The Affordance Landscape: The Spatial Metaphors of Evolution

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Abstract The adaptive landscape is a metaphorical device employed to depict the evolutionary change in a population or lineage undergoing natural selection. It is a powerful heuristic and didactic tool. This paper has two objectives. The first is to dig beneath the adaptive landscape in order to expose certain presuppositions about evolution concealed there. The second is to propose and motivate an alternative spatial metaphor, one that embodies a wholly different set of presuppositions. I develop the idea that adaptive evolution occurs on an 'affordance landscape.' The conception of adaptation—both the process and the product—that follows from adopting the affordance landscape metaphor is a significant departure from the conception of adaptation embodied in orthodox Modern Synthesis biology.

Spatial metaphors abound in evolutionary biology. Biologists speak of genotype space, phenotype space, and a 'map' between them. Phylogenetic propinquity is measured as a distance in an abstract space of nucleotide sequences (Nei 1972). Molecular evolution is envisaged as occurring in a 'protein space' (Maynard Smith 1970). Morphological diversity is represented by a manifold of dimensions of morphospace (McGhee 2007). Such spatial metaphors contribute to evolutionary thinking in myriad ways. Like scientific metaphors in general, they make recondite theoretical concepts accessible and tractable. They point toward ways in which our theoretical concepts may be extended, expanded and revised. They suggest to us sometimes surprising implications of our theories, and in turn help generate empirical predictions. But they do not come free of cost. In giving form to inchoate concepts, they may also constrain or bias our use of them in subtle and subliminal ways. Such impositions, in turn, may obscure from our view what might otherwise

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G. Barker et al. (eds.), *Entangled Life*, History, Philosophy and Theory of the Life Sciences 4, DOI 10.1007/978-94-007-7067-6_11,

be perfectly obvious interpretations, or empirical consequences, of our theories. The use of metaphors may well be essential to scientific thinking: “Metaphor and simile are the characteristic tropes of scientific thought, not formal validity of argument” (Harré 1986, 7). Nevertheless, it imposes a burden on scientific practice: “The price of metaphor is eternal vigilance” (Lewontin 2001a, 1264).[1]

The adaptive landscape is among the most vivid, pervasive and enduring spatial metaphors in biology. It is a device employed to depict evolutionary change in a population or lineage undergoing natural selection.[2]

> The idea … has become a standard imagination prosthesis for evolutionary theorists. It has proven its value in literally thousands of applications, including many outside of evolutionary theory. (Dennett 1995, 190)

So powerful is it as a heuristic and didactic tool, that we seldom enquire into the ways it might immure our thinking about adaptive evolution. Nor, for that matter, are we inclined to question the commonly held presuppositions about the process of adaptive evolution that make the adaptive landscape such an apt representation. But the ‘price of metaphor’ suggests that we should.

This essay has two objectives. The first is to dig beneath the adaptive landscape in order to expose certain presuppositions about evolution that the metaphor conceals. The second is to propose and motivate an alternative spatial metaphor, one that embodies a wholly different set of presuppositions. I outline the idea that adaptive evolution occurs on an ‘affordance landscape.’ The adaptive landscape and the affordance landscape underwrite strongly divergent conceptions of adaptive evolution. The crucial difference resides in the role that each accords to organisms in the process of evolution. Whereas the adaptive landscape entrenches the Modern Synthesis view that organisms make no substantive contribution to adaptive evolution, the affordance landscape underscores the way that the distinctive capacities of organisms create and constitute the conditions under which evolution occurs.

1 The Adaptive Landscape

The adaptive landscape is a pictorial device used to portray the evolution of populations and lineages. Adaptive evolution is depicted as a trajectory traversing a multi-dimensional surface. This surface resides in a space whose axes represent traits, one dimension for each trait. Each point in the multi-dimensional ‘design

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[1] With characteristic modesty, Lewontin credits this dictum—an allusion to a similar saying about the condition or price of liberty—to Rosenblueth and Wiener. However, I was unable to find it in any of their co-authored papers. It appears unattributed, though enclosed in quotation marks, in Lewontin (1963, 230).

[2] Some productive uses of it can be found in Lande (1976), Flyvbjerg and Lautrup (1992), Niklas (1997), and Sloman (2000).

space' thus corresponds to an individual organism's total phenotype or form.[3] There is a further axis in addition to the trait dimensions; each individual total phenotype has a fitness, represented as an altitude on the landscape. Individuals with higher fitness, so the story goes, generally beget phenotypically similar individuals with comparably high fitness. As evolutionary novelties are introduced into a population, some will confer yet higher fitness on their bearers. So long as the selection coefficients are sufficiently high, that is to say, the slopes are sufficiently steep, a population undergoing selection will be drawn inexorably toward a local fitness optimum. The local fitness optima are 'adaptive peaks,' good locations in 'design space.' Populations at these optima are well adapted to their conditions of existence. A population inhabiting a valley may split, each moiety moving toward a different adaptive peak. The adaptive landscape device thus illustrates the way populations undergoing natural selection become both increasingly well suited to survival and reproduction in their respective environments *and* increasingly diverse. All in all, it is an elegant way to represent adaptive evolution. "The value of an adaptive topography is that it is easily visualized and so makes the evolutionary dynamics of the population intuitively clear" (Lande 1976, 315).

Adaptive evolution, then, is visualized as a process in which a population or lineage traverses a fitness surface under the influence of evolutionary forces; its trajectory is explained exclusively or primarily by the topography of that surface.

> Adaptive evolution is a search process—driven by mutation, recombination, and selection—on fixed or deforming fitness landscapes. An adapting population flows over the landscape under these forces. The structures of such landscapes, smooth or rugged, governs both the evolvability of populations and the sustained fitness of their members. The structure of the fitness landscape inevitably imposes limitations on adaptive search. (Kauffman 1993, 118)

1.1 Evolution on the Adaptive Landscape

Unpacking the adaptive landscape metaphor discloses a number of non-trivial, but widely endorsed, preconceptions about adaptive evolutionary change. The landscape suggests that adaptive evolutionary change is robust, in the sense that it is relatively insensitive to initial or perturbing conditions. A population will move toward its local summit, even if it is deflected by deleterious mutations, or impeded by constraints.

