

2 THE ECOLOGICAL CAUSES OF DIVERSITY

shihō yori / hana fuki irete / nio no nami

*From all four quarters / cherry petals blowing in. / To Biwa's
waters!*

—Basho, 1690

We seldom hear about chimprillas or gorpanzees. If you are lucky enough to find yourself in a forest in Central Africa—and happily there are such forests quite close to lakes I have visited—you might, with a little luck or effort, see chimpanzees. With some more effort you might see gorillas. Either way, you will not come across any creatures that are halfway in between, whether for ear shape, brain size, skull shape, testis size, or any of the long list of characteristics that separate these relatives of ours. And you certainly won't happen on a population of apes in which each individual possesses a haphazardly assembled collection of chimpanzee and gorilla features and traits. Rather, you will encounter members of distinct species, and where they occur side by side it will not be hard to distinguish one from the other, even if the odd chimp is big enough to be mistaken initially for a gorilla.

As most of us know intuitively, this is what we usually find in nature, especially in the sorts of animals and plants that can be seen with the naked eye. At any particular location, the diversity of life is separated into pretty much discrete packets that are known as species. Each species comprises populations of individuals that share many traits with each other, but differ in a variety of ways from members of other species. There are exceptions of course (there almost always are in living systems), but for most organisms in most places, the great majority of individuals are readily assigned to one species or another. This is why field guides are useful, and why they are profitable enough that they keep being published. There has been a modest amount of argument among biologists about the reality of species, with the opposing view being that they are arbitrary constructs of the human mind, but most of us find the concept useful and rely on it in our work.

Still, perhaps this is not how things had to be. Why *is* life organized into these more or less nonoverlapping units? How exactly do we decide when we have two species rather than one? And are there better ways to describe biological diversity than just counting species?

Let's start with a definition. Unfortunately, coming up with a species definition that a good number of biologists can agree on turns out to be no small thing, and several are in use. Even philosophers have gotten in on the act and generated a surprising volume of verbiage concerning what a species is from a philosophical perspective. But a great many biologists, and especially those whose research focuses on how species are formed, mainly rely on a single definition. It states that a species is a set of populations (or members of a single large population)

that actually or potentially interbreed and exchange genes only with each other; this is known as the biological species concept. Oddly enough, it is not something that Darwin handed down to us, at least not explicitly. Although his most famous work was titled *On the Origin of Species by Means of Natural Selection*, Darwin for the most part treated species as extremes of the varying forms he saw throughout nature. He did not give much special attention to this unit in the *Origin*—though he did comment on it here and there, and considerably more in some of his unpublished writings.

The biological species concept was due mainly to Ernst Mayr, a remarkable scientist with whom I briefly overlapped, to my good fortune, while starting my graduate studies at Harvard in the late 1980s (there is a photo of him in chapter 4). Professor Mayr was then in his own eighties and still publishing regularly—something he carried on doing almost continuously until he died at age 100. I well recall his aggressive questions and comments at seminars, and he is reported to have remarked, “I’m not dogmatic, I’m simply right!” We students held him in awe.

The main problem with Mayr’s “BSC,” as it is often known, arises when dealing with sets of populations that have wide distributions. Things really go downhill when there are breaks in distributions. In the Malili Lakes of Sulawesi, for example, there is a ricefish (*Oryzias marmoratus*) that is found in more than one lake and varies somewhat between lakes. Since the lakes are separated by rivers that are likely more difficult for the fish to traverse, movement between lakes and opportunities for interbreeding may be rare. Would fish from different lakes interbreed if placed together, and would their offspring

survive and themselves be able to breed? Maybe, but with so many millions of species of animals and plants we can rarely do the necessary tests to address these questions—certainly not for every break in the distribution of every species—and it is often necessary to make a judgment call (highlighting these challenges is the fact that the evolution of *O. marmoratus* has become an increasingly complex matter just during the writing of this book). With more molecular data now available, we frequently have a better idea just how genetically distinct different populations are, but judgment is still involved in deciding when we have two or more species rather than just one.

Distinct species that live alongside one another yet occasionally interbreed can also complicate life for the biologist trying to apply the BSC. It can be tough to decide just how much interbreeding is too much and at which point one species should be treated as two. In addition, the BSC only works when reproduction is sexual and thus interbreeding is a possibility; no sex means no interbreeding and an irrelevant BSC. This was long perceived to be a major problem for many microorganisms, especially bacteria. Lately, however, microbiologists are finding that exchange of genes with similar individuals, much like what happens in sexual reproduction, is more common than once thought for a wide range of microscopic creatures. Hence the BSC, its difficulties notwithstanding, may apply even more broadly than once supposed. In fact, it is now clear that even viruses can exchange genetic material when different strains infect a single host at the same time. Moreover, they exchange genetic material much more often with genetically similar viruses, contributing to clusters of individuals much alike in genes and form, and surprisingly comparable to the

clusters that comprise an animal species. All in all, then, the BSC remains the species definition of choice for most, but those who study speciation appreciate its limitations and are increasingly bypassing them by treating speciation as a process that leads to a continuum of levels of reproductive isolation, rather than to necessarily discrete outcomes. Taxonomists, however, have to assign species names and are obliged to use their best judgment in this sometimes arduous task.

IS BIODIVERSITY THE NUMBER OF SPECIES?

Well-defined species concepts are important in the study of biodiversity in part because they enable us to delineate species in a reasonably consistent way and count the number present in a lake, or whatever sort of unit one is interested in. We can then compile counts for different lakes as one way to compare biodiversity across localities, or we can use slightly more complicated indexes that are based on relative abundance as well as species counts. For instance, a lake with five clam species in it, all equally abundant at 20 percent of the total numbers each, might be considered more diverse than a different five-species lake where 98 percent of the clams are of one type, with few of each of the other four. There are also some quite different approaches that can be used to quantify the biodiversity of a lake. One important one, which is gaining in popularity for conservation work in particular, is based on calculations of how much unique evolutionary history is represented by the organisms in the lake.

