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Fitness Landscape: a scientific tool, its epistemological status, and the quest for synthesis in evolutionary biology.

"Fitness landscape" (henceforward, FL) is a diagram, a graphical method for visualizing genetic information, as well as evolutionary variation and adaptation, inside a biological population. Invented in 1932 by Sewall Wright, the intuition of FL was made possible by the elaboration – throughout the first decades of Nineteenth century – of the mathematical theory of evolution based on mendelian genetics. In short, FL is constructed (1) by mapping on a 2D surface all the individual genotypes (i.e. combinations of alleles) that are virtually possible in a given biological population at a given time, in a way that genotypes which are more similar are found near or contiguous on the surface; (2) by assigning each point an "altitude value" which corresponds to the fitness value of the correspondent genotype; (3) by marking those points on the surface which correspond to genotypes actually realized in living individuals at the considered moment.

The visual look of FL, a surface with adaptive peaks and valleys and the population moving on it, had an extraordinary success among many influential evolutionists such as Theodosius Dobzhansky (1937), George Gaylord Simpson (1944), Niles Eldredge (1989) and Richard Dawkins (1996), but it can be shown that the several interpretations completely changed the nature of FL by unlinking it from the original context – i.e. the genetic constitution and recombination inside a mendelian population. Given this, various distinctive features of FL went lost or radically modified:

population was displayed as a point instead of a *cloud* of points; mean fitness was represented instead of *individual* fitness values of unique genetic combinations; phenotype was represented instead of *genotype*; several species were considered together in opposition to considering *one* population; genetic mutation was seen as the main source for movement instead of genetic *recombination*; surface of FL was treated as continuous and not *discrete* etc. Arguably, all these changes occurred without sufficient epistemological analyses and warnings.

Recently, some advanced studies by mathematicians such as Sergey Gavrilets and colleagues (1997; 1999; 2004) triggered a lively debate in philosophy of biology about FL, bringing forth a reconsideration of its merits, limits, usefulness, legitimacy and exposure to misinterpretation in evolutionary biology.

We point out that, for the great part, these discussions themselves suffer from the said cumulate interpretations, failing in re-establishing the original features of FL completely.

Moreover, we argue that the debate fails in assuming the correct epistemological status of FL, variously discussed as a model, a family of models, a metaphor, a tool for theory testing and so on. In Wright's formulation, indeed, FL was nothing more than a 3D visualization of a fundamental mathematical model, where the model is fully autonomous and the diagram is totally dependent. Actually, Gavrilets himself (2004) labeled FL as a "metaphor"; however, he used the term in a technical sense: metaphors would be similar to mathematical models, but «the requirements for metaphorical pictures are much less strict than for exact mathematical constructions» (note that the mapping function of FL has always retained a high degree of approximation, due to the huge quantity of dimensions involved as well as to the difficulty in assigning fitness values to gene combinations). Yet we argue that outside mathematics, where "metaphor" bears a more liberal sense, to tag FL as a metaphor allows it to drift away from its foundational model, leaving epistemological turns implicit, latent, and ultimately misleading; we analyze some examples of this in evolutionary biology.

Gavrilets' work encompasses more than seventy years of research in two domains: (1) genetics, e.g. with the remarkable increase of the known number of genetic *loci* in respect to Wright's hypothesis; (2) modelling, with computers now capable to manage a huge amount of data and operations, differently from Wright's rough "back of the envelope" calculations.

We sustain that Gavrilets' studies affect characteristics and behaviour of the mathematical model of population genetics, and *only as a consequence* its mapping on FL (for example, a greater neutralism in the model would reverberate in FL as a flatter surface, with the absence of remarkable peaks and valleys; the presence in the model of definite groups of low-fitness genotypes would be visualized as a holey surface in FL, and so on). Gavrilets himself seems to be aware of this distinction and asymmetrical relationship when he states that «…there is a clear distinction between a *fitness landscape* […] and the *metaphor of fitness landscape* by which one means a two- or three-dimensional visualization of certain features of multidimensional fitness landscapes». Yet, some philosophical work seems to be necessary in order to clarify the epistemological status of FL (in particular whether it is a metaphor, and in what sense); to make a taxonomy of the several (mis)interpretations of FL and of the underlying epistemological moves; to evaluate viable future possibilities for such a scientific tool.

We believe that the case for FL highlights issues which are crucial for the now proposed "extended synthesis" (e.g. Pigliucci 2007) in evolutionary biology. They are: (a) correct identification of the *epistemological status* of scientific tools (e.g. is FL a way of visualization? a model? a theory? a metaphor?); (b) consideration of scientific tools in their proper *context of origin* and *domain of applicability*, also (even especially) in occasion of updates and revisions; (c) profiting by limits and overinterpretations concerning particular tools *as opportunities* for clarification and correction of misunderstandings, rather than as flaws and reasons for leaving that tools behind.