The adaptive landscape places other, less conspicuous, demands upon the relation between evolutionary trajectories and the space they move through. Most importantly, 'adaptive space' is autonomous of form, inert and unchanging. A location in design space has its adaptive value (its fitness) whether or not it is occupied.

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[3] The first use of this device seems to have appeared in Simpson (1944). It is not to be confused with Sewall Wright's (1932) fitness landscape (although it often is) in which the axes are allele frequencies.

Form and landscape are asymmetrically related; form evolves in response to the landscape, but not vice versa. This asymmetry is necessary if adaptive evolution is to be thought of as form *conforming* to the exigencies of design space.

Further, the adaptive landscape can represent adaptive evolution at any scale, from sub-population to kingdom.[4] That being so, adaptive evolution would appear to be scale-independent. The same processes and dynamics that apply within a population within a generation also apply to the evolution of classes, phyla, and kingdoms, over vast stretches of time. The adaptive evolution of higher taxa is simply the adaptive dynamics of populations scaled up. It consists in the introduction of small random mutations and the gradual progression of populations up adaptive slope, and the divergence of lineages toward adjacent slopes.

1.2 Convergence and Contingency

This conception of adaptive evolution forms the backdrop for a number of disputes about the tempo and mode of large-scale evolution.[5] It is most notably evident in the debate concerning the convergence and contingency of evolution. Simon Conway Morris (2010) has consistently maintained that macro-evolutionary trajectories are convergent (and non-contingent).[6]

> What we know of evolution suggests ... [that] ... convergence is ubiquitous and the constraints of life make the emergence of the various biological properties very probable, if not inevitable. (Conway Morris 2010, 283–284)

Stephen Jay Gould (2002) steadfastly argued for the contrary view, that evolutionary change is non-convergent and highly contingent (Beatty 1995). As historical processes, evolutionary trajectories are subject to all the vagaries of history, the unpredictable occurrences thrown up by chance. The history of any given lineage might easily have turned out very differently than it did. Gould illustrates the contingency of evolution with the metaphor of rewinding a tape:

> You press the rewind button and .... go back to any such time and place in the past. [A]ny replay of the tape would lead evolution down a pathway radically different to the road actually taken. (Gould 1989, 50)

This is a heated and complicated issue. It is not my intention to resolve it, but merely to point out an interesting feature of the dialectic. These diametrically opposed

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[4] There may be differences in landscape topology as we investigate different levels of detail (Wilkins and Godfrey-Smith 2009), but the processes are the same at every scale.

[5] Indeed the adaptive landscape metaphor figures explicitly in many discussions of macro-evolutionary change (Simpson 1944; Stanley 1998).

[6] See Beatty (1995) for an extended discussion of contingency in evolution. On convergence and parallelism in evolution, see Powell (2007, 2012) and Pearce (2012).

positions arise from a shared conviction—viz. if evolution is adaptive, then it is convergent and non-contingent. The adaptive landscape provides support to this supposition. The trajectory of a lineage undergoing *adaptive* evolution is determined principally by the contours of the landscape (therefore, it is non-contingent). Given that ex hypothesi there are few peaks (few good locations in design space), over time biological lineages will tend to converge upon them, no matter their starting point.

> The phenomenon of convergent evolution means that there are a limited number of ways of making a living in nature, a limited number of ways of functioning well in any particular environment. … We can model this reality in an adaptive landscape by specifying the location of adaptive peaks for particular ways of life. (McGhee 2007, 35)

1.3 Niches

If the adaptive landscape illuminates the significant features of adaptation as a *process*, then another standard spatial metaphor, the niche, neatly captures the presumptive nature of adaptation as a *product*. A (non-metaphorical) niche is a space into which something—say, a statue—might fit. An evolutionary niche is a set of properties of an organism's environment, to which organismal form may fit.

The niche concept codifies a particular relation between organism and environment, thought to be integral to a genuine understanding of adaptation. Organismal form and the niches to which it adapts are decoupled and asymmetrically dependent.

> To make the metaphor of adaptation work, environments or ecological niches must exist before the organisms that fill them. Otherwise environments couldn't *cause* organisms to fill those niches. The history of life is then the history of coming into being of new forms that fit more closely into these pre-existing niches. (Lewontin 2001b, 63)

Lewontin claims that the decoupling of form and niche is made obligatory by the concept of adaptation:

> So long as we persist in thinking of evolution as adaptation, we are trapped into an insistence on the autonomous existence of environments independent of living creatures. (Lewontin 2001b, 63)

This conclusion follows from the commonly held conviction that adaptation is adaptation *to* some external feature. Lewontin (reluctantly) reaffirms:

> Adaptation is the process of evolutionary change by which the organism provides a better and better "solution" to the "problem," and the end result is the state of being adapted. (Lewontin 1978, 213)

A nice illustration of this use of the niche concept appears in the very issue of *Scientific American* in which Lewontin first questions its coherence. In explaining the distinctive mode of life of New Zealand's three kiwi species (*Apteryx* spp.), William A. Calder III says,

> I prefer to look on this curious bird as a classic example of convergent evolution. In this view an avian organism has acquired a remarkable set of characteristics that we generally associate not with birds but with mammals. … When there were no mammals present to lay claim to the niches in this hospitable environment, birds were free to do so. (Calder 1978, 142)[7]

Insofar as a trait is an adaptation, then, it must be identifiable as a response to pressures exerted on form by the niche or external environment. That, in turn, requires that we are able to bracket off the contributions that the environment makes to evolutionary change from those of the internal features of biological form. There is an asymmetric relation between environment and organismal form. As Peter Godfrey-Smith notes, in this standard picture...

