

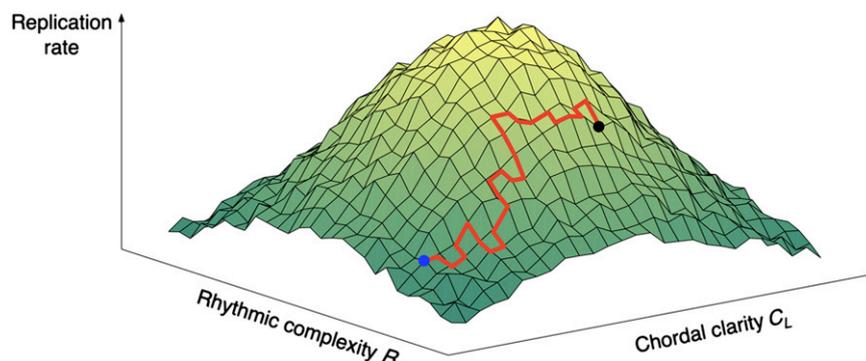
# Adaptive walks on the fitness landscape of music

Christoph Adami<sup>1</sup>

Department of Microbiology and Molecular Genetics and BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI 48824

The evolution of musical abilities in man was an area of intense interest for Charles Darwin: in his book *The Descent of Man, and Selection in Relation to Sex* (1) he discussed the emergence of voice and musical powers in terms of sexual selection and made the case that “the vocal organs were primarily used and perfected in relation to the propagation of the species” (p. 315). Although music has been performed by people at least as far back as the Paleolithic (2), musical styles have changed dramatically throughout the ages and differ significantly across geographic regions. We could therefore ask whether musical preferences change according to laws that are similar to those of biological evolution, namely via inheritance, selection, and variations of tunes that are induced by chance. In PNAS, MacCallum et al. (3) present an experimental approach to study how music evolves, by encoding sounds into programs that can evolve via random mutation and recombination. Using computer programs to study evolution is of course not new (4), but in this case selection was at the hands of people, who listened to the musical phenotype of these programs over the Internet and scored them according to their personal preference. Within a population of “looping polyphonic sound sequences”—or “loops,” for short—those sequences that generated higher ratings by users were given more offspring, and their genetic materials recombined. In this manner, the prevailing music in the population changed over many generations. However, did the music get any better? To assess this, the authors sample loops from the entire evolutionary trajectory and ask a different set of consumers (not those who selected the loops in the original experiment) to rate the quality of the music. This average rating—the musical appeal  $M$ —increased significantly over the first 600 generations, but then seemed to flatten out. Over the remaining 2,100 generations of the experiment, the appeal of the loops remained essentially flat. What happened?

In evolutionary biology, we are used to patterns of adaptation that are consistent with rapid change followed by stasis (5). A handful of different causes are usually advanced to explain the slowdown. When a population adapts to a new niche, it can be thought of as climbing a fitness landscape, using the metaphor of the fitness landscape introduced by the mathematical ge-



**Fig. 1.** An adaptive walk on a rugged landscape defined by the two traits  $C_L$  and  $R$ , beginning at the blue circle and ending at the black circle. The height of the surface is given by the replication rate of a loop with a given set of traits (the landscape depicted is an idealization of the landscape in ref. 3).

neticist Sewall Wright. If there is only a single peak (or if higher peaks are unreachable from that location), then adaptation must stop when the peak is reached: every step upward leads to diminishing returns (6, 7). However, there are other reasons why adaptation may slow down or stop. One of them is particularly interesting from the point of view of genetics and may be at the root of the stasis observed in this experiment. Although recombination of genetic material is a great way to create novelty, it is an equally good way to destroy sets of genes that are finely tuned to work with each other, by ripping them apart in the recombination process. The loops do not have well-defined sets of genes, but individual traits can be examined. For example, the authors use two traits that are commonly used to classify music genres—the clarity of the chords  $C_L$  and the complexity of the rhythmic signature  $R$ —to assess the fitness of each loop. Both traits can be measured objectively (and without error) for each loop, and even though they explain only a small percentage of the overall musical appeal, they correlate with it. Moreover, both  $C_L$  and  $R$  increase within the first 600 generations, when the appeal is also increasing. Importantly, the authors show that, in control experiments in which loops evolved in the absence of selection, both measures remain at low levels. These two traits now can be used to parameterize the fitness landscape of music in this experiment. Interestingly, the traits are not independent: rather, the topology of the landscape implies that they interact synergistically; that is, loops that have a high value in one trait are especially fit if they also have a high value of the other. In

genetics, such interacting traits are called “epistatic,” and they are at the very heart of everything that makes evolution interesting. In particular, it has been hypothesized that synergistic epistasis between genes is necessary for the evolution of sexual recombination to begin with (8). Indeed, according to that theory, the synergy between deleterious mutations ensures that they do not accumulate in the genome, and therefore keep the mutational load of a population low. However, a low mutational load implies a reduced genetic variance, which leads to reduced adaptive potential via Fisher’s Fundamental Theorem of evolution (9). Thus, sexual recombination may be detrimental to the future adaptive potential if the synergistic epistasis is too strong.

