Chapter 7

Landscape Revolutions for Cultural Evolution: Integrating Advanced Fitness Landscapes into the Study of Cultural Change

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Introduction

In 1932 Sewall Wright introduced the idea of the fitness landscape at the Sixth International Congress of Genetics. His landscapes, presented at the conference as a series of drawings, were visual metaphors—tools to help his biologist colleagues conceptualize the mathematics underlying his new theory of evolutionary dynamics in small populations. In their most basic form, Wright’s landscapes diagrammed the mutational paths between genotypes and demonstrated the increase in dimensions necessary to depict a complete set of all possible gene combinations in a simple example where a maximum of five genetic variants (allelomorphs) were considered (Fig. 7.1). Wright then proposed reducing this complexity to a simple illustration where the movements of populations driven by drift and selection could be visualized in a two-dimensional geographic space (Figs. 7.2 and 7.3). On these fitness landscapes, the combination of all possible genetic variants represents genotype space along the X and Y axes, while the fitness assessed to each variant genotype represented the height of the landscape on the Z axis. The landscapes depicted were what we refer to today as rugged (following Kauffman and Levin 1987) as fitness differences between genotypes gave rise to highly topographically variable terrain.

Wright’s drawings, however, not only staked out this theoretical geography, but they also demonstrated the process of movement along the landscapes as small, subdivided populations interacted through migration and were moved across the landscape by a combination of drift and selection. Selection, Wright proposed, should move populations to the top of fitness peaks and hold them there, even if the landscape contained significantly higher peaks. The evolutionary problem then was one of “peak shifting”—how might populations stuck on a peak move to alternative, often higher peaks without risking extinction traversing the low-lying valleys in between? According to Wright and his now (in)famous shifting balance theory, movement across these rugged landscapes is a dynamic, complex interaction between the evolutionary processes of selection, drift, and migration with small populations evolving and speciating (i.e., diverging) more rapidly than those with larger effective size.

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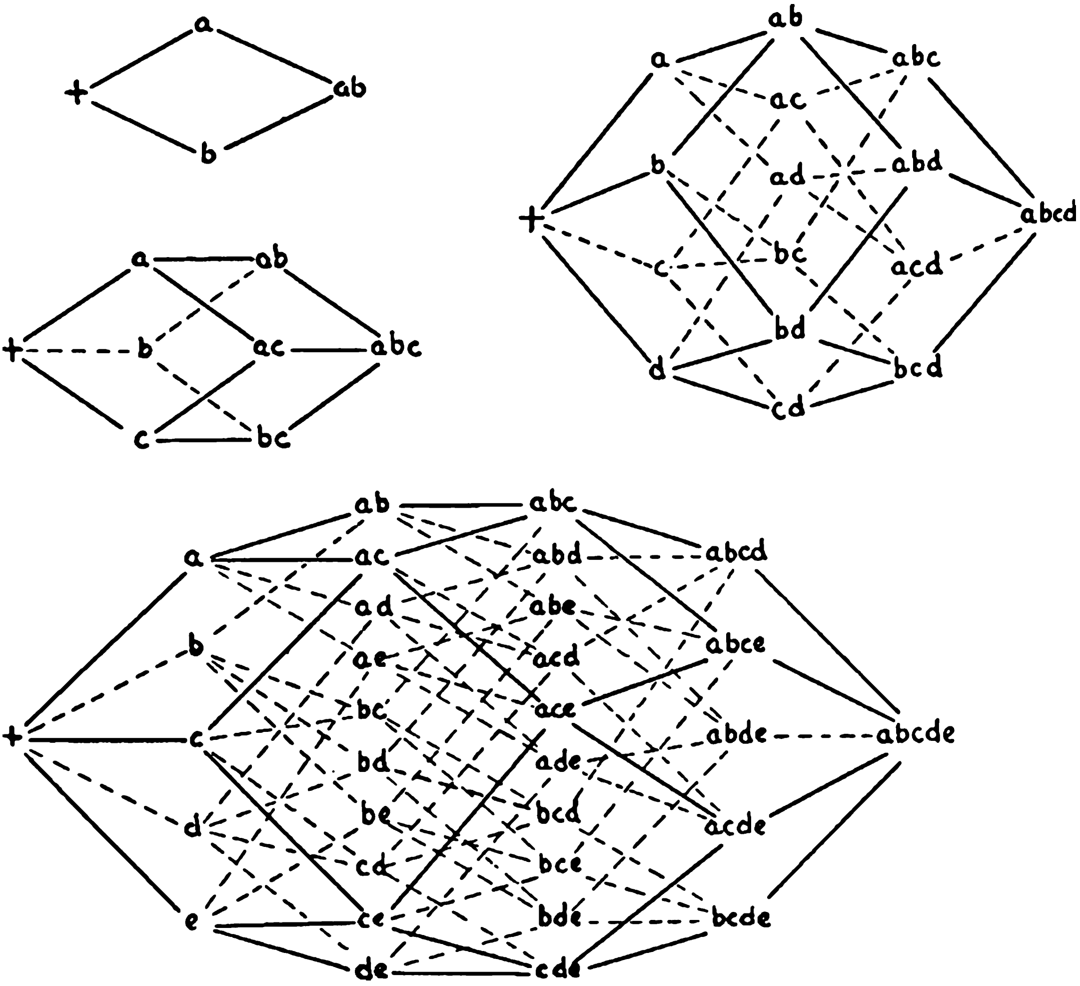

Fig. 7.1 Wright's (1932) depictions of two to five paired allelomorphs

Despite widespread criticism of the theoretical paradigm they were developed to explain, 70 years later Wright's images of evolutionary change have permeated the study of complex systems in disciplines from biology to economics and have held a sustained place in the study of cultural evolution. During this time, fitness landscapes have been used and interpreted in a wide variety of ways; they are variably employed as metaphors and images for illustrating evolutionary processes as well as powerful theoretical models that allow the generation of hypotheses and the subsequent derivation of explanations for evolutionary changes seen in the past.[1] However, as recent critics of fitness landscapes note, models and metaphors are quite methodologically distinct, as are the tools and techniques that help us explain something versus merely describe it. Indeed, some theorists now contend that landscapes as metaphors are the least productive application of landscape theory and in fact landscapes used in this way may mislead us in many situations (see Gavrilets 2004). This

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[1] Much less frequently they represent real data linked to a formal set of mathematics or equations; although with the rise in gene sequencing data, empirical fitness landscapes are becoming increasingly common (De Visser and Krug 2014; Poelwijk et al. 2007).

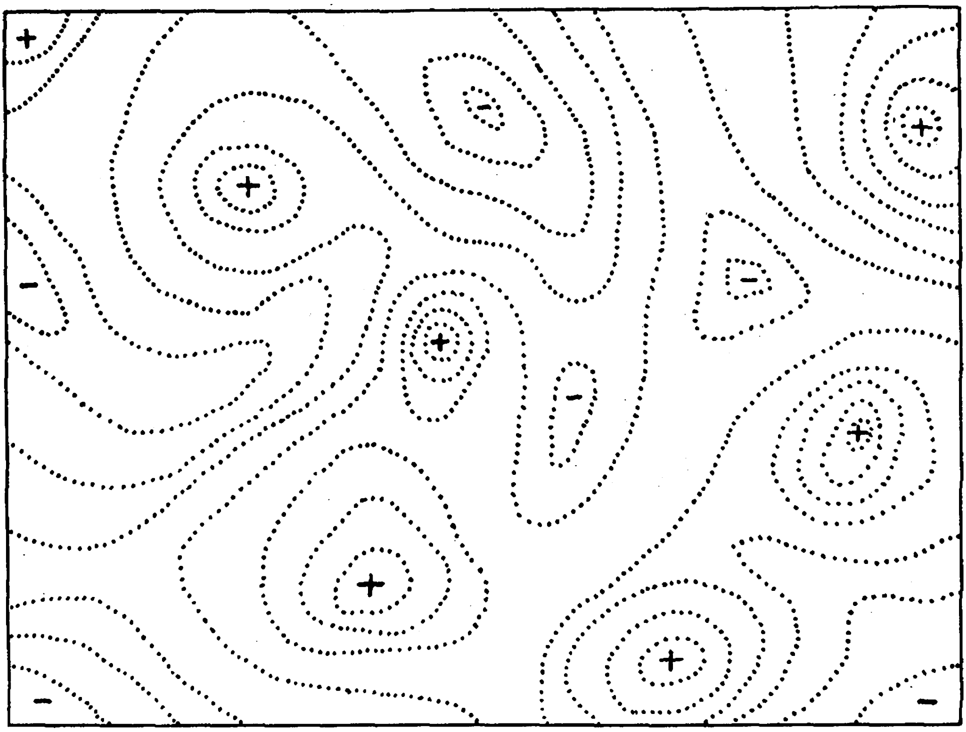

Fig. 7.2 Wright's (1932) diagrammatic representation of the field of gene combinations in two dimensions. Dotted lines represent contours with respect to adaptiveness