> organisms respond to the environment, but the environment is largely autonomous with respect to the organisms. The environment is seen as either stable (as far as the time scale of the evolutionary process in question is concerned) or else as changing according to its own intrinsic dynamics. (Godfrey-Smith 2001, 254)

The separation of organism and environment conjoined with the explanatory primacy of environment over form conspire against any substantive role for organisms in the process of adaptive evolution.

> In this view the organism is the object of evolutionary forces, the passive nexus of independent external and internal forces, one generating "problems" at random with respect to the organism, the other generating "solutions" at random with respect to the environment. (Lewontin 2001b, 47)

The traditional niche concept complements the adaptive landscape metaphor nicely. Niches confer on the landscape its fitness structure. If niches are 'extra-organismal' and are the principal determinants of the fitness structure of the landscape, then it follows that the determinants of the fitnesses of biological form are extrinsic to form itself. This seems to accord with the general usage: the fitness that selection increases is a measure of the ability of organisms to meet the exigencies of the extra-organismal environment.

1.4 The Occupancy of Adaptive Space

Another feature of the adaptive landscape trope is immediately apparent, but less obviously significant—viz. that the conception of space encoded in the adaptive landscape metaphor is a decidedly classical, Newtonian one. Newtonian space is a mere container: non-substantival, inert, and unchanging. Its intrinsic properties are exhaustively described by Euclidean geometry. Because space is a mere container,

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[7] Notice how naturally convergence falls out of the traditional conception of organism/environment relations.

it does not interact with matter. Consequently the properties of a region of space and the relations between spatial regions—relative extensions, displacements, accessibilities—are completely independent of whether that region is occupied. Moreover, the geometrical properties of Classical space are scale-independent. Take a collection of objects. If they were all to be moved in the same direction by the same distance, their spatial relations (relative proximity, accessibility, the angles subtended by any three etc.) would not change. Nor would these relations change if the region these objects occupy were to be doubled in size. Furthermore, doubling the region of space that an object occupies (i.e. doubling its size) may have no effect on its shape.[8] For example, a trajectory that describes a triangle in Classical space, *of any size*, encloses a sum of internal angles of 180°. Consequently, the dynamics of objects moving through space are scale-free.

There are evident analogies between the classical conception of the occupancy of space and the modern synthesis conception of the occupancy of adaptive space. Form does not influence the properties of fitness space. Locations in adaptive space have their properties—in particular their fitnesses—independently of whether they are occupied by biological form.[9] That a location in adaptive space is occupied has no effect on its relations of access to other locations in adaptive space. Most particularly, the dynamics of evolutionary trajectories through adaptive space are independent of location and scale. Selection causes form to move up fitness gradients, and that applies equally to sub-populations within generations and high-level lineages over large time scales. This scale-independence of evolutionary trajectories is manifested in the supposition that the dynamics of macro-evolutionary processes are simply those of micro-evolution scaled up.

2 The Affordance Landscape

It isn't clear, however, that Newtonian space provides the most salutary analogy for the relation between biological form and the space of adaptations. One significant *dis*analogy is that the fitness consequences of a location in adaptive space are not detached from the properties of the form that fills it in the way that objects are from Newtonian space. For example, the traditional niche concept holds that for each environment there is a location in adaptive space that corresponds to the problem posed by the environment. The properties of this location—and hence what would count as a solution to the adaptive problem—are fixed quite independently of the

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[8] Nerlich (1991) calls the independence of spatial relations from spatial properties the 'Detachment Thesis': "thing-thing relations are logically independent of thing-space relations" (172).

[9] There is a further, related, Newtonian analogy to be considered. Most philosophers of biology seem to hold that adaptive space is inert. Consequently, extraneous causes or forces, like selection and drift, are required to propel form across the adaptive landscape.

features of biological form. The problem with the analogy is that extra-organismal features radically underdetermine what might count as a solution to an adaptive problem. Consider the case of the adaptive solution to 'the problem' of locomotion in water. Paramecia and porpoises have both solved it, but in very different ways. The differences are due to the way that water is *experienced* by organisms of different sizes. A harbour porpoise experiences water in much the way we do; for a porpoise water flows easily. A porpoise swims by setting up smooth laminar flow across its body. Porpoises have evolved a terete shape, a strong caudal fin and a narrow muscular caudal peduncle to concentrate the propulsive power of the tail stroke, as adaptations to the problem of locomotion in water. At a length of approximately 200 μm, a paramecium experiences the viscosity of water differently, much as we would experience being immersed in corn syrup (Purcell 1977). A paramecium cannot displace water by setting up laminar flow. Instead it possesses helical bands of cilia, whose rhythmic beating serves to 'screw' the organism through its thick medium.[10] These are two radically different 'design solutions' to the same environmental feature. The upshot is that the concept of an adaptation is not simply that of an evolutionary response to an environmental condition.

I don't claim that the adaptive landscape metaphor is incapable of accommodating the form-dependence of adaptation. I merely wish to suggest that the detachment of form from the determinants of fitness that is engendered by the metaphor is not the most perspicuous way to think of biological adaptation. The point is that we cannot specify what would count as a solution to an 'adaptive problem' independently of the features of form that solve the problem. In order to identify an adaptation we must cite the way that the environment is *experienced* by the organism. Any metaphor that draws our gaze away from the importance of the *experienced* environment has the very real potential to lead us astray. Conversely, taking the notion of the *experienced environment* seriously ought to occasion a significant shift in our conception of adaptation.

My objective is to motivate an alternative conception of adaptive evolution, one that accords due significance to the way that organisms experience, constitute, and alter their conditions of existence. The alternative is encapsulated in the slogan that *adaptation is an evolutionary response to affordances*. That, in turn, introduces an alternative spatial metaphor for adaptive evolution—the *affordance landscape*. My hope is that the contrasting spatial metaphors will underscore the differences between these conceptions of adaptive evolution.[11]

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[10] A *Paramecium* actually has three 'gaits,' only two which involve the asymmetric beating of cilia. See Hamel et al. (2011).

[11] Some of the implications of seeing evolution as a response to affordances are discussed in Walsh (2012).