Basically, the patterns on an evolutionary tree for a group of creatures are used as the basis for calculating how much

unique history is present in any one species. This can be noteworthy for its own sake and can also be a guide to how unusual the organism might be for characteristics of interest but not yet examined—say, its immune system if biomedical issues are the focus. An evolutionary tree, known to biologists as a phylogeny, shows the relationships among a group of species as a branching pattern extending from an ancient ancestor to modern descendants, with intermediate ancestors at the branching points. The longer a branch (in time, DNA sequence differences, or more often both) leading to a species and its near relatives, and the fewer near relatives it has, the more unique history it possesses (figure 2.1).

Evolutionary trees are roughly analogous to family trees (genealogies), so here a family tree can help illustrate the idea. Suppose there were two sisters, each with children. Sister Alice had five children while sister Viola had one. Each of Alice's children also had five offspring, who in turn had five each. By the third generation of her descendants, Alice has accumulated 125 great-grandchildren (this is actually a bit like my Grandmother Thompson's family from rural Canada, but I digress). Meanwhile, Viola's only child kept up the family tradition and also had an only child, who did the same. After three generations, Viola has just one descendant, Victor. Victor is the sole receptacle for three generations of his family's genetic history. He is pretty unique, even if his family reunion picnics are a bit quiet and lonely. In the meantime, over on Alice's branch of the family tree, her great-grandchild Andrew goes to huge picnics. He has plenty of company from folks who are a lot like him, and you could hardly say there is much unique about Andrew—with four siblings, twenty first cousins, and 100 more distant

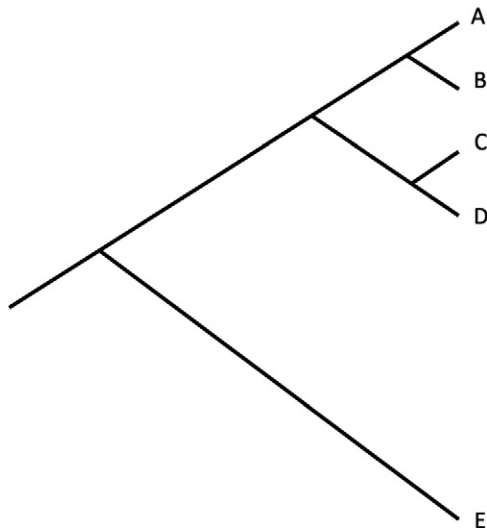


Figure 2.1

Evolutionary tree, or phylogeny, on which modern species “E,” alone at the end of a long branch, has more unique evolutionary history, shared with no other species, than does species “A,” or any of the other species shown. The past is on the left, and the present is on the right.

cousins (not to mention all the uncles and aunts, great-aunts, and so on). If you were charged with choosing the person who carried in their genes the most unique history, you would have to go with Victor over Andrew. Lose Victor and a long tree branch is gone; lose Andrew and a small twig is lost from a bush.

For an evolutionary example, we can compare the ricefish lineage in Lake Matano, Sulawesi, to the lineage of sailfin silversides found there. Ricefish, mentioned briefly earlier, are a group of small fish—the size you would come across in a pet shop—that are found in East and Southeast Asia. There are about thirty-six species in total, with more on Sulawesi than

anywhere else. They have become important as a model system for basic research; the medaka, *Oryzias latipes*, a Japanese ricefish, is used for a wide variety of biomedical investigations. There is just one ricefish in Lake Matano, which we will assume for our illustration has been evolving there on its own for about as long as Matano has been a lake—something on the order of one to two million years. We will assume the sailfin silversides started evolving in Lake Matano at about the same time, but were more prolific, with about ten silverside species now living in the lake. So if you were to consider only the fish in the lake and ask which fish has a more unique evolutionary history, the ricefish or Matano silverside, *Telmatherina prognatha*, you would probably have to go with the ricefish. This sort of approach can be used as the basis for prioritizing areas to protect or designing sets of protected areas that conserve as much evolutionary history as possible. Some folks working in conservation and management are now grinding through these sorts of calculations. Usually they take into account what the risk of extinction is for each species as well. For now, such sophisticated approaches may not be practical for the ancient lakes covered in this volume. But as management of the lakes gets more intense and evolutionary data accumulate—which is happening quickly—this could change.

The third approach you might take to quantifying biodiversity, the last one we will consider, would be to use form and function. This approach requires more data, but sometimes it is possible. Rather than just counting species, or calculating how distinct one or more species are in terms of their location on a family tree, one can calculate how distinct a species is (or set of species are) for one or more traits. Thus, a fish with an

unusual diet, for example, or that is exceptionally big or tiny in size, might be considered more distinct from a functional perspective than one possessing a common diet or that is of an average size for its lineage. Thinking back to Alice's large family and Viola's modest one, suppose Alice's great grandson Andrew was 7 feet (213 cm) tall and everyone else on either side of the family tree was around 5'10" (178 cm) plus or minus a few inches—including Viola's one great-grandchild, Victor. If we were focused on distinctiveness in terms of height rather than family history, we might now reverse our original ranking and decide Andrew was more noteworthy than Victor.

This approach can be applied to our fish example. Our Matano ricefish seems so far to be a fairly typical ricefish—with nothing especially distinctive about it. *Telmatherina prognatha*, however, is a bit unusual for a lake fish in that as an ecological specialist that preys on other fish, it has evolved a torpedo-shaped body and wide jaw gape. This is distinctive because most fish species in freshwater lakes, especially from its family, eat invertebrates. So despite the fact that it has several close relatives and does not possess as much unique evolutionary history as the ricefish, it is more distinctive in terms of its feeding ecology and the features it has evolved that help it make a living feeding extensively on other fish. Consequently, if our focus was ecological distinctiveness, we might rank *T. prognatha* above the Matano ricefish. And we might rank lakes that possess a higher number or proportion of ecologically unusual species more highly in terms of their biodiversity than those filled with more conventional creatures—even if those conventional creatures embody a lot of independent evolutionary history (features at the ecosystem level are sometimes also emphasized).

In practice, though, differences in form and function are often correlated with uniqueness in terms of tree position and branch length, so we don't have to choose between them. Moreover, tree measures are sometimes used as a proxy for form/function, when only limited information is available about the ecology and natural history of the creatures in question.