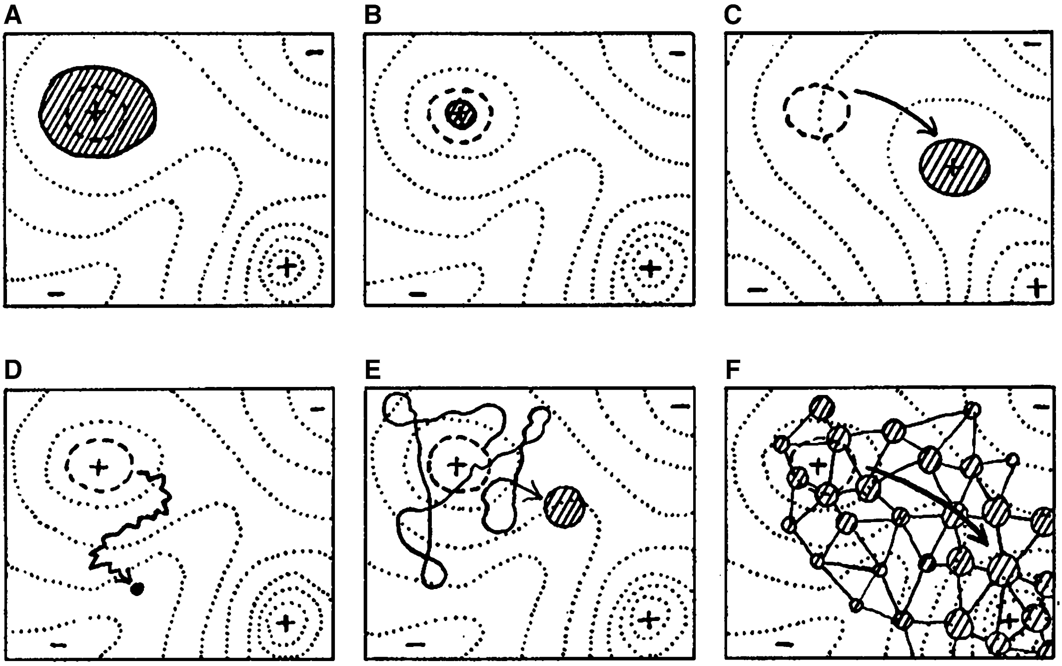

Fig. 7.3 Wright's (1932) diagrams showing gene combinations occupied by a population under various evolutionary scenarios. (**a**) Increased mutation or reduced selection 4NU, 4NS very large. (**b**) Increased selection or reduced mutation 4NU, 4NS very large. (**c**) Quantitative change of environment 4NU, 4NS very large. (**d**) Close inbreeding 4NU, 4NS very small. (**e**) Slight inbreeding 4NU, 4NS medium. (**f**) Division into local races 4 nm medium

is the crux of the recently proposed “landscape revolution,” which claims that traditional landscape images are in need of renovation, replacement, or even abandonment (Calcott 2008; Kaplan 2008; Plutynski 2008). According to proponents of this position, inaccurate landscape metaphors often obscure the processes they seek to reveal and in some cases may even create false explanations when researchers “reverse the relationship between imagery and reality . . . projecting the simplicity of [landscapes] onto their predictions of how the real world works” (Pigliucci and Kaplan 2006, p. 178). For those already familiar with the mountainous geography of the landscapes originally drawn by Wright and commonly employed since, this is likely intuitive—a static landscape comprised of permanent, rugged peaks and low-lying valleys depicts certain evolutionary dynamics well and others not at all. Indeed, decades of research since Wright have revealed the existence of fitness landscapes capable of modeling numerous complex evolutionary scenarios including spatial variation (Lewontin 1978), temporal variation (Richter 2014), the evolution of diversity as a response to the underlying complexity of the fitness landscape itself (Niklas 2004), and the role that interactions between traits plays in evolutionary dynamics (Kauffman 1993, 1995; Kauffman and Levin 1987; Kauffman and Weinberger 1989). In particular, recent approaches to studying highly multidimensional landscapes have led to important insights regarding the role of nonselective evolution in the process of adaptation (Gavrilets 1997, 2004).

Here we join the above-cited scholars in proposing that the landscape metaphors commonly used in the study of cultural evolution are in need of renovation. Indeed, a survey of applications of fitness landscapes in the cultural evolutionary literature indicates that many cultural evolutionists still rely on Wright’s original images, despite decades of both theoretical and methodological advancement. Here we provide examples of major advances in fitness landscape research and examine some of the potential theoretical implications of those advances for the study of cultural change. Despite the fact that the implications of these advances discussed are theoretical in nature, we hope scholars will see the research presented here as a platform for integrating these advancements into quantitative fitness landscape models of cultural change.

Before turning to examples of major advances in fitness landscape research and examining the potential implications of those advances as metaphors or models for cultural change, we give a brief introduction of some of the fundamental modeling concepts that underlie fitness landscape theory and a survey of the literature applying landscapes to the study of cultural evolution.

Landscape Fundamentals

All landscapes models share three basic properties: a set of configurations, a way of measuring the evolutionary distance between configurations, and a function for determining how adapted configurations are relative to each other. Together these properties give rise to the topographical structure of the landscape as well as the evolutionary dynamics that can occur on the landscape space.

Configurations On landscapes developed to depict biological evolution, the configuration is a set of all possible genotypes or phenotypes evolving in a particular environment,[2] where genotypes are

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[2] Each type of landscape is privy to a unique set of theoretical and methodological issues (for an exhaustive review, see Kaplan 2008). While detailing all of these is outside the purview of this paper, we note that the types of landscapes most often relied upon by cultural evolutionists, phenotypic adaptive and phenotypic fitness landscapes, are no exception. In the case of adaptive landscapes, the assumption is made that mean population fitness can be mapped onto frequencies (rather than distributions) of traits within a population (Kaplan 2008, p. 628), ignoring the fact that major evolutionary movement on landscapes, guided by selection, is dependent on the differential reproductive success of the individuals traversing it. For this reason, adaptive landscapes should be viewed as descriptive, rather than explanatory of the

the genetic structures of individuals and phenotypes are the physical characteristics that interact with the environment. Landscapes may then be either genotypic (where non-fitness axes represent combinations of alleles or loci) or phenotypic (where non-fitness axes represent morphological traits). In either case fitness is mapped directly to the phenotypic or genotypic configurations under consideration allowing a direct representation of their adaptive implications.

Here it is helpful to differentiate between fitness and adaptive landscapes as well, as the two terms are often used interchangeably but refer to very different landscape structures based on the set of underlying configurations. Specifically, fitness landscapes map individual genotypes or phenotypes against a measurement of relative adaptiveness or fitness with populations represented as clouds or clusters of points, and adaptive landscapes map genotypic or phenotypic frequencies against the fitness mean for an entire population, which is then represented as a single point.

