

# Biogeography, or How Plants and Animals Got Where They Are

*Biogeography* is the study of the distribution of organisms on Earth — it's all there in the name. This means determining not only where different species live and where they don't live (their *distributions*) but also the historical processes by which they achieved those distributions.

Evolutionary biologists can use biogeographic patterns (distribution, fossil record, phylogeny, *etc.*) to test hypotheses of biogeographic process (*e.g.*, vicariance, dispersal, extinction, and speciation).

During the middle and late parts of the 1800s, biogeography was on the cutting-edge of the study of “natural history” (geology, botany, and zoology, *etc.* — the term *biology* had not yet achieved common usage). Some of the most important natural historians of the time were biogeographers: Lyell, Hooker, Gray, Wallace, and, of course, Charles Darwin, to name a few. As might be evident from this list of scientists, the early development of biogeography was closely linked to the rise of evolutionary thought. The objectives of this essay are to (1) demonstrate that the study of biogeography has relevance to modern-day evolutionary biology and (2) suggest how biogeographical problems might be approached through the scientific method (*i.e.*, hypothesis testing). We will first address the kinds of patterns of use to the biogeographer, followed by a discussion of different biogeographic processes. Finally, the example of the Gondwana lungfishes will be examined, and you will have the opportunity to test and discuss similar biogeographic problems.

## Pattern

### *Endemism, Provincialism, and Disjunction*

No species occurs everywhere. Even widespread species like *Homo sapiens* (that's us) have limited distributions: people don't live in the oceans. Consider a less striking example, the spotted skunk, *Spilogale putorius*. *S. putorius* occurs only in North America. It is *endemic* to North America, as opposed to a species that is ubiquitous, or *pandemic*, occurring everywhere. The *distribution* of a species, or other monophyletic taxon, may be depicted by a range map (Figure 1). Such an illustration does not imply that spotted skunks occur at every point within the shaded area. Rather the range boundaries merely encircle the collection of points from which the taxon is known. Why one can find *S. putorius* at some places within its present distribution but not others is generally due to local, contemporary processes — competition, predation, climate, *etc.*, and these are generally problems for the ecologist. The biogeographer, on the other hand, is more interested in the larger, historical aspect: How did such a pattern of endemism come to be?

Often many taxa share the same pattern of endemism. The Cumberland Plateau is a mountainous area of Kentucky, Tennessee, and, to a lesser extent, Alabama, Virginia, and North

Carolina (Figure 2). Several species of fishes and mollusks (e.g., snails and clams) are endemic to the Cumberland Plateau. A localized region of endemic forms is referred to as a *province*. As the figure shows, the river systems of eastern North America can be divided into several provinces based on the distributions of freshwater mussels. It is this sort of provincialism that lends another level of complexity to the questions of individual species' endemism. If several taxa share the same basic pattern of endemism, isn't it reasonable to hypothesize that they share the same historical cause for their present distributions?

Another pattern of interest to biogeographers is *disjunction*. Consider a monophyletic taxon that occurs in two, non-adjacent provinces. For example, the present distribution of marsupial mammals is limited to the Australian region and the Americas (Figure 3). Is it appropriate to include the Pacific Ocean as part of their range? No. The ocean is a *dispersal barrier* — how far do you think a koala or opossum can swim? When a taxon occurs on both sides of a barrier, it is said to have a *disjunct distribution*. But, bear in mind that what constitutes a barrier varies from group to group.

#### *Phylogeny, the Fossil Record, and Historical Geology*

When we make a hypothesis about the distribution of a species or some higher taxon, we are also implicitly making a statement about phylogeny. In the marsupial mammal example of the previous section, the observed disjunction is only interesting because one natural group occurs on two isolated continents. Consider Old and New World “porcupines” — the family Erethizontidae occurs in North and South America, the Hystricidae in Asia, Europe, and Africa. That is apparently quite a disjunction. However, analyzing the phylogeny of “porcupines” in the context of other rodents reveals that “porcupines” are not monophyletic. Instead, each “porcupine” family shares a more recent common ancestor with other rodents on their respective sides of the Atlantic Ocean than they do with each other. Rather than a case of disjunction, the “porcupines” are exemplars of convergent evolution.