2.1 Affordances

The leading idea behind the experienced environment is captured nicely in J.J. Gibson's concept of an affordance:

> The affordances of the environment are what it offers the animal, what it *provides* or *furnishes,* for good or ill. ... I mean by it something that refers to both the environment and the animal .... It implies the complementarity of the animal and the environment. (Gibson 1979, 127)

For an organism to experience an environment, or a condition of existence, is for that condition to '*provide*' or '*furnish*' something to the organism. That, in turn, depends heavily on the capacities of the organism. We can explain an adaptation as a response to a challenge faced by the organism, only once we understand how the features to which form adapts are *experienced* by organisms 'for good or ill.' One salutary suggestion, then, is that an adaptation is not so much a response to a niche or environment, traditionally construed, but to an affordance.

There is a considerable amount of debate about how to precisify this notion of an affordance. If, as some authors have argued (e.g. Turvey 1992), an affordance is simply a dispositional property of an organism's environment, then it would be possible to reconcile the orthodox Modern Synthesis account of adaptive evolution with the idea that an adaptation is a response to an affordance. Porpoises and paramecia simply respond to different dispositional properties of their shared environments.[12] Construed this way, an affordance could simply be part of a traditional niche—something wholly independent of biological form—and no change in our conception of adaptation would be occasioned by adopting the maxim that an adaptation is a response to an affordance.

It is becoming evident, however, that if the affordance concept is to do the work initially required of it by ecological psychology, it must be a much richer notion (Stoffregen 2003; Chemero 2003).[13] "Affordances are opportunities for action; they are properties of the animal–environment system that determine what can be done" (Stoffregen 2003, 124). They may be considered intrinsic emergent properties of the organism/environment system (Stoffregen 2003) or "relations between the abilities of organisms and features of the environment" (Chemero 2003, 181; see also Heft, this volume).[14] It doesn't much matter for my purposes so long as

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[12] Which dispositional properties are represented as Reynold's Number (Purcell 1977).

[13] A sympathetic reading of Gibson (1979), I believe, suggests the same.

[14] It is interesting that in those sciences in which the niche concept plays a genuine theoretical role, *e.g.* community and population ecology, the niche concept is often defined more in the way an affordance is. The niche concept seems to have originated with Elton (Hutchinson 1978) and was defined in terms of resource utilization. Odum (1959) likens a niche to an organism's 'profession.' See Beatty (1995). I thank Sahotra Sarkar for pointing this out to me.

an affordance is jointly constituted by the capacities of the organism and the conditions of existence.[15]

Further, if the concept of an affordance is to play its intended role in ecological psychology, then an affordance must imply something of significance for the organism. To perceive the affordances of one's environment is to perceive the *significance* of the opportunities it presents.

> The perceiving of an affordance is not a process of perceiving value-free physical objects to which meaning is somehow added ... it is a process of perceiving a value-rich ecological object. (Sanders 1993, 290)[16]

To respond to an affordance is to respond to the value or meaning of that feature for the organism.

2.2 The Implications of Affordances

There are two crucial implications of the affordance concept that make it a radical departure from the traditional niche concept. The first concerns the form/affordance relation. Affordances are not 'autonomous' from organisms, nor is there an asymmetrical dependence of organisms on affordances. There is a reciprocity between organisms and their affordances that does not hold between organisms and their niches or environments. What a feature of the environment affords an organism depends (in part) upon the organism's capacities, and the capacities of the organism in turn depend (in part) on the features of the environment. Organisms and their affordances are co-constituting and 'commingled.'[17]

The second implication is that, unlike a niche, an affordance implies a purposive system. A statue can have a niche, but only a goal-directed system can have an affordance. Purpose defines affordances: an affordance is an opportunity for, or an impediment to, the attainment of a goal. Conversely, affordances define purposive systems: a purposive system is an entity for which features of its conditions of existence constitute affordances. A purposive system is a system capable of responding adaptively to affordances.

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[15] One additional advantage of not seeing affordances as dispositional properties of an organism's environment is that it relieves us of the temptation of thinking that all affordance-presenting features are external to organisms. Inner workings of organisms present affordances too.

[16] In the case of organisms, 'value' may be read, often enough, as 'survival value.'

[17] I borrow the term 'commingled' from Haugeland (1998). The relation between organisms and their conditions of existence I envisage includes but extends beyond what Gillian Barker (2008) calls 'selective interaction.' The principal difference is that selective interaction emphasises the ways in which organisms causally influence their conditions of existence. The 'commingling' of organisms and their affordances underscores the way in which the capacities of organisms partly *constitute* those conditions. See Walsh (2012) for a discussion of the distinction.

In order to respond to an affordance, a system must have two features. Firstly, it must be able to experience its conditions *as affordances*. That is to say that it must generally be capable of responding to propitious conditions *as propitious* by exploiting them, and to unpropitious *as unpropitious*, by ameliorating them. Secondly—and concomitantly—a system must also have an adaptive repertoire. That is to say that on any occasion, there must be a range of possible outcomes or activities that the system or its parts could implement. Which elements of the system's repertoire are actualized on an occasion must generally be biased in favour of those that are conducive to the attainment of the system's goals.

Following the suggestion that adaptation is an evolutionary response to affordances, I would like to explore an alternative metaphor for adaptive evolution. We should think of evolution as occurring on an 'affordance landscape.' An affordance landscape is the complete set of affordances—conditions 'for better or ill'—that impinge on an organism. That is to say, it is the complete set of conditions experienced by an organism as impediments to, or as conducive to, its goals of survival and reproduction.

These implications of affordances have special significance for adaptive evolution. Because the capacities of biological form and affordances are co-constituting, any change in one is a change in the other. Form and the affordances to which it evolves co-evolve. Furthermore, as affordances are reflections of purposiveness, then the adaptive goal-directedness of organisms structures and conditions the affordances on which evolution occurs. I discuss these implications of affordances for evolution in turn.