Neighborhood, Distance, Nearness Together with the configuration set, the distance metric used to describe the possible relationships between configurations gives rise to the topographical surface of the landscape. Each point in space, as noted above, represents a distinct genotype or phenotype (or the average frequency of either in a population). The accessibility (nearness) of one genotype or phenotype from another is simply the number of mutations necessary for the offspring of individuals to move from the space occupied by their parents to another space on the landscape. Using bit strings comprised of 0's and 1's as an example of genotypic alleles or phenotypic traits, it is relatively obvious that it only takes one mutation (one transition of a 0 to a 1) to move an individual from the genotype space 0001 to the genotype space 0011 but two steps to move the same individual to the genotype space 0111. Thus, the individual with genotype 0001 is a "one-step neighbor" to individual 0011 and is closer on the landscape to the individual with genotype 0011 than it is to individual 0111.

Fitness Assignment When the landscape is constructed, each configuration on the space is assigned a numerical fitness value,[3] which demonstrates the degree to which configurations are optimal or adaptive, relative to each other. These fitness assignments give rise to the shape of the landscape, including the presence and height of any peaks, the depth of valleys, and the width of plateaus or other fitness neutral spaces. In the simplest case, all configurations share the same fitness, and the landscape is completely flat and entirely "fitness neutral" as no configuration provides an adaptive advantage or disadvantage over any other. In most cases, however, some configurations are more

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evolutionary process, and scholars of cultural evolution should use appropriate terminology to reflect this. In the case of fitness landscapes, there are often problems of accurate representation, for example, there is an inherent inability to meaningfully situate individual, discrete genotypes along a continuous axis, a problem that has now been widely commented on in the literature (Calcott 2008). There is also the issue of constructing a fitness function that provides a meaningful quantification of adaptive success with often limited knowledge of the genotype and population structure necessary to map genotypes to individual fitness values (in the case of genotypic fitness landscapes) or genotypes to phenotypes to fitness values (in the case of phenotypic fitness landscapes) (Pigliucci 2012; Pigliucci and Kaplan 2006, p. 185).

[3] Fitnesses on non-flat landscapes are assigned in a number of ways, including completely randomly, manually, or based on more complex functions. While an exhaustive account of all of these is impossible here we provide an example of landscape correlation in order to demonstrate the degree to which the process of fitness assignment impacts the topographical structure of the landscape. Uncorrelated fitness landscapes result from the random assignment of fitnesses to configurations on the space. In other words, on an uncorrelated landscape knowing the fitness of one configuration will reveal nothing about the fitness of its one-step neighbors. For example, on the well-studied NK landscape model evolutionary relationships between configurations depend on the interaction between traits (epistasis). The NK model has two parameters, N and K, where N is the number of traits and K is the number of interactions between traits and the K parameter determines the ruggedness of the fitness landscape. The $K = N-1$ landscape is an example of an entirely uncorrelated landscape space that is extremely rugged, with numerous peaks that are low and steep. The $K = 0$ landscape is highly correlated and knowing the fitness of one configuration does provide some information about the fitness of each of its one-step neighbors. On this landscape, the surface is smooth and there is a single, high peak with gradually increasing sides.

or less advantageous, and when this is the case, more complex topography begins to emerge. On low-dimensional landscapes, adaptive peaks and low-fitness valleys develop as a result of fitness differences between configuration, while on highly multidimensional spaces, the landscape (which can best be visualized as a hypercube) is punctuated by networks of fitness neutral configurations (Gavrilets 2003). In all cases, fitness assignments determine both the lowest and highest points on the landscape, including the presence of locally and globally optimal peaks on rugged landscapes, and the width of low-fitness holes in multidimensional spaces.

Evolution on Fitness Landscapes Once fitness values are assigned, they are then used to determine the probability that an individual configuration will be replicated in the next generation. New generations are created as the fitness of existing configurations (the parent generation) are fed to a stochastic selection algorithm that determines the likelihood that they will reproduce based on their fitness relative to other fitnesses in the population. The configurations of the offspring generation are then mutated with a pre-defined probability known as the mutation rate, and this new generation is then established on the landscape space (e.g., a parent configuration 0001 is mutated to 0011, and the offspring "point" is now located on the later configuration).

In natural populations, random drift and selection interact in complex ways to drive large-scale evolutionary patterns. Selection as noted above determines the replication rate of individuals based on their fitness; drift on the other hand is the intervening hand of random chance that allows some individuals to survive and reproduce despite the fact that they are less fit than others in the same population. Along with the shape of the fitness landscape, drift, selection, and mutation determine the patterns of movement that occur on the fitness landscape. In the case of an entirely neutral, flat landscape, drift determines the fate of new mutations; as offspring are produced with mutation, they are sampled entirely randomly for reproduction in the next generation, and the population moves across the space in a "random walk" fashion. As the fitness effects of mutations become increasingly non-neutral, however, the landscape becomes increasingly rugged, and new mutations are more frequently located up or downhill from the population. In this case selection will begin to favor the reproduction of individuals possessing higher-fitness configurations, including offspring with mutations that provide an adaptive advantage relative to existing individuals. Under the pressure of selection, populations will tend to move upward over time as less fit individuals are winnowed, with both the size of the population and the selective advantage of new mutations determining the effectiveness of selection and the rapidity with which populations ascend peaks. Here we note that for populations evolving on rugged landscapes, the process of evolution is likely to slow toward the top of adaptive peaks due to the fact that most new mutations will be downhill (and thus deleterious) relative to configurations already present in the population.

Finally, we note that while the fitness effects of variants may appear to result in a landscape geography that is stable, a great deal of research has demonstrated the inherently fluid nature of landscape space (Lewontin 1978). Topographical shifts on fitness landscapes occur due to environmental changes (Grefenstette 1999; Richter 2009; Wilke et al. 2001) or to coevolution, the process whereby evolving entities deform the landscape topography for other organisms or entities populating it (Kauffman and Johnson 1991). On rugged landscapes, either of these factors might change the locations of peaks as the fitnesses of configurations are adjusted to new conditions. Based on these dynamics, populations that occupied peaks prior to such changes may suddenly find themselves in low-fitness valleys, or vice versa, and the meaning of neutrality may shift as well, with previously neutral configurations becoming either adaptive or maladaptive.

Fitness and Adaptive Landscapes in Cultural Evolution

What do these parameters and dynamics mean for the study of cultural change? To begin it is important to distinguish between ideas of biological and cultural fitness and selection. Biological fitness, as used in fitness landscape theory, indicates the degree to which a physical entity or organism is adapted to its environment and thus is able to survive and reproduce. Fitness in cultural evolutionary research can be used to indicate the degree to which elements of culture or technology impact human survivability and reproduction (e.g., there may be cultural selection for technologies that enhance biological fitness). Cultural selection may also work on the level of artifacts themselves; in other words, a group of people crafting stone tools may select the best examples as templates for future copying, thereby increasing the frequencies of particular characteristics. Finally, cultural selection may act directly on human biology, increasing the frequencies of certain culturally valued biological characteristics in human populations (for a review of these concepts see Shennan 2009). The appropriate usage of selection and fitness in cultural evolutionary studies thus depends greatly on the context. Fitness landscape-based research that is macroevolutionary in nature (see examples below) tends to define fitness and selection in terms of the implications of cultural and technological packages on the survival or persistence of cultural groups. Microevolutionary research, on the other hand, often uses fitness as a way of thinking about the differential reproduction of particular characteristics within a certain artifact or cultural type, with selection acting directly on the objects in question to increase or decrease their frequencies.