The distribution of a species, genus, family, *etc.* is the sum of the distributions of the individual populations that comprise it. That includes extinct representatives as well. The fossil record is a rich (though incomplete) source of data on the past distributions of plants and animals. At the very least, a dated fossil provides a minimum age for the taxa to which it belongs — if a paleontologist finds a fossil turtle 10 million years old, then turtles are at least 10 million years old — and a *paleo-distributional* data point. As the example below will show, the collective dates and distributional points of clade-mates living and dead are a valuable resource for testing hypotheses of biogeographic process.

The study of biogeography also requires a knowledge of Earth history — at least the latest 15% or so since the rise of macroscopic life. Whereas the study of contemporary processes often forces the simplifying assumption of a constant environment, over longer time-scales the world is a busy, dynamic place. During the last 300 million years, the continents have collided, split apart, and then

re-fused; sea level has risen and fallen; and, as recently as 15,000 years ago, a good portion of North America and Eurasia was covered in thousands of meters of glacial ice. All this geologic action has had a profound evolutionary effect. This will become more evident during the following discussion of biogeographic process.

## **Processes**

### *Speciation and Extinction*

*Speciation and extinction*, analogous to the birth and death of species, have an obvious affect of the diversity of species that inhabit a particular region. For example, if the rate of speciation is high in a particular province, it will likely be inhabited by a high proportion of endemic forms. But would the same pattern of high diversity be observed in a province with a low extinction rate? Is a low extinction rate the same thing as a high speciation rate? Consider the example of Darwin's finches on the Galapagos Islands of the eastern, tropical Pacific. This small chain of volcanic islands is home to some 13 finches that occur on the Galapagos and no where else. If we hypothesize that this provincialism is due to a high speciation rate, we would then predict that the speciation that lead to this diversity of finches occurred on the islands. On the other hand, a low extinction rate model would suggest that the ancestors of these birds were once more widespread. They persist on the islands, but the finches have gone extinct everywhere else. What would we need to test these hypotheses? How would the predictions of a low speciation rate or high extinction rate differ?

Extinction as a process can also result in disjunctions, and the mammal family Camelidae is a prime example. Presently, the group is represented by a pair of camel species in Asia and northern Africa and by llama species in South America; the Camelidae are absent from North America. The fossil record shows, however, that camels *did* occur in North America. Within the last few million years, the Camelidae had a reasonably continuous distribution from Asia onto the Americas across the Bering Land Bridge, a low sea-level stretch of land connecting Siberia and Alaska. The North American species spread across the Isthmus of Panama into the South America, but then went extinct in North America, as so many of the large mammals did at the close of the Pleistocene. However, this explanation raises an important consideration — Should North America be considered a barrier to camel dispersal?

### *Dispersal and Vicariance*

The principle mechanisms hypothesized to explain most observed disjunctions are *dispersal* and *vicariance*. When a species or more inclusive natural group occurs on both sides of a barrier, one of two hypotheses must be true:

1. The barrier is imperfect; it allows at least a small amount of dispersal across it.  
The barrier was there first, and the taxon got across it.
2. Or, the barrier arose to divide the once continuous range of the taxon. So, the taxon was there first, and the barrier appeared and divided its range.

The former model is known as dispersal, the latter is vicariance (Figure 4). To which of these classes of disjunction mechanisms does the example of the Camelidae belong?

For dispersal to lead to new populations by the *founder effect*, only a single dispersal event is often all that is necessary. The barrier separating the two disjunct provinces can not be perfect. If it is (and always has been), then dispersal is impossible. On the other hand, if dispersal is too frequent, the question is raised whether the barrier is in fact actually a dispersal barrier. Consider again the Galapagos finches. Ecuadorian finches have a disjunct distribution — populations on the Galapagos are separated from the mainland populations by a substantial *dispersal filter*: about 900 km of open ocean. This is well beyond the cruising-range of a little finch. However, if a few finches (with at least one member of each gender) were blown off course by a tropical storm, they could found a new, isolated population where ever they end up. The presence of finches on the Galapagos suggests that a rare dispersal event of this kind must have taken place.

