

Genome research elucidating environmental adaptation: Dark-fly project as a case study

Naoyuki Fuse



Organisms have the capacity to adapt to diverse environments, and environmental adaptation is a substantial driving force of evolution. Recent progress of genome science has addressed the genetic mechanisms underlying environmental adaptation. Whole genome sequencing has identified adaptive genes selected under particular environments. Genome editing technology enables us to directly test the role(s) of a gene in environmental adaptation. Genome science has also shed light on a unique organism, Dark-fly, which has been reared long-term in the dark. We determined the whole genome sequence of Dark-fly and reenacted environmental selections of the Dark-fly genome to identify the genes related to dark-adaptation. Here I will give an overview of current progress in genome science and summarize our study using Dark-fly, as a case study for environmental adaptation.

Address

Graduate School of Pharmaceutical Sciences, Tohoku University, Japan

Corresponding author: Fuse, Naoyuki (nfuse@m.tohoku.ac.jp)

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Introduction

The polar bear lives in the Arctic, and its body is covered with warm white hair that camouflages it in snow- or ice-covered landscapes and that maintains its body temperature in the cold climate. The polar bear also possesses unique features of metabolism, predominantly consuming fatty acids as its energy source, which it obtains by feeding on marine mammals with high fat content. All of those traits are thought to be adaptive for living in the Arctic environment. Like the polar bear, many other organisms that have expanded to diverse areas around the world have acquired specialized morphology, metabolism and behavior for adapting to local environments during their evolutionary history. Given that the genome is the fundamental blueprint of life, the question arises:

what is the genomic basis of environmental adaptation? This is one of the fundamental questions of evolutionary biology.

Whole genome sequencing

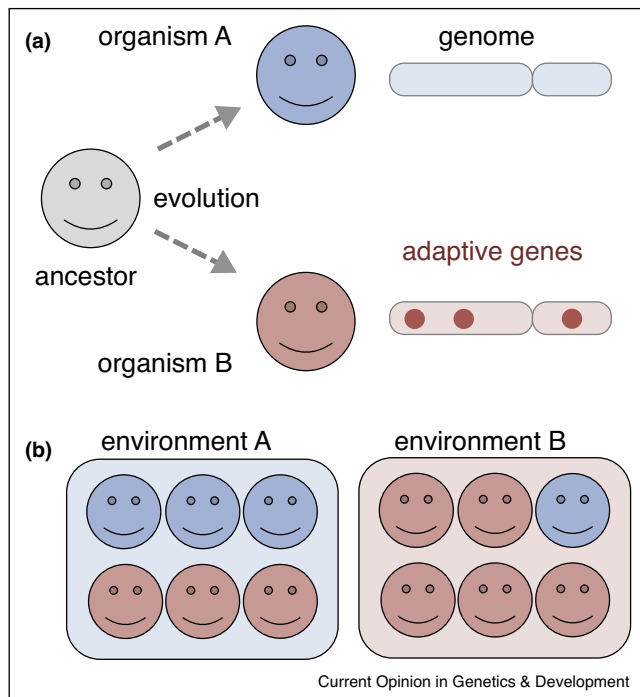
Next generation sequencing (NGS) technology has provided an opportunity to approach the whole genome sequences of organisms [1], and has been applied for studying environmental adaptation and its evolution [2*,3,4*]. For example, the whole genome sequence of the polar bear (*Ursus maritimus*) was determined, and statistical comparisons of the genome sequence between the polar bear and the brown bear indicated that genes associated with fatty acid metabolism contributed to the evolution of the polar bear [5]. As another example, Tibetan people, who reside on high-altitude plateaus, possess specific physiological responses against low oxygen, and genome sequence analyses revealed adaptive evolution of hypoxia-responsive genes during Tibetan history [6,7]. As one more example, Darwin's finch is a symbolic organism for evolutionary biology. Genome sequencing of finches identified genes controlling the diversity of beak shapes evolved in specific habitat environments [8**]. Thus, genome science has identified various genes associated with organisms' adaptation.

Identification of adaptive genes

Identification of adaptive genes is a primary goal for studying environmental adaptation. Let me consider a hypothetical model: organisms A and B have evolved from a common ancestor, and organism B is adapted to environment B (Figure 1). The adaptation would be evaluated by fitness of organisms in an environment. Organisms A and B are equally propagated in environment A, but organism B dominates over organism A in environment B. To identify adaptive genes of organism B, we would compare the genome sequences between organism A and B. However, the story is not so simple, because there would be many differences of the genomes between organism A and B that are irrelevant to environmental adaptation. To overcome this problem, two approaches are mainly taken.