Peaks on the landscapes employed in cultural evolutionary theory are variably tied to both cultural strategies—complete packages that enable groups to meet needs of shelter, mobility, and subsistence—and to the adaptive advantages that individual artifacts provide. Indeed, peaks may be thought of as "felicitous evolutionary solutions" (Bettinger 2009, p. 279) to sociocultural problems allowing human groups to better adapt to or survive in their cultural and natural environments (Richerson and Boyd 1992). As noted above, the rugged landscape images composed of peaks and valleys remain critical in cultural applications of fitness landscapes, and the problem of "peak shifting", as introduced by Wright, is still of enormous importance to cultural evolutionists. Indeed, Wright's shifting balance theory is still widely employed alongside these images and has been a formative theoretical perspective in the study of cultural diversification and change, particularly that occurring in human prehistory. Peaks and valleys in this context are highly meaningful metaphors for the process of adaptation when population sizes were fragile and when technological failure was potentially catastrophic for small, isolated groups. Microevolution in these depictions can be visualized as movement up and around peaks, as cultural groups fine-tune aspects of their social, economic, or political practices, or refine single technologies to better meet group needs. Peak shifts—movements across valleys of less fit strategies to other more adaptive strategies—represent changes in technology use or shifts in optimal combinations of technologies, skills, and cultural practices. These shifts imply alterations in the interactions between people and the landscapes that they inhabit and have important implications for the larger cultural packages in question, including social and economic organization, technological repertoires, mobility, and resource acquisition (see Prentiss and Lenert 2009 for discussion).

Fitness landscapes in cultural evolutionary theory are predominantly used to explain macroevolutionary processes (but see Mesoudi 2011) and tend to orient around broad themes of cultural divergence and large-scale transitions. In fact, a survey of the literature indicates that landscapes are often employed in explanations of major cultural diversification and that they are particularly useful in describing the pace and potential directionality of such change. For example, Prentiss and Lenert (2009) draw on fitness landscapes in order to explain transitions between socioeconomic strategies in the prehistoric arctic, and both Spencer (2009) and Flannery and Marcus (2000) use landscape theory to think through primary state formation occurring in chiefdoms. While Prentiss and Spencer both utilize the concept of peak shifting to aid in their explanations of the process of these large-scale cultural transitions, Flannery and Marcus draw from Wright's ideas of subpopulation isolation and communication to help explain the tempo of cultural change observed in the case of Olmec Meso-America. Bettinger (2009) similarly uses landscapes to help explain the rapid cultural change experienced by humans during the Holocene, noting that increasingly rapid cultural transmission possibly resulted in the establishment of multiple, local optimal solutions to cultural problems. In this volume, Spencer extends use of the fitness landscape metaphor to explain the transition from autonomous villages to chiefdoms and further notes that peak shifts involve both quantitative and discontinuous qualitative cultural changes. Further, such explanations of rapid transition are often extended to the potential directionality of cultural evolution. For example, Bettinger (2015) used landscapes to theorize the persistence and intensification of hunter-gatherer strategies in the precontact Great Basin, Kuhn (2006) to describe the trajectory of Middle Paleolithic technological evolution, and Lombard and Parsons (2011) to explain the disruption of bow-and-arrow usage in Upper Paleolithic Africa.

However, fitness landscapes are not only used to theorize obvious or rapid cultural evolution but to explain periods of stasis and the ways in which such times of little or no change integrate with larger evolutionary dynamics revealed over long time spans. Prentiss and Lenert (2009) discuss the idea that evolutionary stasis can be extrapolated from the archaeological record and interpret the transition from Pre-Dorset forager strategies to Dorset collecting in the Canadian Arctic in terms of Wright's shifting balance theory. Chatters (2009) similarly notes evidence for long periods of stasis in the archaeological record and suggests that cultural continuity often emerges as a strategy for remaining on top of local adaptive peaks. Both Chatters (2009) and Bettinger (2015) look at the often punctuated nature of cultural stasis—what Bettinger describes as periods of "change-stasis-change"—and the authors provide explanations of these periods in the context of demography and isolation and cultural transmission, respectively.

Finally, fitness landscapes are sometimes employed in order to depict the adaptive value that a particular technology provides a cultural group. For example, Lansing and Kremer (1993) use landscapes to examine the complex systems composed of water temples, agricultural production, and religious activity in rural Bali and propose that water temples represent adaptive solutions to the problem of managing irrigation for rural Balinese farmers. Similarly Mesoudi and O'Brien (2008a, b) and Mesoudi (2011) constructed fitness landscapes for the simulated innovation of projectile points and examined the role that underlying fitness functions played in the innovation of new technological forms. Marwick (2013) uses a landscape containing multiple optima to help explain shifts in stone tool technology based on ecological conditions and resource proximity. While such microevolutionary models are rare, they provide valuable insight into the differences between fitness and adaptive landscapes, as they are employed in the context of cultural evolution.

Neutral Networks and Landscape Exploration

In most cases, fitness landscapes are assumed to represent the complete set of all possible configurations possible in a particular evolutionary scenario. Depending on the number of traits and variants of those traits that must be represented to achieve this, the number of configurations on realistic landscapes can be extremely large and with increases in the number of configurations comes an increase in the number of dimensions required to accurately represent them. In the context of a configuration space that is sequence-based, as described in the section on configurations above, dimensionality can be defined as the length of the sequences present on the landscape. Despite the absence of a multidimensional representation in his original images, the highly multidimensional nature of realistic fitness landscapes did not escape Wright. Indeed, he believed that the comprehensibility of his landscape metaphor depended on "some enormous simplification" (Wright 1988,

p. 117) most notably the reduction of the multidimensional configuration space he determined to be a realistic representation of the genotype he was modeling to the three dimensions of his classic rugged configuration space. However, although Wright noted that his models were simplifications, he incorrectly assumed that the reduction in dimensionality would not impact the dynamics he described (Pigliucci and Kaplan 2006). This turns out not to be the case, and research continues to demonstrate that the dynamics of evolution in high dimensions are often fundamentally different from those occurring in low-dimensional spaces (Gavrilets 1997; Pigliucci 2012).

While there are numerous evolutionary implications of increasing the number of dimensions on a fitness landscape, here we highlight the emergence of configurations with identical functions and fitness, a property called redundancy (Vassilev et al. 2000). Redundancy results naturally from the process of mapping configurations to fitness values when there are large numbers of configurations present on the landscape. This is due to the fact that there are a limited number of fitness values that are both realistic and that result in discernable differences in configuration function, while there may be significantly more configurations that those fitness values must be mapped to (Gavrilets 1999). The result of this is that multiple configurations are assigned identical (or practically identical) fitness values with the level of redundancy increasing along with the number of configurations added and, quite intuitively therefore, along with increases in the dimensionality of the landscape. Redundancy results in neutrality due to the presence of configurations with the same fitness effect. In other words as redundancy increases, there are an increasing number of evolutionary movements that evolving organisms can take that do not result in significant changes to their fitness. This implies potentially large regions of the landscape where evolutionary movements do not result in fitness changes (Derrida and Peliti 1991) due to the fact that one-step neighbors have equal fitness and similar functions or phenotypes, despite differences in their underlying configuration. This is consistent with the neutral theory of evolution (Freese and Yoshida 1965; Kimura 1968), which states that most genetic diversity level is the result of neutral mutations that produce no effect on the fitness of the organisms in which they occur. Based on this, the neutral theory predicts that most genotypic evolutionary change should be the result of genetic drift, rather than selection (Hughes 2007).

