

O N E

IN ORDER TO FORM A MORE PERFECT UNION

Without [the light of evolution, biology] becomes a pile of sundry facts some of them interesting or curious but making no meaningful picture as a whole.

—Theodosius Dobzhansky, “Nothing in biology makes sense except in the light of evolution”

Do frogs grow legs because thyroid hormone induces growth of legs or because legs evolved as an adaptation to life on land? Clearly, both explanations are true. The developmental answer addresses *how* legs grow. The evolutionary answer addresses *why* frogs evolved to grow legs. These two explanations do not compete to explain the existence of frogs’ legs. Both explanations enrich our understanding of biology.

We can generalize from frogs’ legs and observe that, at a mechanistic level, most biological diversity results from changes of gene function. In contrast, at an evolutionary level, selection on heritable variation causes biological diversity. These different levels of analysis provide complementary explanations for biological diversity. Failure to distinguish between levels of

analysis can lead to unproductive debates: “Frogs grow legs because of thyroid hormone”; “No, frogs’ legs evolved as an adaptation to life on land.” Usually, it is best to avoid comingling explanations at different levels of analysis.

In recent years, however, data has appeared that does not make sense except when viewed simultaneously from multiple levels of analysis. Here is one example.

In geographic areas with short or harsh summers, mouse-ear cress (*Arabidopsis thaliana*), a small, weedy annual plant, normally germinates in the fall, overwinters, and then flowers in the late spring. These plants require a period of cold to induce flowering, a process called vernalization. However, plants from some populations germinate in the spring and flower without requiring vernalization. These are called “rapid cyclers.” Some rapid cyclers live in areas with long summers. Since the plants do not require vernalization, they can complete more than one life cycle in each growing season. Other rapid cyclers live in areas where harsh winters prevent autumnal germination and survival of seedlings.

In some *Arabidopsis thaliana* populations, mutations that incapacitate a single gene called *Frigida* cause plants to lose their ability to vernalize. These “null” mutations prevent production of a functional *Frigida* protein. These mutations delete all or part of the gene or introduce stop codons that truncate the protein prematurely. Different null mutations of the *Frigida* gene have arisen and spread at least twenty times and contribute to much of the variation in flowering time in natural populations of *Arabidopsis thaliana*.

Production of a functional *Frigida* protein causes plants to require vernalization. It therefore makes sense, from a developmental perspective, that mutations in the *Frigida* gene cause

flowering time variation in natural populations. The null mutations in the *Frigida* gene can be seen as elegant paths to rapidly evolve a faster flowering time.

From an evolutionary perspective, however, the fact that flowering time has evolved by null alleles is compelling evidence that something out of the ordinary has occurred. Plant species closely related to *Arabidopsis thaliana* possess the *Frigida* gene, and even some distantly related plant species contain genes similar to *Frigida*. It is therefore unlikely that null mutations in the *Frigida* gene have contributed much to differences between closely related species; we would not find *Frigida* genes in these species if null mutations conferred a long-term evolutionary advantage. Null mutations appear to have spread in small populations that adapted rapidly to local conditions. The null mutations reduce flowering time, but, since these mutations have not spread widely to other *Arabidopsis thaliana* populations, they are likely to confer disadvantages on plants growing in other environments. This may be an example of short-term evolution leading a gene down an evolutionary dead end.

The natural history of *Arabidopsis thaliana* supports this view. *Arabidopsis thaliana* is native to Europe and to much of Asia, where it grows in recently disturbed ground. It has spread throughout the world, following in the footsteps of human agriculture. The plant reproduces primarily through self-fertilization, so even a single seed can found a new population of genetically similar individuals. Null mutations in the *Frigida* gene, which appear to provide a large advantage in some environments, may spread rapidly in these subpopulations in response to strong selection for rapid cycling.

While an understanding of the developmental role of the *Frigida* protein clarifies why mutations in the *Frigida* gene

generate changes in flowering time, population biology provides a context for understanding why these particular mutations have been selected.

These data contain a second surprising fact. In a mutagenesis experiment to identify genes involved in controlling vernalization, only three out of about 50 mutations occurred in the *Frigida* gene. The remaining mutations occurred in fifteen other genes. In all, mutations in at least 80 genes can affect flowering time. That is, mutations occurring randomly in the genome that affected vernalization would tend not to hit the *Frigida* gene. Why, then, does the *Frigida* gene harbor most of the evolved variation? Is there something special about the *Frigida* gene that makes it a favored target of natural selection?

The questions that arise by considering this example highlight the issues I will address in this book. Development teaches us which genes are available to generate particular phenotypic changes. Evolution teaches us what kinds of mutations may be favored over different time scales.

SUMMARY

Each level of analysis warrants independent investigation by biologists. But new data do not make sense unless considered simultaneously from multiple levels of analysis. Interpretation of these new data requires a synthesis of evolutionary biology—particularly the biology of populations and of closely related species—and development biology.