SPECIATION

Regardless of how you choose to measure biodiversity, to get very much of it requires speciation. Since we are used to thinking about biodiversity in terms of numbers of species, this might seem self-evident—but there is a more subtle and important way in which the formation of new species enhances biodiversity. A new species is an independently evolving unit. A pair of new species cease to exchange genes with each other (or nearly so); they are free to diverge, to evolve in new and different directions, with neither holding the other back. As speciation events and species accumulate, the opportunities for independent evolution and diversification multiply.

The barriers to gene exchange that separate species can take many different forms. Who mates with who is of course critical, and mating between incipient (i.e., not fully isolated, often young) species can slow down or stop for a variety of reasons. Sometimes these new species mate in different habitats or at different times of day or year (or even in different years in the case of some salmon and cicadas!), or reject potential partners of the other species when the opportunity to interbreed does arise. In other cases, they are physically unable to mate, for example, if their genitalia have become too different. Even

if they mate, the eggs and sperm may never find each other, or fail to fuse and begin development. Should things get that far, hybrid offspring may still not develop properly or may be less likely to survive. And even if they survive, they may be sterile or fail to find mates. Things can break down in a lot of different ways.

How and why these barriers evolve are the central questions of research on speciation. In addition to providing us with an influential species definition, Mayr set the direction and tone for fifty or sixty years of research in this area when he argued that in order for incipient species to diverge enough to stop exchanging genes, they each need some time alone. Each would need to spend a period of time evolving independently as a result of a geographic barrier of some sort—say, a piece of land separating two lakes when the water levels fall (for a fish) or a river breaking up a piece of land when the water levels rise (for a squirrel). The key notion is that a temporary physical barrier to gene exchange is needed in order for a permanent biological barrier to have a chance to evolve. Thus, if an ancestral, river-dwelling ricefish colonized two different lakes that had no connection to each other, after some thousands or millions of years the ricefish in each lake may come to differ. They may diverge enough that if the lakes happen to become connected, the two populations do not exchange genes and can persist as distinct forms. They might mate at different depths, at different seasons, or have different courtship behaviors, or maybe they have developmental differences that cause their fertilized eggs to die before hatching. There may be a few different biological isolating barriers preventing the exchange of genes between them.

With Mayr and others arguing aggressively that speciation was nearly impossible without a period of physical isolation to jump-start things, ambitious young biologists were keen to challenge what some saw as a dogma. The problem, though, was proving a negative; it can be difficult to obtain definitive evidence showing that currently overlapping species were never separated in a past that we did not see and cannot visit. Even so, persuasive case studies were eventually documented to the satisfaction of most evolutionists, and some of the most compelling and widely discussed examples came from lakes. Researchers basically showed that the various fish species found only in a single lake were all more closely related to each other than they were to any fish outside the lake—and the shape and history of the lake made a past period of geographic separation seem unlikely. In the most famous cases, these are relatively young crater lakes, which possess simple bowl shapes because they are the remnants of extinct but geologically young volcanoes. One recent example of speciation in a bowl-shaped lake comes from a more ancient water body, Sulawesi's Lake Poso.

This work was conducted by a group of scientists based mainly at the University of the Ryukyus in Okinawa, toward the southern tip of Japan and not so far from Sulawesi, at least as distances go in the tropical Pacific. Nobu Sutra was the lead author on the paper, which also included K. W. Masengi of Sulawesi's Sam Ratulangi University. The team collected tissue samples and made measurements of body shapes from the three ricefish species found in Lake Poso as well as from the nearest populations that they could locate of other ricefish. Using a method that provides extensive samples of DNA sequence spread across every chromosome, they were able to show that

the three ricefish species in the lake are indeed more closely related to each other than to any ricefish from outside the lake, at least for most of their DNA.

An ecological aspect to these speciation events was suggested by differences in shape and size between the ricefish. In addition, they found intriguing evidence for some curious complications to the main findings: their analyses suggested at least one and potentially three episodes of gene exchange occurred between nascent ricefish species, one possibly from a population outside the lake, and the best-documented episode between species within the lake. Such an exchange preceded at least one speciation event and possibly both. Thus, the geographic context of speciation was a little messy—a finding arising time and again as genetic data get better and better, and as our perspective on what is possible becomes a little more flexible. The time frame their analyses suggest is consistent with Lake Poso's estimated age of one to two million years, and Poso's shape would make geographic separation within the lake implausible. It would be helpful to sample more extensively within and around the lake in order to assess these conclusions more definitively, but right now it looks like these ricefish evolved into new species within the lake.

It is increasingly well accepted that speciation sometimes happens with extensive or complete geographic overlap, as in the Poso ricefish example, but the prevailing view among evolutionary biologists is that most speciation indeed involves periods of geographic isolation between incipient species, much as Mayr argued. Speciation in the presence of ongoing gene exchange may occur more frequently when there is only a small level of geographic overlap—say, between fish in a river and a lake.

A shift in speciation research took place in the 1990s, an exciting one. The focus moved from working out the geography of how species form, which was really about the extent to which gene exchange *prevented* speciation, to identifying the processes that *accelerated* species formation by enhancing the evolution of biological barriers to gene exchange. Thus, the shift was from studying what prevented speciation to working on what propelled it. Sounds more positive, doesn't it? Certainly it seemed so at the time, at least to me. Some of the most influential ideas in this area came from the laboratory of Dolph Schluter at the University of British Columbia, where I received valuable and inspiring training at the start of my career. One of Dolph's great insights was to recognize the critical role that ecology, through ecologically based natural selection, could play in causing the evolution of reproductive isolation. Equally important was working out the signature patterns that would help us recognize when natural selection had been the driving force rather than other, more haphazard processes.

