*New Idea***Bridging valleys: Expanding the adaptive landscape concept beyond theoretical space—with applications in ecology and evolution****Constantinos Yanniris and Victor M. Frankel***Constantinos Yanniris (constantinos.yanniris@mail.mcgill.ca), Department of Integrated Studies in Education, McGill University, Montreal, Quebec, Canada H3A 1X1**Victor M. Frankel (victor.frankel@mail.mcgill.ca), Department of Biology, McGill University, Montreal, Quebec, Canada H3A 0C4***Abstract**

Adaptive landscapes embody a concept that has provided valuable services to evolutionary biology over the last 80 years. Its heuristic power derives from its capacity to portray fitness functions in planar representations where environmental conditions are presumed to be static. In an effort to incorporate environmental change into this powerful theoretical tool, we propose an expanded, three-dimensional eco-phenotypic landscape which relates to physical ecological space. This is expected to enhance the ecological applications of the adaptive landscape by providing practical insight into various evolutionary principles including adaptive divergence, gene flow, and sympatric speciation.

Keywords: adaptive landscape, eco-phenotypic landscape, adaptive divergence, speciation, hybrid fitness, gene flow.

evolutionary change. However, the multiple influences shaping the concept of the adaptive landscape have resulted in the lack of a universal definition and have fueled debate over its interpretation and other conceptual issues (Kaplan 2008, Gavrillets 2004, Skipper 2004, Coyne et al. 1997, Ruse 1996, Provine 1986). A major present-day challenge for the concept of the adaptive landscape is to improve its compatibility with the field of ecology. Indeed, the role of ecology in giving rise to dynamic adaptive landscapes has been largely ignored, although recent research better integrates on the role of the environment in shaping the adaptive landscape (MacColl 2013).

A formalization that incorporates ecological change into the adaptive landscape has yet to be developed for improving the applicability of the adaptive landscape for heuristic and educational purposes. Thus, we aim to bridge this gap through the introduction of a dynamic environmental gradient as an expansion of the static adaptive landscape model. In this study, we will develop the conceptual framework and mathematical tools that allow for the introduction of an environmental axis (or axes) to the individual fitness class of functions. This process produces a multivariate extension of the individual fitness function that retains the physical metaphors and the visualization potential of the adaptive landscape. Eventually, the integration of the multivariate individual fitness function over the population's phenotypic distribution generates a multivariate mean

Origins of the adaptive landscape

Since the original visualization of fitness functions by Sewall Wright (1932), the concept of the adaptive landscape has evolved under the influence of Simpson (1944, 1953), Lande (1976), Kirkpatrick (1982), Schluter (2000), Arnold et al. (2001) and others. Over the years, the adaptive landscape was proven to be both an effective summary and a resilient metaphor of the forces driving

Figure 1. Constrained and unconstrained adaptive landscapes. Two constrained fitness functions (top) can be merged into a single fitness function (bottom) that connects the optima between two adaptive peaks. Adapted from Hendry (2016).

fitness function that can be used as a heuristic scheme for describing the strength and direction of selection (see Appendix).

The incorporation of environmental change in graphic representations

Early in the modern synthesis of evolutionary biology, it was understood that fitness peaks constantly shift under the influence of environmental change (Simpson 1953). Since each adaptive landscape is theoretically bound to a specific environment, there is a need for conceptual solutions that can incorporate changing environmental conditions. In an effort to address this issue, Wade and Kalisz (1990) and Mitchell-Olds and Shaw (1987) visualized fitness functions separately for a series of different environments, showing different trait covariances. Hendry et al. (2012) introduced a synoptic approach that advanced the notion of unconstrained adaptive landscapes to include more than one synchronous environment in the same visual representation (Figure 1). This proved particularly useful for the study of geographically dispersed populations.

To the authors' knowledge, MacColl (2011) was the first to use a three-dimensional representation to include both phenotypic and environmental gradients in the same graph. Interested in the causes of selection, MacColl used the mean fitness function to introduce an ecological gradient and named the resulting hypothetical patterns "eco-evolutionary surfaces" in order to discern them from classic adaptive landscapes and other types of

selection surfaces. The present study builds on these previous refinements to the adaptive landscape to demonstrate the value of a multivariate environmental expansion of the individual fitness function for heuristic and educational purposes. These improvements in the conceptualization of the adaptive landscape could greatly enhance the application of adaptive landscapes for pedagogical approaches to evolutionary biology.

