and the total variation within the species will increase [see Gould (2002) for a discussion of drift, drives in individuals, and higher levels of evolutionary change]. Thus random walk along with increase in variation represents drift.



(a)

(b)

(c)

Fig. 7. (a) An ID landscape with two species that cannot evolve via Darwinian dynamics alone. (b) Because of drift, a strategy at the tail of a distribution is able to climb the plateau and evolve to an ESS on the plateau. (c) Two species located on the top of a plateau evolve to an ESS coalition of two.

Drift with Darwinian dynamics allows evolutionary change

Given drift, random walk guarantees there is a non-zero probability of reaching a given point on a featureless plain in finite time. The mean strategy that defines a species need not even reach the edge of a plateau. Only one of the phenotypes in the distribution need do so. Once any variant phenotype strategy reaches the infinite slope of the plateau, it immediately climbs via Darwinian dynamics. This process is simulated using three strategies, two on the plain and one at the cliff base (Fig. 7b). Additional strategies could be shown but would not change the result. Under Darwinian dynamics, the cliff-base strategy immediately jumps to the top of the plateau and then evolves to an ESS. Because this strategy is able to climb the plateau, all remaining strategies on the plain go extinct as verified by their negative fitness in the last panel.

Unless the top of the plateau is also flat, Darwinian dynamics drives evolution to equilibrium points that are often ESS (Fig. 7b). The plateau is a mini adaptive landscape with all the evolutionary features found on such a landscape. For example, two species are able to co-exist on the plateau as an ESS coalition (Fig. 7c).

Our first conclusion, that Darwinian dynamics alone cannot drive evolution on a featureless plain towards a distant lost world plateau, recognizes the undirected nature of Darwin's theory of natural selection, as well as the validity of ID claims that natural selection alone cannot drive features towards irreducible complexity. We do not thereby imply any agreement with the ID claim that true irreducible complexity actually exists in biological systems (see Dawkins, 2006a, and below).

Our second conclusion, that random walks across the plateau have some real probability of finding the cliff, addresses the ID claim that 'irreducible' biological complexity cannot possibly occur by chance. Of course, it could, and the actual probability of this is an empirical question. We note (again without agreement, and as outside the scope of this exercise) that estimating these probabilities has been attempted by Behe and others (Behe *et al.*, 2000); and the relevance of such calculations has been rebutted beginning with Darwin (1859, see Difficulties on Theory) and continuing to the present day (see, for example, discussion in Dawkins, 2006b). ID theorists, of course, are committed to the claim that the featureless plains are vast (*sensu* Dennett, 1995) and uncrossable, whereas biological study finds in repeated examples (the eye, flight, immune systems, bacterial flagella) that the plains are empirically quite small, and in many cases have been crossed repeatedly over small fractions of evolutionary time.

Our third conclusion addresses the narrow scope of the irreducible complexity argument forwarded in ID theory, which we interpret to run something like this: 'If natural selection (alone) cannot navigate the plain and the empirical probability of finding the cliff by random chance (alone) is negligibly small, then the only alternative is an intelligent source for the design'. By coupling random walk exploration of the featureless plain with Darwinian dynamics, our model makes two points: first, that irreducible complexity in ID theory is predominantly an empirical claim about rates of random walks and the size of the featureless plain (rather than a fundamental criticism of the structure of evolutionary theory); and, second, that the ID 'inference to intelligent design' grounded by reference to irreducible complexity cannot be made because alternative explanations have not been considered. In the case of our models, the arrival at the ESS of strategies originally on the plain but near the cliff did occur, through the combination of drift with natural selection. The consideration of phenotypic plasticity, in addition to Darwinian heritable variation, leads to an even more evolutionarily powerful alternative, the Baldwin effect (Baldwin, 1896) discussed below.