3 The Co-evolution of Form and Affordance

The relation between form and affordance landscape is very *unlike* the relation between form and the adaptive landscape—or, for that matter, matter and Newtonian space. The affordance landscape is not inert or 'detached' from the properties of form, nor does it have 'its own intrinsic dynamics.' It is constantly shifting with changes in organismal form. Nor is there a relation of asymmetrical dependence of form on the affordance landscape. Form and the affordance landscape affect one another reciprocally; they co-evolve. A couple of examples might help to illustrate this reciprocal dependence and its importance for adaptive evolution.

3.1 The Origin of Hominin Tool Use

It is generally acknowledged that the advent of tool use in hominins has been integral to their evolution, especially in late hominin lineages leading to *Homo sapiens*. The affordances provided by tools have long been thought to have been intimately involved in human cognitive, linguistic and social evolution (Gibson 1993). It is less clear how those affordances first arose. Recent work in evolutionary developmental biology suggests that the initial conditions that permitted the expansion of hominin tool use may have been a contingent byproduct of the evolution of obligate bipedalism (Rolian et al. 2010).

Tool use requires, at minimum, 'precision grip' (Marzke 1997). This is the capacity to oppose the thumb against one or more fingers. Advanced tool use requires the ability to oppose the thumb against all of the fingertips at once ('higher order precision grip'). Changes in the structure of the ancestral hominoid hand were required in order for this higher order precision grip and opposition of the digits to be possible. These involved, crucially, the increased robustness of the thumb, its extension distally, and the shortening of the fingers (Rolian et al. 2010).

Recent morphological studies on primate hand and foot development demonstrate a considerable degree of integration in the development of both (Rolian and Hallgrimsson 2009). Hands and feet are serial homologues. Their respective development is controlled by very similar developmental architectures (Hallgrimsson et al. 2002). As a consequence, evolutionary changes occurring in the foot may influence the development and evolution of the hand (and vice versa). Rolian et al. (2010) demonstrate that the changes required to the hominin foot required for bipedal endurance running include the strengthening and distal extension of the big toe and the shortening of the lateral digits. These structural changes to the foot that facilitate endurance running are just those changes that in their homologous structures in the hand are required for higher order precision grip.

Rolian et al. (2010) hypothesize that changes in the hand are a consequence of the evolutionary changes in foot structure. Given the developmental integration, or coupling, of hand and foot development, changes in foot structure drag the hands along.

> Developmental constraints caused hominin fingers to evolve largely as a by-product of stronger selection pressures acting on the toes. Simply put, the shorter fingers and longer, more robust thumbs of humans likely evolved because of selective pressures on their respective homologues in the foot. (Rolian et al. 2010, 1564)

Nevertheless, these changes in hand structure conferred on hominoid ancestors new capacities to grasp implements and use them as tools. In other words, serendipitous changes in form dramatically altered the affordances of our ancestors' environments, *without changing the environment*. Changes in our ancestors' hands put tools in their environments. These altered affordances, in turn, introduced new opportunities for adaptive evolutionary change.

3.2 The Origin of Metazoans

The changes in form that usher in new affordances do not have to be adaptive in any way, nor do they need to be underwritten by genetic changes. These lessons can be gleaned from recent work on the origin of the Metazoa.

The morphological and developmental complexity of metazoans vastly exceeds that of any unicellular organism. Yet, the entire panoply of basic metazoan structures, and a fair degree of phyletic diversity, appears to have arisen rapidly in the Precambrian. A fascinating picture is beginning to emerge about this sudden arrival of metazoan complexity (Newman and Bhat 2009). The original coalescence of unicellular pre-animals into vast assemblages of cells appears to have been the consequence of a precipitous change in the ionic constitution of the seas. Kaźmierczak and Kempe (2004) report evidence of a sudden rise in Ca^{++} concentrations in the Precambrian seas. Increased Ca^{++} is known to promote cell-cell adhesion.

These massive aggregations of cells—the proto-metazoans—encountered 'mesoscopic' physical conditions that had never previously affected the development or diversity of organic form.

> The consequent change in spatial scale created a context in which other pre-existing molecules were able to mobilize mesoscopic (i.e., "middle-scale") physical processes and effects that were irrelevant to objects of the size and composition of individual cells. (Newman 2011, 339)

Thanks to the newly encountered "middle-scale" physical processes and effects, these aggregations of cells had the capacity to produce all the characteristic structures of the metazoans—lumena, tissue layers, blastocoels, tubes, differentiated tissues—spontaneously.

> The forms of the earliest multicellular organisms ... were more like certain materials of the non-living world than are the forms of their modern, highly evolved counterparts, and that they were therefore almost certainly molded by their physical environment to a much greater extent than contemporary organisms. ... Stated simply, tissue forms emerged early and abruptly because they were inevitable—they were not acquired incrementally through cycles of random genetic change followed by selection. (Newman 2003, 221)

These new biological structures, the foundations of metazoan form, are not solutions to adaptive problems posed by an external environment. Nevertheless, they confer on biological form novel capacities, which in turn open up new vistas: threats to survival, opportunities for change, potential for new forms.

The nearest living non-metazoan relatives of the metazoans appear to be the unicellular (and sometimes colonial) choanoflagellates (King 2004). Choanoflagellates possess a basic genetic tool kit comprising (*inter alia*) genes coding for proteins that mediate cell-cell adhesions, genes that regulate growth and shape, and extracellular matrix proteins that—in metazoans at least—mediate cell sorting and tissue formation during development. The unicellular precursors of metazoans, then, carried genes that in the new context of multicellular assemblages played entirely new roles in metazoan function and morphogenesis.

> Some components of the protein machinery that mediates animal cell interactions may have originally played other roles in ancestral unicellular eukaryotes before being co-opted to function in signaling and adhesion. (King 2004, 319)

Each of the preceding examples, hominin tool use and the evolution of the metazoans, takes seriously the ways in which biological form partly constitutes the conditions under which evolution occurs. In each of our examples there are reciprocal cycles of changes in form with concomitant changes in affordances, *without changes to the environment*. This suggests that large-scale evolution is not most perspicuously described as the process of form gradually fitting into independently specified problems in static design space. It is the process of form creating and then responding to an ever-changing system of affordances. The affordance landscape metaphor nicely captures this reciprocity of form and conditions in a way that the traditional adaptive landscape metaphor tends not to. The affordance landscape, unlike the adaptive landscape, does not 'obey its own intrinsic dynamics.'