I have mentioned natural selection a few times already, and it will be a central topic in this book, so a definition seems in order. Defining it properly also helps reveal the marvelous simplicity and inevitability of the process given a few quite ordinary conditions. Just as a piece of granite is bound to sink if you drop it in a lake, evolution by natural selection will occur if there is variation in a trait, that variation is heritable (the offspring resemble their parents), and one form of a trait consistently has higher reproductive success than others—that is, individuals with one form of a trait contribute more offspring to the next generation. To illustrate, suppose some fish have larger mouths and some have smaller ones; parents with

larger mouths have offspring with larger mouths (i.e., there is a genetic component); the fish are eating large prey, and fish with larger mouths get more to eat, survive better, and leave more offspring. Each generation, the average mouth size in the population will increase. This is evolution by natural selection. It is that simple. If the conditions are met, selection and evolution happen, just as a rock must sink if the conditions are met of being in a less dense liquid and the presence of gravity. Given certain starting conditions, some outcomes almost *inevitably* come to pass.

In addition to his evolutionary insights, Dolph has a talent for presenting an idea or finding in a memorable, compelling way—an ability often present in the most successful scientists, especially today when the scientific literature is exploding and the competition for attention is fierce, not only attention from readers, but from reviewers of grant proposals. Scientific tools are expensive, and grant reviewers hold the keys to the vault.

As he was developing his ideas about natural selection's role in speciation, Dolph made informal presentations during our laboratory meetings, mainly to the graduate students and postdoctoral fellows. These are often the most exciting settings for science, and it was at one of them that I first heard the term *ecological speciation*. Dolph used it to describe the evolution of barriers to gene exchange that arise, in a diversifying lineage, as a result of contrasting adaptations to different ecological conditions. At the time, numerous types of speciation had already been proposed and the literature was muddled by the sometimes-confusing jargon that accompanied them. I was doubtful about the value of encouraging another bit of specialized speciation verbiage and said so at one of the meetings. But

Dolph knew that this case was different; the term captured a valuable insight and efficiently conveyed an important concept. He also emphasized its connection to natural selection rather than using it more loosely to reference any of the ways by which ecological differences might influence the speciation process.

A straightforward illustration of ecological speciation is when a fish comes to occupy new ecological niches as it colonizes a lake that previously lacked fish, causing one species to divide into two or more. For example, in Lake Matano, Sulawesi, the sailfin silversides comprise most of the fish species and probably had few competitors when the first such fish arrived in the lake. *T. prognatha*, mentioned earlier, preys extensively on other fish, unlike the other members of its lineage and most telmatherinids. Hence *T. prognatha* occupies a fairly distinct niche—and has become substantially reproductively isolated from two closely related forms that feed mainly on invertebrates.

The ecological speciation hypothesis lends itself to experimental and comparative tests, and there have now been many such assessments. I became acquainted with one noteworthy study, led by Jelena Rajkov when she was a PhD student in Basel, because I was involved in the editing of her manuscript. Working in and around Lake Tanganyika, she studied the cichlid fish known as Burton's mouthbrooder (*Astatotilapia burtoni*) in river- and lake-dwelling populations as they diverged into potentially distinct species. She tested for lower survival, as predicted by the ecological speciation hypothesis, of river fish relative to lake fish, in lake environments. The cichlids that had been evolving in the lake for generations should have been better adapted to that environment. In addition, she examined

the survival of the offspring of matings between these populations; offspring of matings between populations should be ecologically intermediate and survive less well than lake fish, though better than pure (nonhybrid) river fish.

She confirmed that river fish survived poorly in the lake environment, and their offspring, whether pure river or from one river parent and one lake parent, also did relatively badly. When I first read her manuscript, I wondered why there was no reciprocal experiment, for example, with the various types of fish all placed in enclosures in a river. The authors explained the reason in the revised final version of the paper, and I found their comments memorable. They first noted the practical constraints of their remote research site—for example, how hard it was to get to and from. They went on to state that owing to “the presence of crocodiles and hippos in the riverine environment, no reciprocal control experiment in river environment could be performed.” Most of my own efforts at field experiments have been with stickleback fish, near Vancouver, Canada. I have occasionally had to deal with a cranky landowner or seagull trying to steal my lunch, but this paper helped me understand one reason there have been relatively few field experiments in the African Great Lakes, especially around rivers. I have seen hippos up close, and they are magnificent but scary. They kill hundreds of people every year, let alone being hard on field enclosures.

One of the most distinctive patterns predicted by the hypothesis of ecological speciation is *parallel speciation*, an idea both clever and audacious. To explain it, let us suppose closely related fish populations are found in physically isolated ponds scattered across a landscape, some with predators, in which a

small body size is selected for, and others with no predators and a large body size favored. Parallel speciation occurs if fish from populations with similar patterns of predation and natural selection evolve similar body sizes and other traits, and will mate with one another, whereas populations from different predation regimes will not. In this scenario, not only do particular traits evolve in parallel across parallel environments, so does reproductive isolation. And this is predicted to happen even though all the populations are evolving independently—the bold part of the prediction.

As with ecological speciation, I encountered this idea in an informal presentation by Schluter at the University of British Columbia. Dolph gave a noon-hour talk about this topic, which he had learned of from two studies of fruit flies in which replicated populations evolved for generations in similar or different selective environments, all completely separate with no movement between them. Remarkably, the predicted parallelism in reproductive isolation was indeed observed. When I first heard this idea and these lab findings presented, I was literally speechless. It was just so original and exquisite in how it linked theory and observation. Moreover, it allowed for a definitive test of a truly unique prediction of the ecological speciation hypothesis. This is important because often in science, the most impassable obstacle we face is to come up with a unique prediction of a hypothesis—a testable prediction for which the data can be readily collected. Parallel speciation was all that. Even better, it turned out to be present in nature, not just a curiosity of laboratory fruit flies.

There seem not to have been any full tests of parallel speciation in the major ancient lake systems, but Joana Meier, then

at Bern, and her colleagues have proposed a closely related yet decidedly novel scenario for Lake Victoria. They suggest that two pairs of closely related Lake Victoria cichlid species have evolved through *parallel hybrid speciation* (figure 2.2). Using *Pundamilia* species and populations, Meier and colleagues conducted detailed analyses of multiple individual genomes from sister species of *Pundamilia* on several islands, including Makobe Island in the main area of the lake and Python Island, which is in Tanzania's Mwanza Gulf and somewhat isolated from the main body of Lake Victoria.