DISCUSSION

We have used a model of Lotka-Volterra competition to illustrate what we take to be universal patterns of OD on fitness landscapes, ED on adaptive landscapes, and ID on intelligent design landscapes. This model is well known and has previously been examined in a number of different contexts to illustrate general principles of fitness-generating functions, Darwinian dynamics, and evolutionary systems (Vincent and Brown, 2005). Our main conclusions are that:

1. The ID argument based on irreducible complexity does not disprove that ED drives evolution.
2. There are some surprising connections between OD and ED that exist such as the fact that they can give identical results and in cases were an ESS does not exist, OD can provide both an initial avenue for co-existence of new species at low diversity, and yet some protection against invasion at a higher diversity.
3. Because horizontal gene transfer may disrupt frequency-dependent ED, OD might play a role in evolution as well.

Rather than attempting to reiterate the details involved with the above three conclusions, we devote this discussion section to some speculation regarding item 3 above. We provided these comments to stimulate discussion as well as to provide some ideas that require further investigation.

OD and ED will generally differ under frequency dependence. Frequency dependence is a common character of selective systems driven by individual selection. However, Woese (2004) has argued that during the early evolution of life, horizontal gene transfer (HGT) prompted evolution driven by reticulated rather than linear descent. In such a system, conditions leading to frequency-dependent selection within a clade may have been rare. Woese (2004) stated that evolution became communal and thus that HGT led to an optimal searching of design space. Although Woese did not formally model this as group selection, we hypothesize that sufficient HGT may lead to OD on fitness landscapes. Another example of OD on fitness landscapes is that of clonal cell proliferation within normal tissue, which has been modelled as an evolutionarily unstable trait (at the cellular, not organismal, level) that gives way to cancer by escaping organismal regulation (Vincent and Brown, 2005).

ED on an adaptive landscape results in an ESS cohort that prevents further speciation. In contrast, OD on a fitness landscape where an ESS would exist under ED, may result in speciation occurring without resistance at first (Fig. 6a), but as the guild size grows, it begins to mimic the ESS, and further speciation is resisted (Fig. 6b). How then shall the differences between OD and ED processes be characterized? Differing outcomes of the design process occur first when peaks of the possible landscapes do not coincide, as for example when the G-function and H-function(s) maxima differ from one another, leading to a different outcome with OD than ED. This difference becomes less when strategies can evolve, with increasing guild sizes on an OD landscape mimicking an ESS on an ED landscape.

The Cambrian explosion recorded in the fossil record has not been satisfactorily accounted for, although tentative explanations abound. In a laundry list of possibilities, Valentine (2004) concludes that the abrupt change in the fossil record is due to imperfections of the record itself; or that the abrupt increase in phyla diversity was real and arose out of physical (e.g. increasing oxygen levels), ecological (e.g. use of vision in predation), or intrinsic evolutionary (e.g. developmental) changes. The modelling exercise presented above suggests the speculative view that intrinsic evolutionary changes related to HGT could account for unique attributes of this faunal transition.

If early life operated without frequency dependence, evolution would have proceeded without ESS cohorts, precluding the further diversification that has characterized the evolution of fauna since the Cambrian. This could allow a proliferation of types (i.e. the divergence of body plans), leading to very rapid diversification across a complex fitness landscape. As frequency dependence became prevalent, constraints on new diversity arose as selection dynamics shifted over to adaptive landscapes and selection favoured stabilization of taxa cohorts around the ESS. This would mimic patterns of rapid diversification of phyla and the subsequent extinction of some and stabilization of others that characterized early faunal evolution.