The eco-phenotypic landscape

In both individual and mean fitness functions, phenotypes are treated as continuous gradients. Similar to the continuous variation found in many phenotypic traits, environmental variables can also be quantified as gradients, as is the case for temperature, salinity, chemical concentration, pH, etc. Environmental gradients can thus be included as a third axis in the adaptive landscape (Figure 2), thus enabling the new representation. A gradual shift of fitness functions can be thus expected as a result of change in the environmental variable.

Bergmann's rule (1847) presents a pertinent example of adaptation to an environmental gradient that allows us to demonstrate how body mass changes depending on mean temperatures (McNab 1971, Blackburn et al 1999). According to Bergmann's rule, fitness peaks will shift towards phenotypes of larger body mass as external temperature decreases (Figure 2). In order to return to the unconstrained landscape of Figure 1, these peaks can be juxtaposed on the same plane.

It then becomes apparent that the peaks of Figure 2 can be considered the scaffold of a continuous, comprehensive 3D graph. By setting the two planar axes to represent phenotype and environment gradients, fitness levels appear as contours, their peaks sticking out towards the reader. Figure 3 provides an illustration of Bergmann's rule as a multivariate individual fitness function. The graph suggests that highest fitness is achieved by large body sizes in lower temperatures, intermediate body sizes in intermediate temperatures, and small body sizes in high temperatures. Also, in extreme temperatures or body sizes, fitness falls to zero. By dissecting the three-dimensional surface along the parallel planes represented here by temperature lines, we can go back to the multiple fitness peaks of Figure 2.

Resembling a topographic map, the emerging *eco-phenotypic landscape* encompasses nuances of spatial environmental gradients. This connection with geography is not trivial: since environmental parameters are spatial functions, axis *E* of the eco-phenotypic landscape corresponds to the natural ecological space. Hence, the vertical axis of Figure 3 could be adapted to represent geographical latitude, with the arrow pointing south in the case of the Northern hemisphere. However, it is important to note that this adaptation must follow the variability of the environmental factor over physical space.

Figure 2. A qualitative representation of Bergman's rule on the unconstrained adaptive landscape (individual fitness peaks shift under the influence of environmental change).

Figure 3. A qualitative representation of Bergman's rule in an eco-phenotypic landscape. It is important to note that the phenotype of the population (represented as the horizontal axis in this landscape) can shift in response to change in the environmental dimension (vertical axis) that drives the strength of natural selection. On the diagram, organisms will follow an upward-left movement for rising climatic temperatures (leading to smaller body sizes), and a downward-right movement for falling climatic temperatures (leading to larger body sizes).

Figure 4. A geometrical attribution of gene flow (θ shift represents adaptive divergence, $\theta - \varphi$ represents gene flow).

For example, the same distance along longitudinal and latitudinal gradients does not represent the same variation in environmental variables such as temperature and rainfall that vary significantly with latitude but less with longitude.

The adaptive ridge depicted in Figure 3 is expected to be a common phenomenon in cases where phenotypes are selected along environmental gradients. Many prominent environmental gradients are predictable and consistent over time (for example, temperature decreases at higher latitudes and altitudes, just as the concentration of sulfur compounds increases with decreasing distance from hydrothermal vents). As a result, adaptive ridges of the likeness of Figure 3 could have sustained their geometrical forms for enough time to create pressures of divergent selection on populations.

The role of adaptive divergence and gene flow in shaping the eco-phenotypic landscape

Populations whose distributions extend over different environmental conditions can be exposed to different

directional selection forces that lead to adaptive divergence (Björklund and Gustafsson 2015, Hendry et al. 2004, Hendry et al. 2002, Barton 2001). The opposite effect is typically caused by gene flow which suppresses genetic variance and tends to drag the populations back to intermediate (central) forms (Rousset 2000, Leblois et al. 2003). Gene flow will then have a direct effect on the population distribution by inhibiting peripheral populations along the environmental gradient from evolving to their local optima (Garcia-Ramos and Kirkpatrick 1997). Eventually, gene flow causes the population distribution continuum to deviate from the fitness optimum (Figure 4).