This is not to say that the adaptive landscape could not be 'adapted' to accommodate at least some aspects of the reciprocity of form and the conditions under which it evolves. It is well known that organisms change and 'construct' their environments. We might allow that the adaptive landscape may deform as organisms alter their external conditions of existence. We could even make the concession that the adaptive landscape represents the conditions of existence as *experienced* by organisms. We could, for example, stipulate that in our swimming example the properties of the adaptive landscape represent organism-indexed parameters, such as Reynold's number, rather than intrinsic properties of the environment, such as viscosity.

But while these amendments to the adaptive landscape metaphor would be significant and salutary, they still would not capture the import of the notion that adaption is an evolutionary response to *affordances.* The reason is that, as discussed, affordances imply purposes; it is purposiveness that turns conditions into affordances. The fact of organisms' being purposive, adaptive entities plays no role in the standard Modern Synthesis conception of adaptive evolution. It is hardly surprising, then, that its principal spatial metaphor should decline to represent organismal purposes either explicitly or implicitly. In taking the conditions to which biological evolution responds to be affordances, the affordance landscape does represent organismal purposiveness as a factor in evolution. Here, I believe, is the watershed. The affordance landscape metaphor earns its keep—and distinguishes itself from the traditional adaptive landscape—only if the purposiveness of organisms makes some decisive contribution to adaptive evolution.

4 Affordance and Organismal Purpose

Organisms are highly robust, goal-directed entities. They are capable of building themselves and maintaining their viability despite the considerable vagaries of their conditions (Gibson 2002). Kirschner and Gerhart label this distinctive property of organisms 'dynamic restoration.'

> The organism is not robust because it is built in such a manner that it does not buckle under stress. Its robustness stems from a physiology that is adaptive. It stays the same, not because it cannot change but because it compensates for change around it. The secret of the phenotype is dynamic restoration. (Kirschner and Gerhart 2005, 108–109).

The hallmark of this ability to adapt to, and to compensate for, conditions of existence is phenotypic plasticity. West-Eberhard identifies plasticity as

> the ability of an organism to react to an environmental input with a change in form, state, movement, or rate of activity. . . . The words "responsiveness," "flexibility," "malleability," "deformability," and *developmental plasticity* are all synonyms of phenotypic plasticity as defined here. (2003, 34–45)[18]

4.1 Plasticity and Evolution

Phenotypic plasticity contributes to adaptive evolution in the following way. An organism faces a challenge from an environmental perturbation, or a mutation, and proceeds to make an adaptive, compensatory change in its phenotype. As organisms are highly functionally integrated entities, a change in one feature of its phenotype requires concomitant changes in others. This capacity of an organism to make compensatory changes in one part of its phenotype in order to accommodate changes elsewhere, is called 'phenotypic accommodation': it is simply one aspect of phenotypic plasticity.

> Phenotypic accommodation is adaptive mutual adjustment, without genetic change, among variable aspects of the phenotype, following a novel or unusual input during development. (West-Eberhard 2003, 98)

Adaptive evolutionary change requires a considerable degree of orchestration amongst an organism's various subsystems. For example, the increase in the mass of a muscle in response to the demand for greater force also requires changes in the origin and insertion of the bones. It further requires increased vascularisation, innervation, and changes in associated connective tissue.

On the standard Modern Synthesis conception of adaptive evolution, organisms do not initiate or orchestrate evolutionary change. Each evolutionary novelty is initiated by a random mutation, or by recombination of genes. But given the demand for functional integration, if each phenotypic change required just the right mutation (or combination) in each contributing subsystem, adaptive evolution might never occur.

> In contrast to the rapid response produced by plasticity, if the production of newly favored phenotypes requires new mutations, the waiting time for such mutations can be prohibitively long and the risk of subsequent loss through drift can be high. (Pfennig et al. 2010, 459–460)

Phenotypic accommodation facilitates adaptive change by providing the requisite adaptive 'orchestration.'

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[18] I would suggest an amendment to West-Eberhard's definition. Plasticity should be seen as the capacity to react to an input from *any* source, not merely an environmental input.

> Phenotypic accommodation finesses the problem of correlated change: a genetically-caused modification in one system need not wait for a genetically-caused change in associated systems, even when both must change for either to be adaptive. (Sterelny 2009, 99)

Phenotypic plasticity enters into the process of adaptive evolution by initiating *adaptive* responses to the organism's conditions of existence and then further making adaptive (accommodating) responses that maintain or promote viability. Often enough, adaptive responses, underwritten as they are by the developmental robustness of organisms, are intergenerationally stable. They can be passed from one generation to the next, and hence are candidates for being evolutionary characters.[19]

The adaptive plasticity of organisms is underwritten by the fantastic phenotypic repertoire immanent in development.

> Through its ancient repertoire of core processes, the current phenotype of the animal determines the kind, amount and viability of phenotypic variation the animal can produce . . . the range of possible anatomical and physiological relations is enormous. (Gerhart and Kirschner 2007, 8588)

Phenotypic plasticity is the capacity of an organism to marshal its phenotypic repertoire in response to the challenges and opportunities it encounters. It is a manifestation of organismal purposiveness. Organisms make adaptive changes in form or function to those features of their environments, genomes, or developmental systems that threaten or promote their viability. Thus the plasticity of organisms consists in a goal-directed capacity to respond to, and to create, *affordances*.

4.2 Plasticity and the Affordance Landscape

If adaptive evolution is change in response to conditions of existence, then in altering the conditions of existence the adaptive plasticity of organisms contributes to the process of evolution. When an organism makes an adaptive response to its conditions of existence, it also changes those conditions of existence. These changes, in turn, introduce new evolutionary challenges and opportunities. In this way, organisms are participants in adaptive evolution, not mere objects of it.

