Is Adaptive Landscape in Biology a Metaphor or a Quantitative Concept? or Both?

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Abstract

Some biologists accept Wright’s adaptive landscape idea, believing it is one of most profound concepts in evolutionary dynamics. Some wouldn’t, believing that "the idea that there is such a quantity remains one of the most widely held popular misconceptions about evolution." The two groups usually have very limited communication with each other. The paper of Poelwijk, Kiviet, Weinreich, and Tans (Nature, 445: 383-386(2007)) is an example. Sometimes such isolation can be good, because it protects budding ideas in a harsh environment. Thanks to the theoretical and experimental progress during past few years, time may have arrived to consider both sides seriously. Present letter is an attempt to bridge this gap, by pointing out two misrepresentations and one resulting error in Poelwijk et al.
Wright’s adaptive landscape and the associated potential function have been controversial in biology even since they were proposed some 70 years ago [1]. In his recent textbook Rice stated that "there is no general potential function underlying evolution. ... the idea that there is such a quantity remains one of the most widely held popular misconceptions about evolution" [2]. Despite such strong negative opinion, the explanatory power of Wright’s idea is evident and remains attractive. So went the 2007 paper of Poelwijk et al [3] on the numerical construction of the landscape for protein evolution paths. In their dash, however, Poelwijk et al made two misrepresentations and one error.

**Does the adaptive landscape really have a meaning beyond its metaphoric role?**

By ignoring the abundant objections such as that of Rice Poelwijk et al chose to present a consensus picture. However, apart many intriguing "counterexamples” in literature, Rice emphatically stressed the simple limit cycle type dynamics as a "counterexample” for nonexistence of adaptive landscape. To my knowledge there is no work to head-on addressing such objection, other than those in Ref.’s [4, 5], which are not cited by Poelwijk et al. Fortunately, the general conclusion of the existence of quantitative adaptive landscape in Ref.’s [3, 4, 5] all agree with each other, a rather happy coincident.

**What is the effect of noise?**

Poelwijk et al did notice that there are some situations that the landscape seems ill-defined, such as "the situation in which environmental fluctuations are fast relative to selection timescales”. They suggested that "recently theoretical considerations may provide promising approaches to address these questions more generally.” This leads to their second misrepresentation: Such general theoretical framework has already existed since 2004 [4, 6, 7], again not mentioned in their work. Specifically, it was already shown in 2005 that the existence of the Wright adaptive landscape is a general property of Darwinian evolutionary processes [4]. The noise, both genetic and environmental, is shown to be able to affect the adaptive landscape in a profound and quantitative way [4, 5, 6, 7, 8]. Here is then another and more impressive happy coincidence.

”Intelligent design” vs Evolution.

The exaggeration and negligence, or vision and boldness if putting alternatively, are abun-
dant in literature. For example, in a recent Nature paper the results were presented in such a way it appeared the adaptive landscape in biology started with them\textsuperscript{9}. Hence, experienced readers would ask: What is the real fuss on such issue? Well, the reason was actually been suggested by Poelwijk \textit{et al.}: To fight the misunderstanding on evolution we have to be extra careful. It is known that the advocates of "intelligent design" have the habit to ignore overwhelming inconvenient evidence and to selectively pick up ones "supporting" their theories. As scientists, we naturally cannot operate on such "professional" level. Otherwise, it would not improve the credibility of science. There is an already known example of such rash in 1990’s on the evolution of eye: The researchers were not careful enough on assumptions and gaps in their simulation. They led others to believe a definite conclusion was already reached. Till these days there are still ongoing experimental efforts to understand the evolution of eye\textsuperscript{10}. With this in mind, it is worthwhile\textsuperscript{11} to point out the works neglected by Poelwijk \textit{et al} as well as their misrepresentations.

\textbf{Importance of drift.}

Poelwijk \textit{et al.} did ask important questions such as ”Is neutral genetic drift essential for a new trait to emerge?” However, it appears wrong for them to conclude that ”neutral genetic drift is not essential in case studied.” Let me ignore their rather restrictive use of drift and focus on two facts showing in their work. First, without the drift, the wondering in the flat part of landscape in their Fig.1c would not happen. Second, if they perform a large sampling, they should be able to obtain distribution determined by their adaptive landscape as discussed in Ref.[4], even for single adaptive peak. There would be no such distribution if there were no drift. Thus, drift cannot be ignored.

There are two additional reasons that their negative conclusion on drift is not correct. There is a so-called fundamental theorem of natural selection\textsuperscript{12} generalized in Ref.[4]: The rate to approach to the peak is proportional to the drift or variation. Zero drift would imply the impossibility to reach the adaptive peak! Furthermore, as discussed by Wright\textsuperscript{1,4}, the drift would make the transition from one peak to another, such depicted in their Fig.1b. A report on the quantitative agreement between experimental and theoretical studies of such behaviors in the phage lambda may serve as a nontrivial example of such transition\textsuperscript{8}. The real problem seems to be time scales. It is likely that in their numerical experiment Poelwijk \textit{et al} had not run their time long enough to reveal such features.
I do not believe Poelwijk et al had deliberated ignored relevant prior works: Once the two misrepresentations and one error are corrected, their main conclusion of the existence of adaptive landscape becomes stronger.

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[3] Poelwijk, F.J., Kiviet, D.J., Weinreich, D.M. and Tans, S.J., Empirical fitness landscapes reveal accessible evolutionary paths, Nature 445: 383-386 (2007).
[4] Ao, P., Laws in Darwinian Evolutionary Theory, Physics of Life Reviews, 2: 117-156 (2005).
[5] Zhu, X.-M., Yin, L., Ao, P., Limit cycle and conserved dynamics. Intl J. Mod. Phys. B20: 817-827 (2006).
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[7] Kwon, C., Ao, P. and Thouless, D. J., Structure of stochastic dynamics near fixed points. Proc. Natl. Acad. Sci. (USA) 102: 13029-34 (2005).
[8] Zhu, X.-M., Yin, L., Hood, L. and Ao, P., Robustness, stability and efficiency of phage lambda genetic switch: dynamical structure analysis. J. Bioinf. Compt. Biol. 2: 785-817 (2004).
[9] Acar M., Becskei A., van Oudenaarden A., Enhancement of cellular memory by reducing stochastic transitions, Nature 435: 228-232 (2005).
[10] Jacobs, G.H., Williams, G.A., Cahill, H., Nathans, J., Emergence of Novel Color Vision in Mice Engineered to Express a Human Cone Photopigment Science 315:1723 - 1725 (2007)
[11] This note was submitted to Nature on March 16 after 15 days waiting for reply to my private communications sent respectively to Weinreich, D.M. and Tans, S.J.. None from them so far. In 2004, the PI of [9] promised to consider papers of [8] and [6] for his genetic switch and stochastic projects. For unknown reasons, Ref.’s [1, 6, 8] were not in his 2005 paper (Ref. [9]). Until a few months ago this PI maintained that there were no general construction of potential function in the absence of his discussion on the generic construction published since 2004. The
recent record of this PI of [9] on this matter is unclear.

Consistent with Nature’s position not to publish correction due to its own errors on this matter, this comment was naturally declined by Nature: The issue on severe missing prior references on adaptive landscape in one of Nature papers was already raised to Nature in 2005.

[12] Fisher, R.A., *The Genetical Theory of Natural Selection*. Clarendon, Oxford (1930).