
Preface

The Adaptive Landscape is one of those classic concepts in evolutionary biology that seems to emerge again and again despite having been declared dead many times. It was first formalized by the late population geneticist Sewall Wright in 1932 (Wright 1932), 80 years ago, and is the topic of this volume. Wright's idea immediately caught the attention of some leading evolutionary biologists, including Theodosius Dobzhansky, who popularized the idea in several books and articles. Eventually, the Adaptive Landscape became intimately connected to the Modern Synthesis in evolutionary biology, which started in the late 1930s with several influential volumes (Dobzhansky 1937; Mayr 1942; Simpson 1944), and which remains subject to much controversy and discussion even today (Pigliucci & Müller 2010). It was probably the highly appealing visual aesthetic of the Adaptive Landscape, as well as Dobzhansky's charismatic personality and strong influence that contributed to the popularity and success of the Adaptive Landscape concept.

The editors of this volume (Erik Svensson, ES; Ryan Calsbeek, RC) got our research training long after the Modern Synthesis was completed, and long after the death of Sewall Wright, yet the Adaptive Landscape has been with us since we first entered our PhD programs in Sweden and California, respectively. This influence of the Adaptive Landscape was part of our formal curriculae, but we also encountered it on various other occasions, such as at scientific meetings, but often in also quite unexpected contexts. For instance, ES went on field excursions with some other Swedish PhD students to the Galápagos Islands in 1993, and while standing watching giant tortoises from the slope of one of the five volcano peaks (Alcedo) on the large island of Isabela one of his colleagues (Anders

Hedenström, currently a professor at Lund University) remarked: "These volcano peaks remind me about Sewall Wright's Adaptive Landscape." Anders was neither the first nor last person who has drawn the analogy between physical (geographic) landscapes and the landscape of fitness that Sewall Wright described in the powerful metaphor he formulated in 1932. A few years later, ES went to California to pursue postdoctoral research on side-blotched lizards (*Uta stansburiana*), where RC had just started as a graduate student. We both did our fieldwork on the hilly grass-covered slopes at Los Banos (Merced County) in Central California. These rolling hills also provided a natural visual connection to Sewall Wright's Adaptive Landscape. Interestingly, Sewall Wright actually spent at least one vacation in Central California during the critical time period when the Adaptive Landscape was formulated (Provine 1986), so it is actually possible that he was partly inspired by the very same hilly landscape that caught our attention.

After his postdoc, ES published a paper from his postdoctoral research that reveals the inspiration of the Adaptive Landscape in evolutionary ecological field studies: "Experimental excursions on Adaptive Landscapes: density-dependent selection on egg size" (Svensson and Sinervo 2000). Over the ensuing decade, we both published several more papers containing fitness surfaces and selection gradients as part of our research programs in field evolutionary ecology using insects, reptiles, and amphibians (see Chapter 7 for a review of this and many other selection studies).

The Adaptive Landscape has certainly also been popular outside of our research environments, otherwise we would probably not have been able to publish our studies. In fact, the Adaptive

Landscape seems to hold a central position in some fields, which are almost impossible to imagine without the concepts of adaptive fitness peaks and valleys. These include, for instance, the ecological theory of adaptive radiation and ecological speciation (Schluter 2000; Rundle and Nosil 2005). The study of local adaptation and fitness trade-offs between environments, for instance, postulates the existence of fitness valleys between fitness peaks that can be revealed by reciprocal transplant experiments (Schluter 2000). Moreover, in evolutionary genetics, fitness epistasis and multiple fitness peaks are central topics of research, and these topics are very difficult, if not impossible, to understand without referencing the Adaptive Landscape (Whitlock et al. 1995; Wolf et al. 2000; Phillips 2008). Finally, in comparative evolutionary biology and phylogenetic studies of adaptation there is often a strong link to the Adaptive Landscape in formal theoretical modeling (Hansen & Martins 1996; Hansen 1997).