The first approach is 'case and control study' comparing the genome sequences of many individuals (Figure 2a). In this approach, many individuals are divided into two groups: case (exhibiting adaptive phenotype B) and control (lacking an adaptive phenotype). Statistical comparisons of genome sequences of the two groups ignore the rare variations that occur randomly in individuals, and

Figure 1

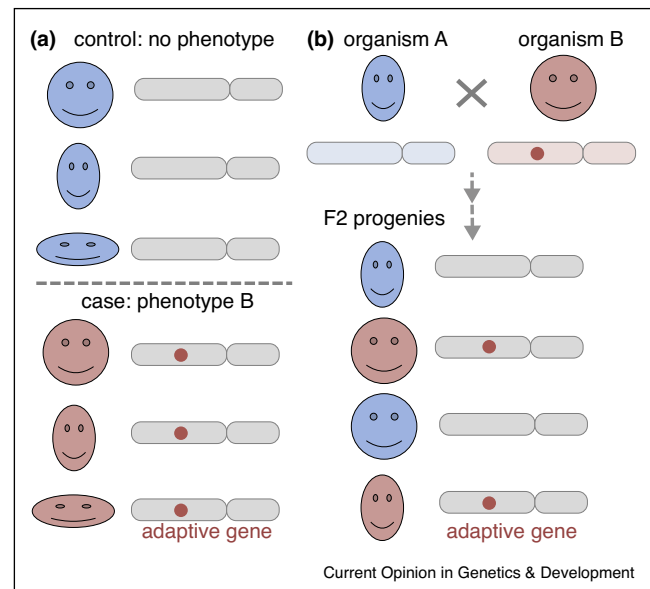


A hypothetical model for the study of environmental adaptation. **(a)** Organism A (colored blue) and B (colored red) are evolved from a common ancestor. Organism B carries adaptive genes (red dots) in the genome. **(b)** Organism B dominates over organism A in environment B, but not in environment A; that is, organism B is adapted to environment B.

detect the variations that are commonly different between case and control and thus are related to phenotype B. Many statistical methods for comparing multiple genomes have been developed and are now available [2[•]]. The studies of the polar bear, Tibetans and Darwin's finches described above took this kind of approach. The genome wide association study (GWAS) is also an example of the case and control study, and has been used by many researchers to identify causal variants associated with human diseases, such as Alzheimer's disease and inflammatory bowel disease [9,10].

Another approach for identifying adaptive genes is the 'segregation study' comparing many progenies derived from the organism of interest (Figure 2b). In this approach, many progenies are collected from breeding of two parents, one of which exhibits adaptive traits. Each progeny is categorized according to a visible adaptive trait, and genome sequences segregated from the parents are compared between individual progenies. Quantitative traits loci (QTL) analysis is a type of segregation study that has long been performed by many researchers, even before applications of NGS technology. As a recent example of QTL analysis, the cavefish genome was analyzed to search for adaptive genes. Cavefish (*Astyanax*

Figure 2



Genome analyses of environmental adaptation.

Schematic drawings of **(a)** case and control study and **(b)** segregation study to identify the genes related to environmental adaptation. An adaptive phenotype is represented by red color, and other phenotypes unrelated to adaptation are represented by the various shapes of the cartoon faces. See text for details.

mexicanus) has evolved in Mexican caves, and is famous for its odd morphology, such as eye loss and albino skin [11]. These traits are thought to be adaptive in darkness because they let the cavefish save energy by avoiding production of useless tissues. As the advantage for study, cavefish is able to breed with the surface-dwelling sister species with normal eyes and pigmented skin. QTL analysis of breeding between cavefish and surface fish identified causal variants for eye loss, one of which is mapped to a gene encoding a developmental signaling factor (Shisa2, an inhibitor of the Wnt-signaling pathway) [12]. Since genome sequencing of multiple individuals is still laborious and expensive, more cost-effective approaches using pooled genomes have been taken recently by some researchers, and statistical methods have also been developed for the analysis [13].

Demonstration of adaptive genes

Analyses of whole genomes have identified adaptive genes in diverse organisms. However, when such genes are thus identified, it is still unclear whether the gene variation found in the organism is responsible for environmental adaptation. Genome editing technology, such as the CRISPR/Cas9 system, enables us to address this issue [14]. Again, let me consider a hypothetical model for demonstrating the role of an adaptive gene (Figure 3). Using genome editing technology, a gene variation of organism B is introduced into organism A, and the knock-

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