Recent work using theoretical fitness landscapes demonstrates the importance of neutrality in producing long-term macroevolutionary patterns. In order to illustrate the impact of neutrality on evolutionary dynamics, Gavrilets (1997, 2004) (see also Gravner et al. 2007) uses a simplified landscape of two fitnesses, viable and inviable, and assigns these fitnesses randomly to configurations on the space. Gavrilets shows that there is a critical threshold (i.e., the percolation threshold) above which the emergence of a large network of viable configurations (i.e., a giant component) is extremely probable. Percolation specifically describes the probability that there is a connected path across a space of interest (typically a graph or fitness landscape), while a giant component in the context of fitness landscapes is mathematically defined in relation to the size of other connected components. Gavrilets shows that this is complexly related to both the probability of viability for each configuration and to the dimensionality of landscape; assuming a branching process defined by a Poisson distribution, Gavrilets shows that for a Poisson mean greater than 1, the probability of a giant component scales inversely with the number of dimensions. This means that as dimensionality increases, lower probabilities of viability for each configuration will result in the percolation of a giant component across the landscape. In other words, when these conditions are met, increasing the dimensions of a landscape nearly assures the emergence of large networks of configurations with identical fitnesses (i.e., they are all viable and the path connecting them is entirely neutral). Critically, when giant components are present on the landscape, a random (neutral) walk beginning at any viable point is highly likely to lead evolving entities across the entire landscape space. According to Gavrilets, this indicates that populations are extremely likely to traverse the entire landscape via neutral networks, rendering the classic problem of peak shifting largely obsolete.

Both biological and artificial evolution models have largely supported Gavrilets conclusions regarding the pervasiveness of neutral networks on realistic fitness landscapes and the degree to which populations may undergo large evolutionary changes through neutral one-step mutations. Schuster et al. (1994) found that RNA sequence space contains extensive neutral networks and noted that finding novel configurations from neutral mutation and small amounts of selection should be relatively common. Building from this, Huynen et al. (1996) described the prevalence of neutral networks and the "high diversity phenotypic neighborhoods" that lay along them. He noted that the implication of neutral networks is "perpetual innovation" (Huynen et al. 1996, p. 166), whereby organisms evolving through neutral mutation are incredibly likely to be constantly evolving novel, high-fitness configurations through neutral mutation with an innovation rate that is defined by the number of novel configurations that are accessible with each new mutation. Similarly, Andreas Wagner (2011) recently showed the existence of vast neutral networks of genotype configuration corresponding to the same phenotype in biological metabolic and regulatory networks. Wagner confirmed that these networks contained connected components that tended to percolate through genotype space, making them spatially proximate to most other genotypes on the landscape. He demonstrated the neutral property of these landscapes via random walks and found that these walks typically traverse configurations that are very far from their point of origin.

The implications of this research for theorizing evolutionary change are profound. First, these results highlight that in complex evolutionary scenarios, the number of configurations and thus the number of dimensions on the landscape is likely to be quite large. As shown above, increasing dimensionality is very likely to result in an increase in the number of neutral changes that are possible when evolving entities move across the landscape space. Archaeologists using fitness landscapes as aids for the study of cultural change should thus be aware that the complexity of the evolutionary scenario being described (e.g., all possible characteristics of a Clovis point vs. those of a digging stick), including any interactions between the configurations present on the landscape, should help the careful theorist construct the appropriate model or metaphor. Second, cultural evolutionists should be aware that a great deal of cultural change (particularly in more complex evolutionary scenarios) may occur entirely outside of the influence of selection. This indicates that explanations of major shifts in patterns of artifact use or manufacture seen in the archaeological record need not always be explained by mechanisms of culturally biased selection. Indeed, the property of perpetual innovation describes how large quantities of cultural diversity may manifest solely from the accumulation of minor, fitness neutral changes, particularly over long periods of time.

Neutrality, Stasis, Potentiation

While the fitness landscape research described above illustrates how neutral evolution may lead to rapid exploration of the fitness landscape, often resulting in the acquisition of novel configurations, one of the most compelling insights of recent advances in landscape research is the idea that phases of neutral evolution are potentiating of later periods of adaptive change. Such periods of neutral drift on fitness landscapes are often referred to as "metastable episodes" and may appear largely static as populations move across large portions of the landscape space without accruing visible changes in fitness or phenotype (Adami 1995; Barnett 1998; Elena et al. 1996; Fontana and Schuster 1998; Newman and Engelhardt 1998; Van Nimwegen et al. 1997). Some scholars claim that such metastable periods are generic on evolutionary landscapes, particularly those containing neutral networks (Barnett 1998). Even though these long, apparently stable phases may visually seem to lack change, however, they are actually highly productive periods of time (Vassilev et al. 2000, p. 255) that often have surprising evolutionary outcomes.

The fact that most variants fixed during drift have been shown to be very slightly deleterious, rather than entirely neutral (Ohta 1992), suggests that periods of stasis should be brief as they may be expected to result in the inevitable degradation of mean group fitness (Lande 1994). However,

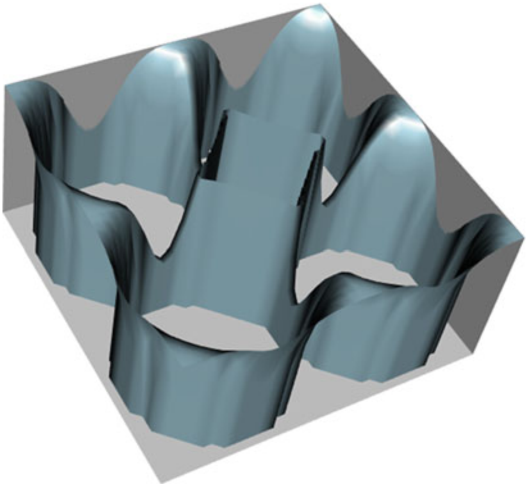

Fig. 7.4 A holey adaptive landscape formed by genotypes within a narrow fitness band. Evolution along a holey landscape is nearly neutral

recent research has resulted in the discovery of an entire class of weakly beneficial mutations and the corresponding idea that the degrading effects of drift are often corrected for across long time spans (Stephan 1996). These results suggest that populations may drift for very long periods of time without suffering severe fitness losses as novel, higher-fitness configurations are discovered accidentally or through two critical processes—potentiation and compensation. According to Lynch and Walsh (2007, p. 70), the accumulation of slightly deleterious variants during drift, while immediately detrimental to population fitness, can ultimately "provide a potential setting for secondary adaptive changes," and Huynen et al. (1996) found that evolution on fitness landscapes was often best described by punctuated equilibria, with long periods of stasis corresponding to neutral drift followed by significant fitness increases resulting from the discovery of beneficial mutations (see also Elena et al. (1996)). Research in experimental biology has since validated this claim through the discovery of neutral and slightly deleterious mutations whose interactions with the organisms in question are "potentiating" of future beneficial mutations (Blount et al. 2012). Further, research has also revealed how long periods of neutral drift may increase the probability of mutations with beneficial effects, a process known as "compensatory evolution" (Hartl and Taubes 1996; Stephan 1996). Phases of stasis, defined by neutral drift, may thus be both prolonged and common and extremely important to large-scale evolutionary patterns and outcomes that emerge only over long periods of time (Barnett 1998).

One such outcome of neutral and nearly neutral evolution, according to Gavrilets (1997, 2010), is the process of population divergence or speciation. Again, Gavrilets demonstrates how the discovery of novel phenotypes through neutral evolution may occur as populations drift along interconnected neutral networks of "viable" configurations, which are punctuated randomly by inviable, low-fitness "holes" (Fig. 7.4). A population that evolves into an inviable hole faces impending extinction, according to Gavrilets, while populations that move to the other side of a hole vis a vis their original position have split from the lineage defining their parent population and have become a distinct species. Gavrilets (1997, p. 309) demonstrates that not only *can* such divergences occur via the accumulation of small neutral mutations but that if a population can avoid extinction long enough, speciation is "an inevitable consequence" of evolution on high-dimensional holey landscapes as populations traverse large portions of the fitness landscape.