In the absence of gene flow, the population distribution would follow the fitness ridge (fitness optimum) of the three-dimensional landscape. Instead, if extensive gene flow overwhelms the selection forces of adaptive divergence then the population distribution would pivot to assume a vertical position. Hence, the two opposing forces of phenotypic variance, adaptation and gene flow, assume geometrical attributes in the eco-phenotypic landscape: adaptive divergence tends to shift the population distribution along the adaptive ridge while genetic drift tends to restore the population distribution to the vertical position. Borrowing from the methods of analytic geometry, the effects of adaptive divergence and gene flow on a phenotypic distribution can be quantified as angles θ and $\theta - \varphi$, respectively (Figure 4).

This reasoning allows us to propose the following function as a tentative measure of gene flow:

$$g = \frac{\theta - \varphi}{\theta}$$

Function g is an algebraic value of a geometrical origin, expected in conditions of dynamic stability to assume values from 0 (zero gene flow) to 1 (panmixia). As a dimensionless quantity, it lends itself to comparisons with other measures of gene flow in continuous populations (see also Pigliucci 2013, Pigliucci and Kaplan 2006).

A mechanism for sympatric speciation

This section uses the eco-phenotypic landscape to describe a speciation model within a continuous population distribution. Numerous studies have noted gene flow as an obstacle to speciation (Kirkpatrick and Barton 1997, Rousset 2000, Hendry et al. 2009, Berner et al. 2009). Until recently, the potential of divergent selection to induce speciation in the presence of active gene flow was hotly debated. Contemporary biology holds that speciation can indeed occur in the presence of extensive gene flow between continuous, interbreeding populations as long as the drivers of disruptive selection

are strong enough (Dieckmann and Doebeli 1999, Leblois et al. 2003, Benkman 2003, Rueffler et al. 2006, Rova and Björklund 2012).

In the scenario that follows, changing environmental conditions expose a population to strong divergent selection that leads to speciation. Initially, the population occupies the left lobe optimum of Figure 5A, at temperature T_1 . The dissection of the three-dimensional eco-phenotypic surface along four temperature values (Figure 5A) produces a set of two-dimensional fitness graphs (Figure 5B). Figures 5BI to 5BVII present the chronological order of the speciation scenario. In Figure 5BI, the peak in solid color represents the phenotypic distribution of the initial population; the other two fitness peaks are vacant. A series of cold winters force the population to undergo adaptive change (Figure 5BII, 5BIII) that leads to the evolutionary bottleneck of 5BIV (T_4). After that point, a climatic rebound to warmer temperatures triggers a ‘dimple’ or ‘split of peaks’ speciation scenario (Rozenzweig 1978) as in 5BV and a separated population will hence occupy the intermediate fitness peak (5BVI and 5BVII). The newly occupied peak corresponds to the right lobe of the horseshoe-shaped eco-phenotypic landscape (Figure 5A).

To sum up, this model shows that a horseshoe-shaped eco-phenotypic landscape may have a special significance for sympatric speciation in continuous populations. However, the shape of the eco-phenotypic landscape is not a sufficient condition for sympatric speciation. The pace and amplitude of environmental oscillations, the strength of selection, the covariance with other environmental and phenotypic characters, and the genetic variance and covariance will all have to be accounted for before an accurate prognosis can be made. The value of the eco-phenotypic landscape is that it retains its form over phenotypic or environmental change and can serve as a template that allows for long-term heuristic projections after the integration of the aforementioned parameters.

The three-dimensional eco-phenotypic landscape (Figure 5A) can be viewed as a relatively static mold which produces the ephemeral patterns of fitness peaks that move constantly under the forces of environmental change (Figure 5B). Interestingly, Simpson used the following analogy for the patterns of the original, two-dimensional adaptive landscape:

‘To complete the representation of nature, all these elements [of the selection landscape] must be pictured as in almost constant motion- rising, falling, merging, separating and moving laterally, at times more like a choppy sea than like a static landscape’ (Simpson 1944: 90)

Careful consideration of Simpson’s work (1944) reveals that his conception of the adaptive landscape was far from static. However, it is possible that at his time there was less empirical evidence upon which the scientific community could have expanded on his pioneering work that aimed to bridge evolutionary change in phenotypes with that of change in ecological conditions that vary across geographic landscapes. Today, we revisit his ideas looking for the theoretical and analytic tools that may enable researchers to map the adaptive landscape onto real-world landscapes and identify traits under selection in different regimes established by geographical variations. Thus, placing these ideas in the context of previous considerations of the adaptive landscape by Simpson and others could guide ecologists to identify the primary drivers of natural selection while enabling evolutionary biologists to measure the strength of selection across environmental change and allow both to make predictions on how natural populations respond to environmental change. Finally, this visualization of the adaptive landscape over geographic rather than theoretical space will allow educators in both fields to convey complex ideas developed in theoretical space and move them into any classroom.