Traditional Modern Synthesis biology treats the adaptive plasticity of organisms as, at best, a mere consequence of adaptive evolution (Godfrey-Smith 1996). But it accords organisms no active role in promoting adaptive evolution; organisms are "the passive nexus of independent external and internal forces" (Lewontin 2001b, 47). We encountered the rationale for this view in our discussion of the

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[19] Confusion persists on this point. See, for example, Sterelny (2009, 101) who claims that novelties generated by phenotypic plasticity are "mere ecological events." "Such novelties have no effects on the germline are not inherited [*sic*]" (2009, 94). He muses on how they can be transformed from "mere ecological events" into evolutionary events. My claim is that no transformation is needed; any ecological event that is intergenerationally stable *is* an evolutionary event.

adaptive landscape metaphor, viz. the conditions under which form evolves are taken to be independent of the capacities of form. The external environment is autonomous from biological form and changes, if at all, “according to its own intrinsic dynamics” (Godfrey-Smith 2001, 254).

It is difficult to accommodate the contribution of organisms to evolution within the constraints of the old adaptive landscape trope. Pfennig et al. (2010), for example, try to incorporate the effects of plasticity into the adaptive landscape.

> Phenotypic plasticity also promotes population divergence by facilitating peak shifts or valley crossing on the adaptive landscape. … a population can traverse a valley rapidly, potentially in one generation, by facultatively expressing an alternative phenotype closer to the fitness optimum. (Pfennig et al. 2010, 462)

To claim that adaptive evolution can readily cross valleys or ‘shift peaks’ is to concede that evolution does not follow the contours of the adaptive landscape. But the heuristic value of the adaptive landscape metaphor lies specifically in the notion that in adaptive evolution form follows the contours of the landscape, the topography of which is fixed by extra-organismal conditions. Where this relationship breaks down, so too does the utility of the adaptive landscape metaphor.

The affordance landscape metaphor, in contrast, nicely illuminates the relation between organismal plasticity and the conditions under which form evolves. In responding adaptively to conditions of existence, organisms alter their affordance landscapes. These altered affordances, in turn, redound to organisms. Plasticity, then, amplifies the mutual dependence of the capacities of form and the affordances on which it evolves. The plasticity of organisms is one of a number of factors—including genes and environments—that can alter the affordances upon which adaptive evolution occurs. Indeed, according to the affordance landscape metaphor, the contributions of organisms, genes and environments to evolution are no different in kind. They all contribute to the affordances to which organisms respond. That the affordance landscape metaphor can accommodate the role of plasticity in evolution and the adaptive landscape cannot commend the former over the latter.

4.3 The Occupancy of Affordance Space

If the adaptive landscape metaphor embodies a thoroughly classical, Newtonian conception of the occupancy of space, the affordance landscape suggests a radical alternative. The relation between form and the affordance landscape bears some commonalities with the relation between matter and space (well, spacetime) in General Relativity. In General Relativity, space is thought of as a substance. It interacts causally with the matter that occupies it. Most particularly, the geometrical properties of a region of space are not independent of whether that region is occupied. There is a relation of reciprocal dependence between the local properties of spacetime, and the capacities of matter (say, to attract other bodies). The trajectory of a body is influenced by the structure of spacetime around it, which in turn is altered by the motion of bodies.[20] The relations of access and relative proximity between spatial points are not independent of scale, or of the way that spacetime is occupied (Dainton 2001). In curved space, spatial relations change with scale. Because space has no univocal geometrical structure, there is no guarantee that the behaviour of bodies in spacetime is scale free.

Analogously, the features of the affordance landscape—its fitness, the relations of access and proximity between locations—are all influenced by the nature of the form that occupies it. For example, because of plasticity, a given phenotype may be underwritten by a range of developmental mechanisms. Each of these mechanisms, in turn, may have different phenotypic repertoires. Different instances of the same phenotype may differ in the range of conditions over which each is stable, and the kind of adaptive novelties that each can initiate (Ciliberti et al. 2007a, b; Wagner 2011). These novelties, in turn, vary with respect to *other* stable novelties that may be produced. So whether one phenotype is robustly fit, or is close to or accessible from another, may depend upon the way that form affects the array of affordances.

Because evolutionary trajectories are dependent not just on the independent structure of the landscape, but also upon the changes in form itself, there is no reason to suppose that the evolutionary dynamics are scale-independent. There is no reason to suppose that short-range (micro-evolutionary) changes can be extrapolated to long-range (macro-evolutionary) changes. One implication is that even if micro-evolutionary change is convergent and non-contingent, it doesn't follow that macro-evolutionary change is too. This is not to deny that there are convergences in macro-evolution. There certainly are (McGhee 2007). But when they occur they need special explanations.[21] They may be the results of constraints, or reflections of the fact that the same developmental resources are used in different lineages. The point is that convergences are *not* to be expected or explained simply by the fact that evolution is adaptive.

5 Adaptation and Contingency

The affordance landscape is offered here as an alternative spatial metaphor for adaptive evolution. But there is a problem. So different is the process of evolution on the affordance landscape from that on the adaptive landscape that it is questionable whether the former should rightly be considered *adaptive* at all. There are two causes for scepticism. The first concerns the concept of an adaptation. An adaptation is typically thought of as a solution to a 'design problem,' a self-standing, stable,

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[20] One salutary implication, for both relativity and its metaphorical extension to evolution, is that it is not necessary to posit an additional metaphysical category of force to propel bodies through space.

[21] Perhaps ironically, Conway Morris (2010) offers a number of these.

external condition. Affordances are not external, self-standing or stable. "If ... we abandon the metaphor of adaptation, how can we explain what seems the patent 'fit' of organisms and their external worlds?" (Lewontin 2001b, 63). The second cause for scepticism concerns the tempo and mode of evolution. As we saw, the adaptive landscape metaphor reinforces the intuition that large-scale evolution is convergent and non-contingent. We should expect that evolution on the affordance landscape, in contrast, might be contingent and non-convergent. Again, the question arises: "How can such a process be legitimately considered to be adaptive?"