While Gavrilets simplified landscapes reveal critical properties and outcome of stasis and neutral drift, other evolutionary landscapes help us visualize how selection and drift might interact in some circumstances. Huynen et al. (1996) note that in some cases, landscapes demonstrate the property of "neutrality within ruggedness," exhibiting spaces that are defined by both peaks and valleys and pervasive neutral networks. Figure 7.5 depicts the relationship between a rugged landscape and neutral

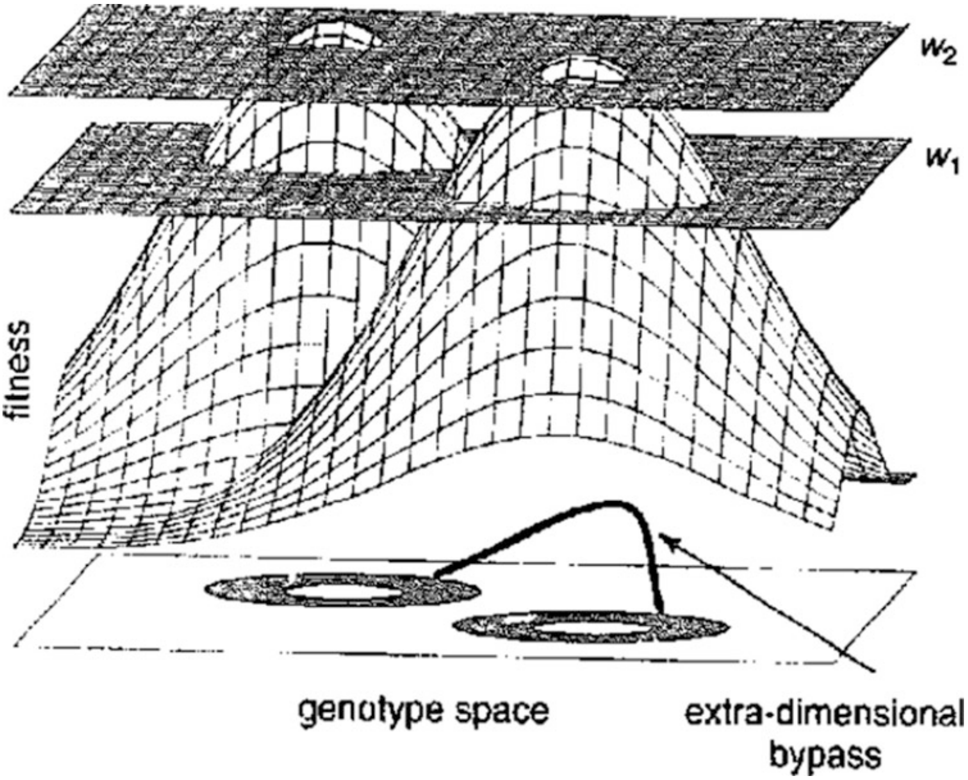

Fig. 7.5 The relationship between a rugged adaptive landscape and a holey adaptive landscape (Gavrilets 1997, p. 311)

plateaus, as one example of how different evolutionary dynamics may be represented on a single space. On the landscapes described by Huynen et al., contact regions between networks of higher and lower fitness may occur, enabling populations to transition to networks of higher fitness at these points of contact or “convergence.” When convergence on a contact region between the occupied network and one of higher fitness occurs, Huynen et al. show that selection acts rapidly to “amplify” members of the population around the point of contact, facilitating the fixation of the variant and thereby allowing the next generation of the entire meta-population to access the network of higher-fitness mutations. According to Huynen et al., on a reasonable time scale, there is no limit to the number of configurations that can be accessed via the neutral network indicating that prolonged neutral evolution can result in the evolution of any possible adaptive change.

Similarly, Derrida and Peliti (1991) show that the combined effects of mutation and previous selection events may fracture populations into small subgroups that share a recent common ancestor on the neutral space of the fitness landscape. These subdivided groups continue to undergo the process of drift, compensatory evolution, and subdivision, spreading out along a single neutral network until, by chance, a highly beneficial mutation enters the population. These beneficial mutations, under the right demographic conditions, provide the opportunity for the entire population to transition to a new neutral network of higher fitness than the one currently occupied (Barnett 1998). Van Nimwegen et al. (1999) also demonstrate how the presence of highly interconnected regions of the space where networks of different fitness levels connect facilitates transitions between networks of higher and lower fitness (Fig. 7.6). Large populations, according to the authors, are more likely to converge on these highly interconnected areas than they are to move stochastically across the space due to the fact

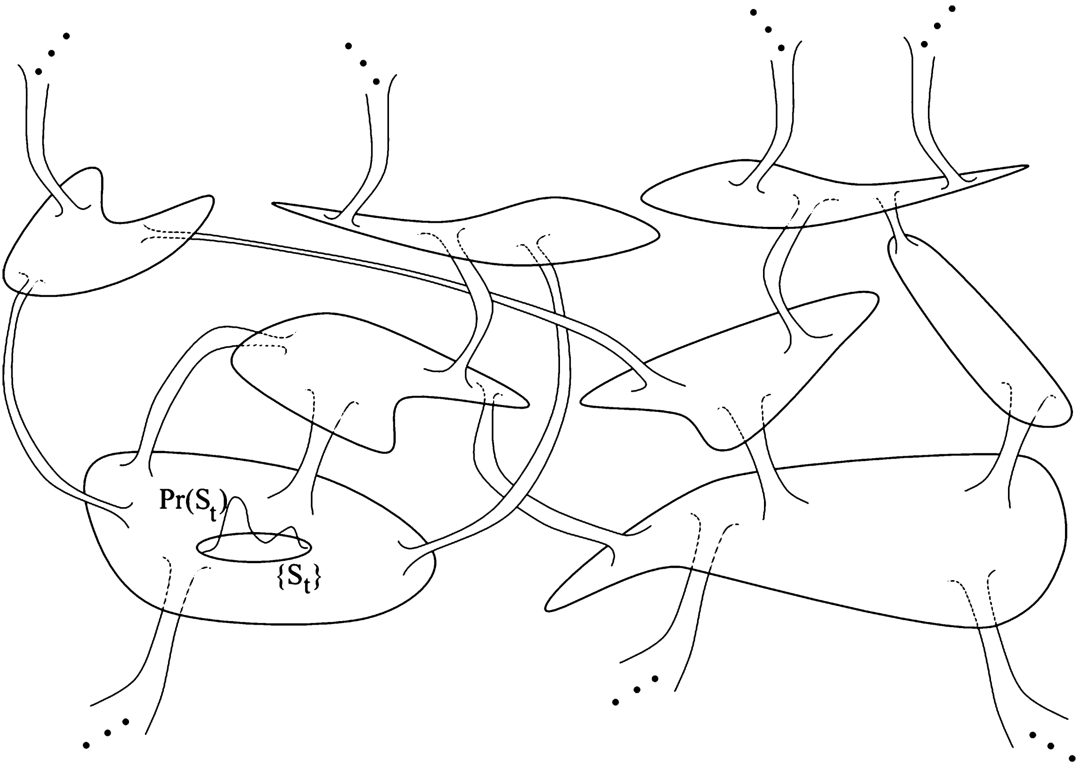

Fig. 7.6 Subbasin and portal architecture underlying macroevolutionary dynamics. A population diffuses in subbasins (large sets) until a portal (tube) to a higher-fitness subbasin is found (from Crutchfield and van Nimwegen 2002, p. 5)

that selection, rather than drift, dominates their evolutionary dynamics, while small populations may encounter, or miss, these contact regions as the result of chance.