Concluding remarks

In this paper we provide the conceptual and mathematical framework for the introduction of an environmental gradient to the adaptive landscape, starting with the individual fitness class of functions. The resulting graphical instrument facilitates the visualization of various evolutionary principles including gene flow, adaptive divergence, and sympatric speciation. Although we present this expansion of the adaptive landscape by introducing only a second independent environmental variable, it is important to note that various independent or interdependent environmental variables could drive adaptive change in the phenotype of a population. Therefore, our expansion of the eco-phenotypic landscape should motivate further elaborations of the adaptive landscape to allow for this multivariate visualization. Eventually, the integration of the multivariate individual fitness function over the phenotypic distribution of actual populations produces multivariate mean fitness functions that can be used to predict the forces of selection over spatially or temporally alternating environments. In addition, the eco-phenotypic landscape demonstrates that the adaptive landscape is not only a resilient and useful tool for understanding evolutionary change, but is in itself an engine for research into the educational and heuristic approaches to understanding that ‘mystery of mysteries,’ evolution by natural selection and the origin of species.

Figure 5. (A) A horseshoe eco-phenotypic landscape (multivariate individual fitness function). (B) A scenario of sympatric speciation driven by environmental change (blue peaks represent individual fitness functions and solid magenta peaks represent phenotypic distributions).

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Appendix: Mathematical formulations

Presently, adaptive landscapes are associated either with individual fitness functions (Svensson and Calsbeek 2012: 181) or with mean fitness functions (Schluter 2000: 88). The *individual fitness* function applies to individual organisms; its graphical representation carries the powerful illustrative potential of the adaptive landscape for conceptualization and didactic purposes. As a graph, it provides insight on selective pressures but cannot provide accurate predictions on the strength and direction of selection (selection gradient) without the consideration of the population's phenotypic distribution.

The *mean fitness* function produces graphical representations where data points stand for entire populations. In the mean fitness function, the population distribution (V) has been integrated and thus the function can produce accurate predictions concerning both the rate and direction of evolution. Indeed, the tangent's slope on the mean fitness function graph represents the selection gradient β (Arnold et al. 2001).

Table 1. Individual and mean fitness functions disambiguation

Function name	Horizontal axis	Vertical axis	Graph sample	Assumptions	Pros	Cons
Individual fitness function	Phenotype (Z)	Individual fitness (W)	<p>Graph includes population distribution (solid magenta)</p>	Constant environment (E)	Retains form regardless of changes in phenotypic distribution	Does not provide quantitative predictions of evolutionary direction
Mean fitness function	Mean phenotype ($\bar{Z}$)	Mean population fitness ($\bar{W}$)	<p>Phenotypic distribution already included in the mathematical reasoning</p>	Constant environment (E) Constant phenotypic distribution (V)	Allows the prediction of evolutionary direction	Changes according to the population distribution

Table 1 is meant to clarify the two types of adaptive landscape visualizations mostly in use today. Understanding the distinction between these forms is important before proceeding to the main argument. Both the *individual fitness* function and the *mean fitness function* (Table 1) can be transformed into multivariate functions of two independent variables as follows, where the independent variables represent phenotype and the newly introduced environmental gradient.

$$\begin{array}{lll}
 W = f(Z, E) & & \{\text{individual fitness function}\} \\
 \bar{W} = f(\bar{Z}, E) & V=\text{constant} & \{\text{mean fitness function}\}
 \end{array}$$

Values:

W=individual fitness
 $\bar{W}$ =mean fitness
 V=population distribution
 Z=phenotype
 $\bar{Z}$ =mean phenotype
 E=environmental gradient

The above algebraic transformations produce the three-dimensional graphical representations referred upon as eco-phenotypic landscapes. These surfaces are mathematically allowed to take all sorts of shapes except from negative or vertical slopes; each point in the diagram corresponds to a single contour (Figures 3, 4 and 5).