From their genomic data, they inferred that the *P. pundamilia*–*nyererei* species pair first evolved in the main area of the lake, including on Makobe Island. The more shallow-dwelling, widely distributed, and likely older species, *P. pundamilia*, which features blue males, then colonized the Mwanza Gulf and Python Island. A little later, individuals from the deeper-dwelling *P. nyererei*, which possesses red-shifted vision and red males, arrived and interbred with the *P. pundamilia*, forming a hybrid population. From this hybrid population, a new shallow-adapted population of *P. pundamilia*-like fish subsequently evolved with blue males alongside a deeper-adapted population of *P. nyererei*-like cichlids with red males. Substantial reproductive isolation also evolved between them.

Because the two species pairs did not evolve entirely independently, they are not quite an example of parallel speciation of the sort that Schluter proposed. And at the genome level, there was a mixture of parallel divergence between the old and young pairs involving the same parts of the genomes, and different regions diverging in the younger pair. But overall, the consistencies across different locations in the lake do suggest an

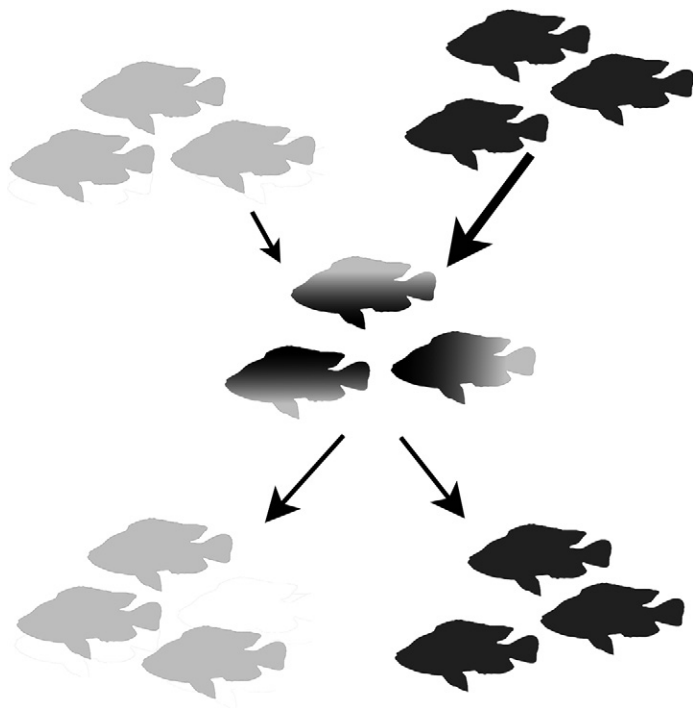


Figure 2.2

Parallel hybrid speciation in *Pundamilia*. *P. pundamilia*, here darker, colonized the Mwanza Gulf and Python Island followed by *P. nyererei*, here lighter. They interbred, forming a hybrid population from which a new shallow-adapted population of *P. pundamilia*-like fish evolved, here darker, alongside a deeper-adapted population of *P. nyererei*-like cichlids, here lighter. *Source*: author, based on figures by Joana Meier.

important role for divergent selection, acting in parallel on similar genetic raw material that became available to the younger pair through hybridization.

ADAPTIVE RADIATION

Ecological speciation is closely linked to the idea and theory of adaptive radiation (though they will not always occur together). Adaptive radiation is an intuitive concept in which a lineage of organisms rapidly diversifies as it adapts to new environments and opportunities. Central to the theory is a guiding role for natural selection in driving divergence in ecologically important traits. It may also contribute to the formation of new species, in particular through ecological speciation. For example, when fish colonize a lake that lacked fish previously, selection often causes some to evolve traits that allow them to feed along the bottom and mainly live in that habitat, while others evolve traits that help them catch tiny free-swimming prey in the open water. Those fish in each habitat that possess genes for traits well suited to their local setting leave more offspring, and genetic differences accumulate over generations—even faster if speciation gets started. Bottom-feeding and open water-feeding fish become more and more different, as each becomes better at feeding and surviving in its preferred habitat.

The term *adaptive radiation* can be thrown around a bit casually, and some use it when discussing any collection of related species. At least in principle, however, a lineage can diversify with a minimal role for natural selection through a haphazard differentiation of physiological, developmental, and other traits that are not always tied to ecology or the

environment. This can occur even for animals and plants that live in environments that vary little, especially if they spend their entire lives in a small area, not moving far even when young. If their habitat is patchy, as for some rock-dwelling cichlids in lakes with mainly mud on the bottom and only occasional patches of rock, populations can easily become spatially divided. They can diverge through the processes Mayr emphasized owing to a lack of gene exchange even if selection differs little between, say, rocky outcrops. Thus, sets of related species are not necessarily products of adaptive radiation. Diversification mainly as a result of physical isolation, though, is generally expected to be slower and less predictable.

Ancient lakes are perhaps best known among biologists and certainly among students for providing case studies of adaptive radiation. Biology texts commonly feature a figure showing how cichlid fish in different African Great Lakes have evolved similar forms and appearances as they have adapted to similar diets and ecologies in different lakes. Those of us who have looked at figures of this sort time and again throughout our careers can easily start to take such convergence for granted. But if I stop and reflect just a moment, it really is a wonder. From ancestors as genetically different from each other as we are from apes, fish in lakes hundreds of kilometers apart have evolved strikingly similar heads, body shapes, and fins when confronted by similar ecological challenges. An example of such is shown in figure 2.3.