So, are the loops evolving toward an “epistatic conundrum” between traits, or did they simply run out of beneficial mutations at the top of a peak? To test this, the authors use a description of evolutionary processes that is more general than Fisher’s Fundamental Theorem, namely Price’s equation (10), and that is able to disentangle the effects of variation, and the strength of inheritance, on evolution. An analysis of Price’s equation shows that the slowdown of the furious rate of adaptation during the early 600 generations is due mainly to the increased production of inferior types via recombination, an effect that is expected if traits interact

Author contributions: C.A. wrote the paper.

The author declares no conflict of interest.

See companion article 10.1073/pnas.1203182109.

<sup>1</sup>E-mail: adami@msu.edu.

synergistically. Over the whole evolutionary history, however, the authors observe a trend of reduced variance instead, which is a consequence of synergistic epistasis under recombination. Indeed, a visualization of the adaptive walk on the landscape spanned by the traits (Fig. 1) shows that the evolutionary process fails to locate the highest peak in the landscape. The same dynamics are observed in control experiments performed with undergraduate students as the selection force rather than over the Internet, suggesting that the observation is germane.

Although the fitness landscape metaphor necessarily abstracts the full evolutionary dynamics by focusing on a few traits only (usually two so that the landscape can be visualized), it is a valuable tool not only to gain a more intuitive understanding of the past unfolding of evolution but also to make quantitative predictions for the future of evolution. Using tools similar to those used here to reconstruct the fitness landscape from actual fitness data, researchers recently reconstructed the fitness

landscape for the evolution of drug resistance in the HIV and showed that epistasis between mutations on that landscape is

## MacCallum et al. present an experimental approach to study how music evolves.

strong and affects recombination between the HIV genes (11). Recombination is a valuable tool that evolution uses when the landscape changes often, as is true for certain viruses, notably HIV. For the musical loops, the environment is fairly constant, so perhaps an asexual model of replication would be better suited and might locate the peak of this landscape.

Do the experiments conducted by MacCallum et al. tell us anything about how music actually evolved in human societies? Certainly, music does not

emerge from a random process only: composers actively create music, albeit influenced by existing music within their culture. Perhaps this influence can be thought of, remotely, as variation and recombination of existing elements. The success of a tune, no doubt, depends on a process akin to selection by an audience, and music spreads via a process similar to replication when performers learn (and thus copy) a new piece. However, maybe the most important role of music in the history of our species is precisely the one that interested Darwin the most: with music we are able to encode, and therefore transmit, complex and deep emotions. For empathic animals such as ourselves, being able to compose or perform music may indeed help in propagating those genes.

**ACKNOWLEDGMENTS.** I thank B. Østman for Fig. 1. This work was supported in part by the National Science Foundation's BEACON Center for the Study of Evolution in Action, under Cooperative Agreement DBI-0939454.

1. Darwin C (1871) *The Descent of Man, and Selection in Relation to Sex* (D. Appleton, New York), 1st Ed.
2. Montagu J (2004) How old is music? *Galpin Soc J* 57: 171–182.
3. MacCallum RM, Mauch M, Burt A, Leroi AM (2012) Evolution of music by public choice. *Proc Natl Acad Sci USA*, 10.1073/pnas.1203182109.
4. Adami C (2006) Digital genetics: Unravelling the genetic basis of evolution. *Nat Rev Genet* 7:109–118.
5. Fitch WM, Ayala F, eds (2005) *Tempo and Mode in Evolution: Genetics and Paleontology 50 Years After Simpson* (National Academies, Washington, DC).
6. Khan AI, Dinh DM, Schneider D, Lenski RE, Cooper TF (2011) Negative epistasis between beneficial mutations in an evolving bacterial population. *Science* 332:1193–1196.
7. Chou HH, Chiu HC, Delaney NF, Segrè D, Marx CJ (2011) Diminishing returns epistasis among beneficial mutations decelerates adaptation. *Science* 332:1190–1192.
8. Kondrashov AS (1994) The asexual ploidy cycle and the origin of sex. *Nature* 370:213–216.
9. Fisher RA (1930) *The Genetical Theory of Natural Selection* (Clarendon, Oxford).
10. Price GR (1972) Fisher's 'fundamental theorem' made clear. *Ann Hum Genet* 36:129–140.
11. Hinkley T, et al. (2011) A systems analysis of mutational effects in HIV-1 protease and reverse transcriptase. *Nat Genet* 43:487–489.