I intend to address these concerns by means of an analogy to two different kinds of 'adaptive' games. In each game the challenge for the player on any given move is to solve a problem. Each of these games presents a player with an affordance landscape, a set of conditions that are propitious for, or impediments to, success. Yet, the relation between the player and the affordance landscape is different in each game. Consequently, the respective dynamics of the games are radically different.

The challenge faced by a sudoku player is to fill in the correct numbers in an array of spaces. The affordances of the sudoku game are the opportunities to fill the empty squares with numbers, and the existing array of filled-in squares. The affordances of the game are (for the most part) largely independent of the state of the game. For instance, what counts as the correct number in any given blank is independent of whether that blank is filled in, or which of the other squares the player has filled. The game has "its own intrinsic dynamics." Consequently, the affordances of the game and the state of the game are (largely) non-co-evolving. The trajectory of a sudoku game depends strongly on the initial conditions. As a consequence of this, the various trajectories of a Sudoku game are convergent and non-contingent. Reasonably adept players will arrive at the same solution to a given game, even if they do so by different routes.

So, the trajectory of a sudoku game is thus rather like the trajectory of adaptive evolution as suggested by the traditional adaptive landscape metaphor. It advances progressively toward the attainment of a pre-specified, unchanging solution to a self-standing problem, the nature of which can be described independently of the trajectory that approaches it. It is convergent and non-contingent because it is adaptive.

The challenge faced by a chess player is much different. At each move the player must respond to the threats and opportunities presented to her by the locations of the pieces, and by their capacities. The capacities of the player at a time and the affordances presented to her are mutually constituting: one cannot be specified without the other. They are also co-evolving. Each change in the location of the pieces, whether it is initiated by the player or the opponent, is a change in the affordance landscape.

The trajectory of a chess game is highly unpredictable. For most arrangements of the pieces on the board there are an enormous number of possible final outcomes. One reason for this is that a player typically has a broad adaptive repertoire. On any occasion, there are any number of moves available to the player that might promote her goals to some degree. Consequently, the trajectories of a chess game are contingent and non-convergent. It is highly unlikely that any two chess games will end up in precisely the same final configuration. Furthermore, unlike sudoku, the trajectory of a game does not depend very largely upon, nor is it predictable by, the initial conditions.

Exploring the contrast between sudoku and chess serves two purposes. First, the chess analogy suggests that we can consider a process to be adaptive even if it is not a progressive convergence upon a solution to an unchanging, independently specifiable problem. Chess moves are adaptive, even if successive moves do not progress toward a single solution. The 'metaphor' of adaptation may not be as constraining as we usually take it to be. Second, the comparison suggests that where an adaptive process is best characterized as the result of an adaptive entity embedded in an interacting system of affordances, there is little reason to expect that process to be convergent and non-contingent. Some processes are contingent and non-convergent *because* they are adaptive.

My suggestion throughout this paper has been that adaptive evolution is such a process. But if so then evolutionary thinking has been ill-served by its most prominent metaphor. The alternative affordance landscape metaphor underscores the important contribution that organisms, as purposive entities, make to adaptive evolution. Adaptive evolution is not to be conceived of as the moulding of passive form to meet the exigencies of an autonomous, external environment. It is the response of form to a mutually constituted set of affordances. Moreover, the affordance landscape metaphor suggests that the process of adaptive evolution should be contingent and non-convergent—not convergent and non-contingent as the adaptive landscape suggests it should be. This is a genuine empirical possibility that has been obscured from our view for much of the history of evolutionary biology, probably through overreliance on the power of a metaphor. Evolutionary thinking has been strongly conditioned by the adaptive landscape metaphor. It may well correctly disclose to us the kind of process that adaptive evolution may and may not be. I think it more likely that the predominant conception of adaptive evolution is just the penalty we incur for not having properly paid the price of metaphor.

6 Postscript: Forging a New Adaptationism

The adaptationist program—so sharply criticized by Gould and Lewontin (1979)—is predicated on a particular conception of the role of organisms in evolution. The properties and capacities of organisms are mere consequences of evolution. Organismal form is an object of evolutionary change. E. O. Wilson expresses the idea vividly. He says of human cognitive evolution,

> however subtle our minds, however vast our creative powers, the mental process is the product of a brain shaped by the hammer of natural selection upon the anvil of nature. (2004, xii)[22]

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[22] I thank Chris Haufe for the quotation.

The blacksmith metaphor is telling. It neatly conveys the idea that form is a mere malleable substance, shaped by the extrinsic forces of evolution—the 'hammer of selection.' If organismal form contributes to the process of evolution it does so only by exerting resistance—the 'anvil of nature.'

But organisms are not mere objects of evolution. A new adaptationism, I suggest, must develop an understanding of organisms as *subjects* of evolution. Such an adaptationism would highlight the ways in which organisms "actively participate in their own evolution" (Ingold 2000, 292). Organisms are self-building, self-maintaining, purposive systems actively engaged in, commingled with, their conditions of existence. Adaptive evolution is the consequence of a constant dialectical interplay between organisms and their conditions; organisms change them and are changed by them. Perhaps an alternative blacksmith metaphor might be more germane. Hegel illustrates his theory of human freedom with "the old proverb that says 'Everyone is the smith who forges his own fortune.'"[23] Organisms are smiths who forge their own evolution.

Acknowledgments I would like to thank audiences in London (Ontario), Dubrovnik, and Stockholm for their lively responses. I am particularly grateful to Fermin Fulda and Susan Oyama for suggested improvements to an earlier draft. In addition, Jacob Stegenga, Cory Lewis, Michael Cournoyea, and Alex Djedovic provided a very helpful discussion. The editors of this volume also provided very helpful suggestions.

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[23] Hegel (1991, §147Z). Quoted in Yeomans (2012, 163). I thank Sally Sedgwick for the quotation.

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