Why would early evolution be characterized by fitness rather than adaptive landscapes? We hypothesize this would result if early evolution was characterized by loosely (rather than tightly) co-adapted gene complexes or modules, as Woese (2004) has argued, and HGT was a dominant adaptive strategy in early microbial evolution that led to highly reticulate molecular phylogenetic patterns. Woese provided some evidence that his hypothesis better accounts for the root(s) of the Moneral-Archaeal-Eucaryote molecular phylogenetic tree than does the hypothesis of common descent. As gene complexes became more tightly co-evolved, the importance (and isolation) of the individual rose, and a phase transition occurred from evolution based on a group optimal fitness under HGT to individual adaptation within reproductive lineages. If major changes in the evolutionary landscape preceding the Cambrian explosion were accompanied by independent modular gene-complexes and their regulation, as has been suggested (Valentine, 2004), this would lead to a leap in the frequency of HGT, and the consequent shift away from adaptive landscapes back to fitness landscapes. Our models suggest that whenever such a shift occurs, it would be accompanied by rapid but self-terminating diversification, a pattern similar to that of the Cambrian explosion.

Design outcomes may depend on whether a given landscape contains discontinuities as proposed by ID. However, there are empirical and theoretical reasons to suspect that discontinuities are unlikely to be maintained on landscapes of any sort, as evolving landscapes characteristically shift under the adaptive forces at work on the biological entities they characterize. The effect of rapid diversification with gradient-climbing algorithms on an OD landscape is to 'approximate' ESS conditions that cannot be found directly by selection. A similar process was first suggested by Baldwin (1896) to allow selectively favoured phenotypic plasticity to become fixed, and Dennett (1995) has argued that this induces learned (that is, intelligent) behaviour to become innate. Phenotypic plasticity allows the exploration, in a single generation, of an area of phenotypic design space around the innate genotype for abrupt changes in fitness (Dennett's 'good tricks'; our lost world plateaus). A continuum of such effects exists, from loosely co-adapted statistical proteins to antibody systems (Woese, 2004) to plastic development (Dennett, 1995; Valentine, 2004) to learning (Baldwin, 1896).

ID theory proposes a landscape composed of plateaus separated by featureless plains. We have shown that genetic drift allows for species to cross such a plain, and once atop the plateau evolution in terms of gradual changes can take place by Darwinian processes. What do the phenotypic plasticity of Baldwin and similar effects do to the shape of adaptive landscapes? In regions near any abrupt increase in fitness, such as a lost world plateau, the Baldwin effect creates an increase in fitness for any phenotype that, while itself still below the plateau, is close enough to it that some phenotypically plastic individual will nevertheless develop or learn plateau strategies. Thus, the otherwise uncrossable featureless plain at the base of the plateau will become a gradually sloping upward rise (see Dennett, 1995). For this reason, although the actual extent of featureless plains on evolutionary landscapes remains an empirical question, the occurrence of extensive plains at the base of lost world plateaus is prevented by the Baldwin effect, which, in evolutionary systems of complex organisms, turns such featureless plains into slopes readily navigated by natural selection. Thus, the argument from ID theory that such landscapes (described as irreducibly complex) cannot be navigated by natural selection is shown to be based on an oversimplification of evolutionary theory and a failure to engage the empirical findings of biology.

If lost world plateaus are biologically discovered and occupied in this manner, what pattern of evolution would emerge?: punctuated equilibrium (Eldridge and Gould, 1972; Gould and Eldridge 1977), where periods of change are very rapid (punctuation), but are preceded and followed by periods of stability (stasis). In a densely populated adaptive landscape, existing plateaus are expected to be occupied. In a sparsely populated landscape (e.g. pre-Cambrian), plateaus may exist as yet undiscovered by the tree of life, or awaiting creation as the landscape shifts under evolving populations. The discovery of broad plateaus would allow evolutionary novelty and support rapid adaptive radiation, as a population leaps to the top of the cliff and radiates across the new landscape. This pattern is similar to that observed in the Cambrian explosion. Each occupied plateau then becomes the (flexible) adaptive landscape of a new radiation, and may itself lead to the formation of new lost worlds still to be discovered. As a speculative example, multi-cellularity led to a landscape that contained lost worlds of bilateral symmetry and a true gut. The occupation of this plateau led to another landscape with lost worlds shaped by developmental processes and regulatory genes. This is the plateau occupied by the major phyla of metazoic life today.

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