Finally, we highlight that despite the emphasis placed on selection in traditional evolutionary theory, landscape-based research continues to reveal the limitations of selection in complex evolutionary scenarios and suggests that we must look beyond this one factor in robust explanations of cultural change. Kauffman and Levin (1987) extensively modeled the interactions between complexity and selection in artificial environments and found that selection is often inefficient at increasing mean population fitness and that it is largely incapable of maintaining populations on adaptive peaks when those peaks are connected by a series of one-step mutations (see Pigliucci and Kaplan (2006) for discussion) indicating that neutral drift, rather than selection, may be the evolutionary "default." Indeed, some theorists contend that populations located next to landscape peaks are highly unlikely to climb at all (Moran 2007; see Plutynski 2008 for discussion) and that, even in cases when they do, the probability of Wrightian style peak shifting is still incredibly small (Gavrilets 2004). Moreover, many of these theorists claim that small populations are far more likely to go extinct than they are to cross a valley and climb a new peak (Coyne and Orr 2004; Gavrilets 2004). Strathmann (1978) linked the probability of a successful climb to the level of evolutionary complexity attained by the organism involved; generalist (less complex) species he thought would be more likely to evolve toward unoccupied peaks than specialists, who would be unable to attain the rapid, adaptive diversification necessary to do so. Other research has shown that in some situations, selection actually leads to a "survival of the flattest" rather than a survival of the fittest effect, where the most mutationally robust, rather than the fittest, variants within a population are retained for future generations (Wilke et al. 2001; Zaman et al. 2012).

These results indicate not only that selection is often surprisingly ineffective at producing uphill, progressive evolutionary change but that traditional ideas regarding the predictability of selection-driven population movement on landscapes are likely inaccurate in most situations. Research on pNK landscapes, which combine neutral and non-neutral spaces, shows that under certain circumstances "reluctant" adaptive walks (movement to a neighboring square with the least fitness gain of all available beneficial moves) and random adaptive walks (movement to the next randomly chosen square), while often immediately *less optimal*, produce long-term payoffs that are often greater than those provided by "greedy" adaptive walks (movement to the neighboring square with the largest fitness gain) (Nowak and Krug 2015; Valente 2014). This indicates precisely the opposite of what we might expect—that organisms that move slowly and risk making less-optimal short-term decisions may actually fare evolutionarily better in the long term, perhaps because their long, slow walks allow exploration of larger portions of the landscape space, thereby opening up access to previously unavailable peaks.

Conclusion: Applying Landscape Revolutions to Cultural Change

What are the implications of all of these new fitness landscapes for the study of cultural change? To begin, we assert that ongoing landscape-based research has fundamentally called into question the pervasiveness of the most commonly used fitness landscape model in evolutionary anthropology—the landscape of peaks and valleys first proposed by Wright. Based on this we must also begin to question the peak-shifting "problem" as the quintessential evolutionary conundrum that cultural evolutionists attempt to solve and to imagine many scenarios in which cultural change cannot be placed on a landscape defined by a rugged topography. Indeed, while explaining evolution via hill climbing and peak shifting holds particular appeal in cultural evolutionary theory, as selection is deemed critical in sculpting major adaptive changes, new landscape research demonstrates the power of neutral evolution to bring about these beneficial shifts as well.

Here we note that the neutral theory has been an important component of research on cultural evolution for more than two decades. However, following from early controversies on stylistic vs. functional cultural traits (Dunnell 1980), the majority of the work on cultural change has continued to highlight the roles of biological and cultural selection in increasing the frequencies of adaptive cultural variants and influencing macroscale patterns in the human social groups. Indeed, the neutral theory has been employed entirely as a null model, and most cultural evolutionists still tend to see selection as the defining force in the production of adaptive cultural forms (Bentley 2008; Bentley et al. 2004, 2007; Lycett 2008; Shennan 2001; Steele et al. 2010).

While fitness landscape modeling has not been a part of all of this research, the metaphor of evolutionary ruggedness has certainly permeated disciplinary expectations. If we return to Gavrilets claim that inappropriate landscape metaphors are capable of misleading us into envisioning the process of evolution in incorrect ways, we begin to see how incorporating fitness landscapes that contain neutral spaces into our landscape toolkit can greatly expand the expectations that we are able to generate and the conclusions that we are capable of drawing from our cultural data. For example, the presence of large connected neutral networks and neutral ridges between peaks provides evolving populations with evolutionary paths not available on the rugged topographies typically imagined. In the context of cultural change, peak shifting and hill climbing cease to be the sole paths to novel, adaptive cultural innovations as cultural groups may feasibly move between peaks solely through the accumulation of neutral variants and the process of random drift. The property of perpetual innovation, now documented in a great deal of landscape research, demonstrates that through the continual discovery of new and often higher-fitness configurations neutral evolution may have critical implications for large-scale patterns of change.

How might we expect this to happen in cultural populations? The process of mutation in cultural models is analogous to that of random innovations (Neiman 1995) or small errors introduced during the processes of manufacture or the cultural transmission of knowledge and skills (Eerkens and Lipo 2005). Because these changes are not purposeful, their effects on the technologies or cultural forms in question are modeled as being entirely random, with the neutral hypothesis stating that many or most of these changes should have little or no effect on the functionality or desirability of the objects or practices in which they occur. This situation seems entirely plausible as individuals make and use technologies in different ways and transmit information regarding cultural knowledge, skills, customs, and beliefs that is subject to small often unnoticeable errors (Cavalli-Sforza and Feldman 1981). Rather than disregarding these theoretically neutral differences as trivial, however, the landscape theory discussed above asks us to consider how such small changes might accumulate in populations over time to drive larger patterns of stasis and change. Based on this we might consider the implications of placing small cultural populations on a landscape of large interconnected neutral networks that allow rapid transitions between dimensions, rather than envisioning their evolution on traditional rugged landscapes. On such a landscape, each small, neutral technological change represents the shift of individuals or populations (depending on the type of landscape) to an alternate space on the landscape with no loss or gain in fitness.

Given that small populations are likely to encounter points of contact with higher-fitness networks only by chance during the process of drift (Huynen et al. 1996), it is easy to envision extended periods of cultural stasis during which a single technological variant dominates and variation emerges only because of the types of errors in perception, skill, or memory noted above. While Gavrilets notes that speciation (what in cultural terms we might envision as ethnogenesis or major cultural diversification) is inevitable if evolving populations drift across the landscape for sufficient periods of time, he also notes that the space on the landscape between extinction and divergence is very slight (often as small as one mutational error). Thus, it is only through chance that small populations go extinct, or persist and diversify, and on landscapes defined by neutral networks, either of these outcomes can be determined through very small, randomly introduced errors alone.

Here we note that the extinction of small human groups in the past must certainly have been the norm, and recent research has shown that cultural fidelity (which would work to reduce error) has major implications for the retention of adaptive technologies and the survival of the groups relying on them (Andersson 2013; Andersson and Törnberg 2016). Poor fidelity in these small populations would have certainly resulted in the accumulation of tiny errors in cultural information and the technologies such information encoded, potentially causing the deterioration of cultural and technological fitness over time. Indeed, the loss of beneficial technologies in small prehistoric populations and the resulting population fragility that ensues have been documented in multiple instances (Henrich 2004; Lombard and Parsons 2011; Prentiss et al. 2015). However, in the event that the same small groups were fortunate enough to survive long enough, they would inevitably have been the beneficiaries of lucky technological moments as well—an encounter with another group possessing a better version of a currently used technology or an individual within the group creating an adaptive modification in order to solve a cultural problem, both of which would have provided “compensatory” sources of change. As noted above, such compensatory evolution corrects for the degradation of fitness experienced by populations over prolonged periods.

Although rare, some of these lucky moments certainly resulted in the creation of entirely novel, highly adaptive technologies as well. In these situations, the coalescence of many small random events would bring a population to a “point of contact” between the network they currently occupied and one that allowed access to a higher-fitness dimension on the landscape. These cultural or technological innovations might then have spread rapidly between subdivided populations (again, there is evidence for the rapid transmission of highly adaptive technologies among closely related prehistoric populations (Boyd et al. 2011; Smith 2001)), and selection would act to "amplify" communicating populations to the same point of network contact, effectively transitioning them all to the new landscape dimension and future evolution on the same new neutral network. It is possible that these innovations might have dramatically altered the resource management strategies (Prentiss and Lenert 2009) of the groups in question, shifting entire cultural and technological packages as a result. In this case, we can envision these evolutionary moments in light of Gavrilets speciation theory and see how prolonged periods of stasis, driven only by neutral drift, might cause entire populations to rapidly acquire novel technologies and to shift entire cultural strategies as a result.