Some of these patterns are also seen even farther afield. In Sulawesi's Lake Matano, for example, one can find thick-lipped fish from a completely different lineage located thousands of kilometers away, in a lake on a different landmass, which are

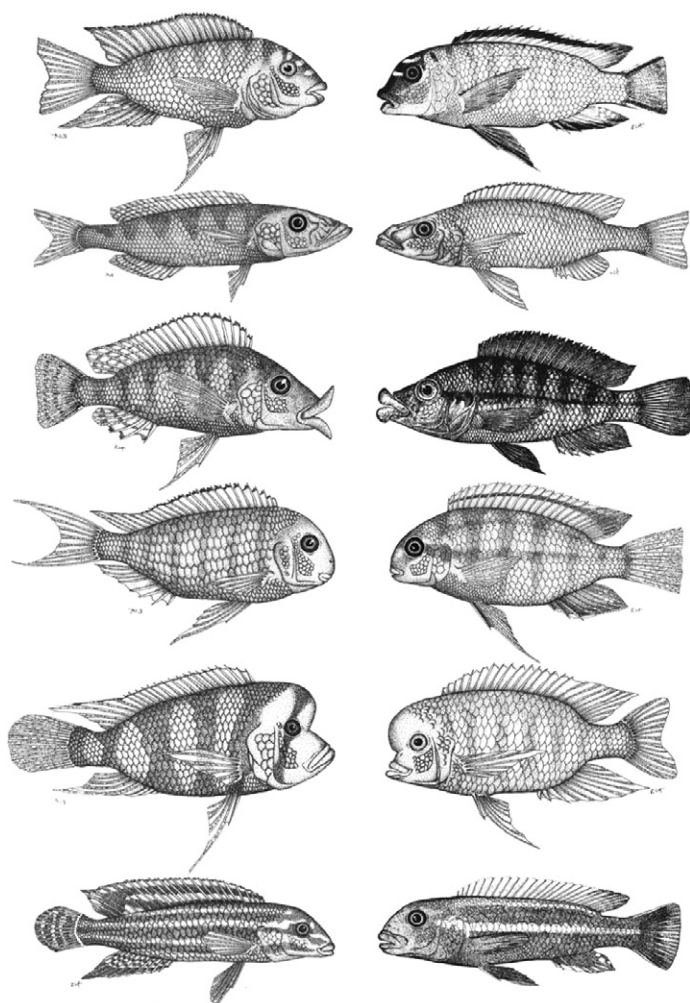


Figure 2.3

Convergent evolution in two ancient lakes. The species in the left column are all from Lake Tanganyika, and the ones on the right are from Lake Malawi. *Source:* Reprinted with permission from Springer Nature, from Albertson and Kocher, "Genetic and Developmental Basis of Cichlid Trophic Diversity," *Heredity* (2006).

reminiscent of forms in the African Great Lakes. In addition, the divergence described earlier, between a shallow-water, bottom-feeding lifestyle versus open water cruising and feeding, is replicated for different groups of fish in different lakes across the entire planet. Just as human economic systems lead to certain similar occupations most everywhere, such as fishing versus farming, fish in different lakes show certain commonalities in how they make a living.

What is less well-known, and arguably even less expected, is that different and relatively unrelated lineages of fish have sometimes diversified in parallel within a single lake. Walter Salzburger and his colleagues at the University of Basel have stressed this pattern for the cichlids of Lake Tanganyika. The cichlids of Tanganyika are special in that they are to the cichlids of the other African Rift Lakes as Africa is to hominins; Tanganyika is the oldest of the trio that also includes Victoria and Malawi, and its cichlids are more genetically diverse than those of the other lakes. In fact, the radiations in the other lakes evolved mainly from lineages within the Tanganyika radiation. The diversity of form present in Tanganyika's cichlids is readily apparent to even the casual snorkeler, and I found Tanganyika's waters and fishes captivating during a brief visit there. It surely deserves more attention from travelers.

Working with Salzburger and Adrian Indermaur, Moritz Muschick analyzed the shapes, ecologies, and evolutionary relationships for a large sample of Tanganyika cichlids encompassing lineages that have been evolving independently for millions of years. Much as for the comparisons between lakes, he documented fish evolving similar feeding habits and adaptations, ranging from jaw shape to body shape, over and over—but these

fish, of different species and from different evolutionary backgrounds, were often side by side in exactly the same habitat in the same small area of the lake. This observation raises questions of how they coexist and how they evolved such convergence in the first place. Possibly some convergent forms originated in different parts of the lake, especially during low water periods when Tanganyika was divided into separate basins since periods of temporary fragmentation are not unusual in the larger and older lakes. Ongoing coexistence may have been aided by differences in other key traits; for example, some of the cichlids studied spawn on the lake bottom whereas in others the female carries the fertilized eggs in her mouth. But these explanations do not always apply, and although within-lake convergence is especially obvious and well studied in Tanganyika, it is not unique to this adaptive radiation. Research into this intriguing topic continues.

Although adaptive radiation is a persuasive and intuitively satisfying explanation for many patterns in nature, it is always important in science to conduct decisive tests of our most fondly held explanations. If ecological opportunity mediates diversification, as predicted, it should be possible to identify which aspects of ecology are important and link opportunity to the diversification rate. This has been done in large-scale comparative analyses initiated by Ole Seehausen (figure 2.4), who I have mentioned before. Ole's group has bases both in Bern, Switzerland, and at a research center in the picturesque Swiss village of Kastanienbaum, on the shores of the exquisite Lake Lucerne—which is itself home to radiations of whitefish and charr. Ole is well-known for the intensity of his fascination with cichlid fish, and I had an enjoyable experience of this during a

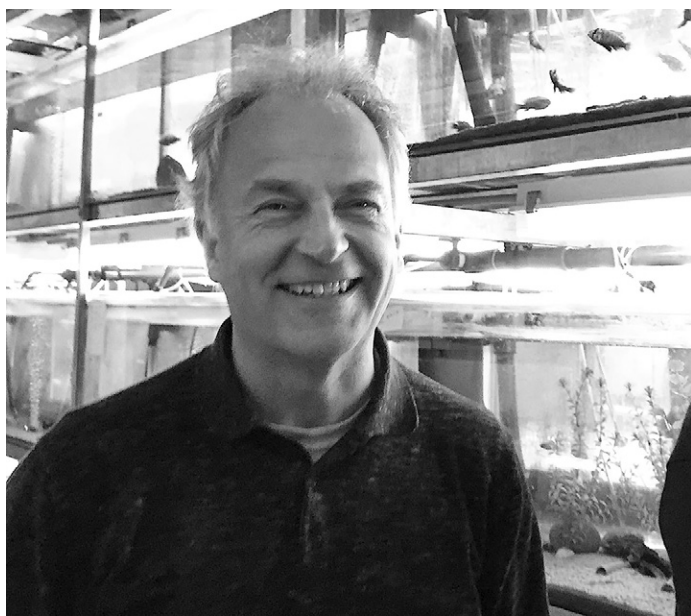


Figure 2.4

Ole Seehausen in his laboratory in Kastanienbaum, 2019.

visit to Kastanienbaum. It was entertaining, inspirational, and informative to spend a few hours with Ole in his fish lab. He had a marvelous tale to tell about every tank, what had already been learned, and what he wished to do next. He chose his words carefully as he spoke, but also with humor and the joy in the work that is a delight to see in colleagues and students. Later, at a group dinner, I was reminded that even elite scientists are people with families and lives when one of Ole's teenage children joined us. My own eldest had recently moved out of our home, and I felt nostalgic watching the affectionate give-and-take between daughter and father.