We, along with many other evolutionary biologists, are obviously strongly influenced by “landscape thinking” in our day-to-day research. Still, we also became aware, quite early on, of the many criticisms and potential pitfalls of the Adaptive Landscape. These criticisms appear at regular intervals in philosophy journals and books (Gavrilets 2004; Kaplan 2008; Pigliucci 2008), and are important, as they challenge supporters of the Adaptive Landscape concept to clarify their points and sharpen their arguments about why it is important and useful. Science and the production of new knowledge is often stimulated as much by discussions and controversies, as by elegant ideas. Science is a process, rather than a product that will be finished with all questions resolved. These criticisms have therefore been as useful and stimulating to us as we prepared this book, as were the many examples and areas where the Adaptive Landscape appeared to have been useful and influential.

This volume aims to present different voices on the Adaptive Landscape, its past, present, and future position in evolutionary biology. We got the idea for this book a few years ago, when we realized that the 80-year anniversary of Sewall Wright’s classic paper was approaching rapidly (2012), and we both felt that it was an excellent opportunity

to summarize the state of the art of the Adaptive Landscape. Our hope is that this volume will be intellectually stimulating to both senior researchers, postdocs, as well as new-comers and fresh PhD students in evolutionary biology and related fields. We also hope that this volume does not mark the end of the scientific discussions about the Adaptive Landscape, but rather a new beginning. And finally, we hope that if the Adaptive Landscape will not survive another 80 years, it will hopefully be replaced by an even better concept or metaphor that will push evolutionary biology forward and increase our knowledge about adaptation, speciation, and the origins and preservation of biodiversity on this fragile planet.

Erik I. Svensson and Ryan Calsbeek

References

- Dobzhansky, T. (1937). *Genetics and the origin of species*. Columbia University Press, New York.
- Gavrilets, S. (2004). *Fitness landscapes and the origin of species*. Princeton University Press, Princeton, NJ.
- Hansen, T. F. (1997). Stabilizing selection and the comparative analysis of adaptation. *Evolution*, 51, 1341–1351.
- Hansen, T. F. and Martins, E. P. (1996). Translating between microevolutionary process and macroevolutionary pattern: The correlation structure of interspecific data. *Evolution*, 50, 1404–1417.
- Kaplan, J. (2008). The end of the Adaptive Landscape metaphor? *Biology & Philosophy*, 23, 625–638.
- Mayr, E. (1942). *Systematics and the origin of species*. Columbia University Press, New York.
- Phillips, P. C. (2008). Epistasis—the essential role of gene interactions in the structure and evolution of genetic systems. *Nature Reviews Genetics*, 9, 855–867.
- Pigliucci, M. (2008). Sewall Wright’s Adaptive Landscape: 1932 vs. 1988. *Biology & Philosophy*, 23, 591–603.
- Pigliucci, M. and Müller, G. B. (2010). *Evolution—The Extended Synthesis*. The MIT Press, Cambridge, MA.
- Provine, W. B. (1986). *Sewall Wright and evolutionary biology*. University of Chicago Press, Chicago, IL.
- Rundle, H. D. and , Nosil, P. (2005). Ecological speciation. *Ecology Letters*, 8, 336–352.
- Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Simpson, G. G. (1944). *Tempo and mode in evolution*. Columbia University Press, New York.

- Svensson, E. and Sinervo, B. (2000). Experimental excursions on adaptive landscapes: density-dependent selection on egg size. *Evolution*, 54, 1396–1403.
- Whitlock, M. C., Phillips, P. C., Moore, F. B. G., and Tonsor, S. J. (1995). Multiple fitness peaks and epistasis. *Annual Review of Ecology, Evolution, and Systematics*, 26, 601–629.
- Wolf, J. B., Brodie III, E. D., and Wade, M. J. (2000). *Epistasis and the evolutionary process*. Oxford University Press, New York.
- Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proceedings of the Sixth Annual Congress of Genetics*, 1, 356–366.