There are numerous examples from the cultural evolutionary literature documenting not only the presence of punctuated equilibria in cultural evolution (Barton et al. 2007; Prentiss and Lenert 2009) but also the degree to which prolonged periods of stasis often had unpredictable outcomes, including extinction or cultural stagnation, cultural diversification, and the rapid innovation, adoption, and spread of novel and highly adaptive new technologies (Henrich 2004; Prentiss and Chatters 2003). For example, the case of agricultural origins in the Near East shows how the accumulation of small-scale changes over a long period of time may work to bring about major evolutionary transitions. In this case, the Epipaleolithic has been shown to be a period of small but varied cultural innovations that when viewed from a certain temporal perspective appears largely random. However, these small innovative changes eventually came together to facilitate the advent and spread of agriculture during the Holocene, an obviously profound shift in the entire cultural strategies of the groups that adopted an agricultural lifestyle (Zeder 2009a, b). Similarly, the transition between the Middle and Upper Paleolithic provides compelling evidence for the degree to which periods of stasis, rather than being stagnant, are often highly productive periods of time that are potentiating later episodes of rapid, innovative change (Hovers and Belfer-Cohen 2006). In this case, the prolonged use of major tool traditions during the extensive periods of both the Lower and Middle Paleolithic results in the rapid explosion of technological and cultural change that characterizes the beginning of behavioral modernity seen in the archaeological record around 50 KYA (Ambrose 2001; Petraglia et al. 2003). In both of these cases, the application of neutral fitness landscape theory provides a way of envisioning how this might occur and challenges our prevailing assumptions regarding the nature of cultural stasis as unproductive and stagnant.

The landscapes introduced above also question the straightforward relationship between human behavior, selection, and evolutionary progress that remains, despite our best efforts, a pervasive part of the narrative on human cultural and technological change. These "myths of innovation" (Watts and Gilbert 2014) and the models that have followed from them (Broughton and Cannon 2010; Henrich and Gil-White 2001; Kennett and Winterhalder 2006) posit human beings as hyper-rational, fundamentally creative and innovative, or inherently optimizing beings. While these models are typically purposeful simplifications of complex socio-natural situations, the idea of humans as rational optimizers has had an obvious impact on cultural evolutionary theory as we tend to view cultural strategies or technological packages as potentially optimal solutions to adaptive problems (Bettinger 2015; Boyd and Richerson 1985; Boyd and Richerson 1987; Boyd and Richerson 1995; Smith and Winterhalder 1992). In cases where theorists note that specific instances of human behavior may be sub-optimal, the conclusion is often drawn that such behaviors are selectively retained due to their interaction with other fitness-enhancing processes, such as social learning (Richerson and Boyd 1992). Further, the application of traditional rugged landscape imagery to such scenarios provides us with a vision of hill-climbing cultural groups that are able to see the contours of the adaptive landscape they are traversing and to use their unique human knowledge of adaptive peaks and valleys to hone future adaptive moves, thereby guiding the process of evolution in a beneficial direction (see Bettinger 2015 and Mesoudi 2008 for opposing perspectives on the role of foresight in evolution).

Indeed, research on the evolution of artificial populations has largely shown that our expectations of population optimization on rugged landscapes are likely entirely misguided, as the height and length of adaptive walks are complexly related to the interaction between the landscape properties and the characteristics of the organisms populating it (Nowak and Krug 2015). More simply, on rugged fitness landscapes, where the traits in question interact (a realistic assumption for the evolution of cultural and technological package with multiple integrated traits or components), the evolution of populations is constrained by the very complexity of those interactions, with highly interactive landscapes tending to permanently trap populations on sub-optimal fitness peaks (Valente 2014). Research on niche construction (see Riede this volume) further indicates the inherently complex interactions that underlie the process of adaptation, and work by Caiado et al. (2016) highlights the degree to which social processes may fundamentally change the shape of the landscape. Even more realistically, according to Gavrilets (2003), rugged landscapes provide us no accurate information about the process of macroevolution at all, including the major innovations or cultural diversifications typically described using peaks shifts. Rather they are solely a way of reasoning through the process of microevolution, and based on this they might give us a great deal of insight into the process of refinement within a single trait or technology, but nothing else. Given the increasing momentum in cultural evolutionary research to integrate understandings of micro- and macroevolutionary processes (Walsh et al. Chap. 2 and Prentiss Chap. 1, both this volume), a theory of fitness landscapes that allows us to do so should be particularly appealing.

New landscape imagery provides examples of evolution that are random and drift dominated yet highly productive, with populations that take long, slow, non-optimal evolutionary paths often experiencing the most productive high-fitness outcomes. This is a particularly timely discussion in light of increasing archaeological evidence for the nondirectional nature of cultural evolution in some contexts. For example, there is now consensus for the abandonment of bow-and-arrow technology at Howiesons Poort (Lombard and Parsons 2011) and for the abandonment of agriculture in many portions of precontact North America (Bettinger 2015). There is also growing acknowledgment for the lack of Mousterian “progress” toward Upper Paleolithic complexes (Kuhn 2006) as well as evidence that the transition from Middle to Upper Stone Age complexes in Africa did not follow a liner, progressive path. Similarly, Arctic Small Tool tradition of the North American Arctic provides an example of nonprogressive losses and gains in Pre-Dorset tool types (ca. 4000–2500 cal. B.P.) that do not in any way predict the comparatively rapid evolution of Dorset socioeconomic strategies and toolkits at later points in time (Prentiss et al. 2015).

Indeed, the ideas that cultural evolution is sometimes nonprogressive and that immediate non-optimal decisions are incapable of predicting later evolutionary developments have been growing among evolutionary anthropologists (Ambrose 1998; Brown et al. 2012; Lombard 2012; McBrearty and Brooks 2000; Tryon and Faith 2013). Likewise is the notion that evolutionary dynamics such as mutation (e.g., innovation and error), drift, selection, and population size are complexly intertwined and thus not easy to either measure or directly predict. Further, while a great deal of evolutionary work on culture does highlight culturally selective biases, many researchers acknowledge that the interaction between neutrality and selection is most likely complex and that both neutral drift and selection may potentially play important roles in cultural evolution (Bentley 2008; Bentley et al. 2004; Brantingham and Perreault 2010). Cultural evolutionary research is thus poised to consider many of the critical topics currently advanced by fitness landscape theory, and the inclusion of these alternative landscape dynamics and topographies could serve as useful tools and visual aids for this purpose. Further, while the implications described in this paper are at this point largely theoretical in nature and involve the use of advanced fitness landscapes as metaphors or visualizations for thinking through complex evolutionary scenarios, we hope this paper provides a catalyst for quantitative applications as well. In particular, we see the integration of neutral and nearly neutral spaces on the fitness landscapes used to model cultural microevolution as an especially reasonable addition to the existing literature. Such spaces would allow integration of neutral (or nearly neutral) microscale changes seen in archaeological contexts, providing the researcher with the ability to explain both periods of stasis within tool technologies or traditions and long-term selective trends. Research using the plethora of data surrounding the Acheulean tool industry might prove particularly useful for such a project as existing models include nuanced discussions of neutrality, fitness, and selection (Lycett 2008).

In conclusion, we note that the examples drawn from this paper are but a small sampling of a very deep literature spanning the decades since Wright's original work. While representing only a brief introduction to the topic, this paper will hopefully be a source of encouragement to scholars of cultural change to consider the "landscape revolutions" described above in ongoing work. In particular, we feel that consideration of recent advances in landscape theory may have major implications for the ways in which evolutionary anthropologists theorize stasis, cultural divergence, and macroevolution, the role of neutral evolution in facilitating the process of innovation, and the complex interactions between selection, drift, and human behavior in determining large-scale patterns of cultural change.

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