Seeking to test hypotheses of adaptive radiation, Catherine Wagner, a young US scientist then working in the Seehausen lab (who later moved to Wyoming), led a series of analyses of cichlid fish and their ecologies across forty-six African lakes. These included the three great lakes we have focused on. Wagner and her collaborators asked what factors made a cichlid newly colonizing a lake more likely to evolve into at least two species, or five or more species. They found that cichlids were more likely to diversify in lakes with characteristics associated with ecological opportunity: greater depth and greater net solar radiation. Depth should provide a wider diversity of habitats to colonize, and more solar energy should support larger populations and/or more species. Surprisingly, lake area was not consistently important in triggering diversification, although large-scale radiations were seen only in the largest lakes. Further, when they looked at the total number of species that had evolved in a lake (a little different from the previous measure), adding up all the different lineages of cichlid present, there were indeed more species in lakes with bigger areas. This could be because of a greater range of ecological opportunities in such lakes, but it could also be because they are large enough for speciation to occur between related populations in different parts of the lake. In lakes in which speciation had taken place, lake age led to greater diversity as well, although the effects of time were not always straightforward.

The Seehausen group has continued these analyses of cichlid diversification in work that expands their data sets to include *every* species of cichlid. This effort was led by Matt McGee, another intrepid US scientist. There are more than 1,700 cichlids (probably quite a lot more; this estimate is likely

low), which comprise more than 5 percent of all teleost fishes; teleosts are what we usually think of when we think of fish. Perch, tuna, salmon, and most other fish are teleosts, whereas lampreys, sharks and rays, lungfish, and a few other groups with fewer species are not. For comparison, there are about 6,400 species of mammals on the entire planet. If the 1,700 cichlids had hair and mammary glands, they would represent over one-quarter of mammals. If they had a land-dwelling adult stage, they would account for more than one-fifth of the 8,000 or so amphibians so far described and named (which are mostly frogs, it turns out). This more comprehensive cichlid data set includes fish from South America, India, Madagascar, and a few other spots as well as Africa, and a large number of river-dwelling species in addition to those in lakes. Perhaps it is not surprising, then, that when the relationships between speciation rate and environmental variables are reanalyzed, things have changed a bit.

As far as external factors go, the biggest development in the new data is the appearance of predators. Analysis of this broader data set suggests that when large, visually oriented predatory fish are present, speciation is slower and species accumulate less quickly (note the new analyses are of speciation rate, which is also a little different from examining whether radiations start or not, or looking at the total number of species—though the measures are all related); possibly predators suppress population densities of the species they eat, thereby reducing competition among prey and thus pressure to diversify to obtain enough food. A dry climate also acts as a brake, not surprising for fish. Deep water still facilitates cichlid speciation in the expanded data set, but the effect is weaker. There are additional

intriguing correlates, more internal than environmental, which we will explore in later chapters. Nevertheless, environmental correlates of diversification remain in this massive compilation of data in which environmental classifications are of necessity somewhat crude. And these correlates are connected to ecological opportunity. Therefore adaptive radiation is supported, though perhaps less clearly than when one considers only lakes.

Most studies of adaptive radiations and the processes that drive them have either looked at large-scale patterns in traits, ecology, and diversity, or sought to measure selection itself in a much smaller number of species, typically one or two. A study of telmatherinid fish from Sulawesi's Lake Matano took a different and notably ambitious approach in an effort to test adaptive radiation theory more directly and comprehensively. For the five or more incipient species comprising the Matano sharpfin group, Jobst Pfaender and his collaborators collected wide-ranging data from over 1,000 individual fish, including feeding habits, habitat, body shape, and relative liver weight, a measure of body condition thought to be indicative of evolutionary fitness. Evolutionary fitness is essentially the relative contribution to the next generation's gene pool—thus whether a trait is becoming more common or disappearing as a result of differential survival and reproduction. Liver weight is sometimes used as an indicator of fitness because the liver carries energy stores. These stores are an index of the energy available to the fish for growth, reproduction, or other functions, and an indicator of how well the fish is doing day-to-day in terms of feeding success, resisting stress from disease, and so on. It can reveal whether an animal is scrawny and scraping by, or plump and prosperous.

Pfaender and colleagues plotted their liver-based fitness index against measures of shape. These composite shape measures summarized multiple features like relative head width and body depth—features that have often been found to affect how successful fish are when feeding on particular prey types. Such plots are referred to as adaptive or fitness landscapes (figure 2.5). A value for a trait (or set of traits) indicates success on a fitness landscape if it is on a fitness peak, and suggests failure if it is in a valley of depressed fitness. If ecological selection acts strongly in favor of members of incipient species and against hybrids, the average value for each species should be on a peak of fitness whereas hybrid values should have low fitness and be in valleys. This is the pattern seen in Pfaender and colleagues' data, in which peaks are generally associated with sets of features characteristic of members of the five known species while areas between species, where hybrids should usually be located, are generally of lower fitness. Not every peak is exactly where it was expected to be, and some statistical results are not definitive, but the overall pattern is clear and provides satisfying support for hypotheses of ecological speciation and adaptive radiation. The tremendous effort involved in the study turns out to have been well justified.

One of the coauthors on this paper deserves recognition here for the contributions she made to this and many more of the studies on Indonesian lake fishes that will be recounted in this volume as well as the taxonomic work that made some of the theoretically focused studies possible. Renny Hadiaty (figure 2.6) was the systematic ichthyologist at the Indonesian Institute of Sciences Research Center for Biology as well as head of the Ichthyology Laboratory and the curator of the fish

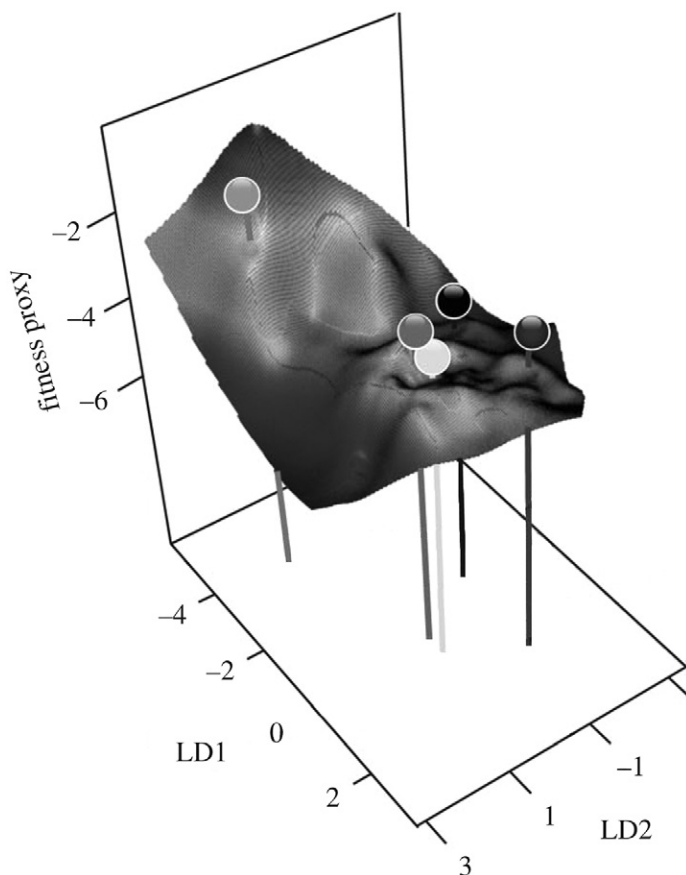


Figure 2.5

Fitness landscape for sharpfin telmatherinid fish from Lake Matano, Sulawesi. The horizontal axes are summary measures of shape, and the vertical axis is a proxy for biological fitness. The “pins” indicate mean values for each species and are mainly on peaks of fitness, with valleys of low fitness between them—where intermediate hybrids generally do poorly. *Source:* Modified from Pfaender et al., “Rugged Adaptive Landscapes Shape a Complex, Sympatric Radiation,” *Proceedings of the Royal Society B: Biological Sciences* (2016), under a Creative Commons CC BY 4.0 license (<http://creativecommons.org/licenses/by/4.0>).



Figure 2.6

Renny Hadiaty (right) with Daniel Lumbantobing and Sopian Sauri during 2010 fieldwork. *Source:* Photo by Lynne R. Parenti, © Smithsonian Institution.

collection at the Museum Zoologicum Bogoriense. In a career that ended too soon with her death in 2019 at age fifty-nine, she published over fifty papers in three languages and made important contributions to the growth of Indonesian fish biology. She also had three fish species named after her!

Our attention is often drawn to isolated radiations as in Lake Matano or spectacular radiations that involve many species as in the African Great Lakes. A quite different pattern of diversification is seen in Japan's somewhat less speciose Lake Biwa, though it occurs to some degree in probably every ancient lake. Biwa is located on the main Japanese island of Honshu, almost midway between the massive urban centers of Nagoya and Osaka, just upstream from the cultural center of

Kyoto. The lake is over four million years old, but underwent substantial geological changes about 400,000 years ago when most of its current deepwater areas were added as a result of a tectonic process known as a *fault-block movement* associated with grabens and half-grabens. These deeper waters, now reaching over 100 meters, are associated with species living entirely in open water, away from the lake bottom. Biwa contains sixteen endemic or semiendemic—confined mainly to Biwa—fish species or subspecies, out of about sixty total species and subspecies (forms that are differentiated, but not quite enough for taxonomists to label them as distinct species).

In contrast to better known ancient lakes, Biwa's endemic species are not mainly the result of a few lineages undergoing repeated speciation events and rapid within-lake diversification. Instead, multiple lineages that are found mainly in nearby rivers have each evolved into one or a few new lake species, often through adaptation to habitats found in the lake yet not present in the surrounding waters. In addition, the lake harbors some lineages now absent from the rest of Japan, or that are genetically distant from other Japanese forms. Thus, Lake Biwa may have served as a reservoir of species and genetic diversity, and made an important contribution to the freshwater fish communities of western Japan outside the lake. This reservoir or refugium (also sometimes described as a museum, in contrast to a cradle) role has also been suggested for some other ancient lakes, at least for some groups of animals. The gastropods (snails) of Lake Tanganyika are a prime example.

Studies of Biwa's snails highlight another important feature of lake radiations: how different lineages can respond differently to the same environments. Snails of the genus *Biwamelania*

resulted from two distinct colonizations of the lake. They diversified into fifteen different species as they occupied new habitats and depths following the lake's expansion and deepening about 400,000 years ago. The study of this system is at a somewhat early stage, but it currently looks like spatial isolation may have contributed to speciation in this system in addition to ecological divergence. Some species are confined to individual islets or river mouths, and lack a free-swimming or drifting open water stage that would help the snails disperse. Hence fish and snail diversity have accumulated in different ways in the same lake. We have made important progress in the study of adaptive radiations, but there is much more to come.

* * *

Counting the species in a location is one way to measure biodiversity. Other methods take into account relative abundance, evolutionary history, and ecological distinctiveness. Biodiversity ultimately arises through the evolution of new species, and ecological differences are increasingly considered to be important to speciation, but spatial isolation, time, and chance can play roles too. During adaptive radiations, lineages of organisms rapidly diversify as they adapt through natural selection to new environments and opportunities, and ecological speciation may occur. Ancient lakes provide support for the theory of adaptive radiation and extraordinary case studies. Ancient lakes may also serve as reservoirs of biodiversity, seeding the areas around them.

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