Because the Earth is a dynamic place, changes often occur that create barriers and break up populations. The marsupial mammals on Australia and South America at one time had a continuous distribution. During the Mesozoic, those two continents were connect with Africa, India, and Antarctica to form a huge super-continent known as Gondwanaland (Figure 5). When those continents rifted apart, dispersal barriers of open ocean formed between them. Thus, the disjunction of Australian and South American marsupials was caused by vicariance. Vicariance events need not take place only on such large scales. Any process that mechanically divides the range of a taxon qualifies.

### Testing Biogeographic Hypotheses: an Example Using the Lungfishes

Hypotheses of the processes responsible for biogeographic patterns are inherently difficult to test because they are outside the domain of experimentation. Regardless of the fact that biogeographical processes act on spatial and temporal scales beyond experimental manipulation, the real philosophical difficulty is that we are talking about actual events that occurred during a history that no one observed. Even if we could manually reunite Gondwanaland and then carefully observe the course of evolution over the following 100 million years, there is no *a priori* reason to suspect that the same biogeographic processes would repeat themselves — *i.e.*, History happened one way once.

Although we can never *know* the exact course of unobserved, ancient history, we can *estimate* it. While it is very easy to construct 'Just-So' stories consistent with observed distributional and phylogenetic patterns, that is inconsistent with the Hypothetico-Deductive tenets of the Scientific

Method. To approach biogeography from a scientific perspective, we need to derive predictions from our hypotheses. Ideally, the predictions should be stated in such a way that if the predictions are false, the hypothesis from which they are derived *must be false*. That is the hard part. The best way to see the application of the scientific method to biogeographic problems is to see an actual example.

### *Lungfishes of the Southern Continents*

The lungfishes (Superorder Ceratodimorpha) are a group of primitive-looking, freshwater fishes presently occurring on the continents of Africa, South America, and Australia (Figure 6). The group is comprised of three genera, each endemic to one of the continents: *Neoceratodus* (Australia), *Protopterus* (Africa), and *Lepidosiren* (South America). As their common name suggests, ceratodimorphs all display at least some degree of air breathing, ranging from *Neoceratodus*, which will occasionally gulp air at the surface, to *Protopterus* which can survive for months in the damp mud of a dry river bed. Our objective here is to see what we can infer about the biogeographic processes leading to this distribution of air-breathing fishes based on their present biogeographic, phylogenetic, and historical patterns.

There are no hard and fast rules to dealing with biogeographic patterns. Each case has unique qualities that bear upon the details of the analysis. However, as described above, there are often broad process-themes that apply widely to different cases — endemism is endemism and disjunction is disjunction, regardless of the taxa involved. Table 1 lists some diagnostic pattern-predictions for alternative, generic biogeographic process-hypotheses. If we can show the predictions to be false, we may also have grounds to falsify one or the other alternative hypothesis.

In the case of the Ceratodimorpha, this is clearly a problem of disjunction (although each of the three genera shows also displays a high degree of endemism). The three lungfish genera are isolated by thousands of kilometers of open ocean, a formidable barrier to strictly freshwater fish. We can hypothesize two alternative processes for this pattern, either dispersal or vicariance. Since we are dealing with three separate disjunct taxa, we could potentially be dealing with both of these processes. From the models presented in Table 1, we can derive specific predictions for each case:

1. If lungfish achieved their present distribution by dispersal, then
  - a. the Ceratodimorpha is monophyletic.
  - b. the fossil record should show that the most recent common ancestor of all three genera did not occur in all three areas.
  - c. the fossil record should show that the most recent common ancestor of all three genera post-dates the formation of the southern oceans.
  - d. Australia, South America, and Africa were not connected (*i.e.*, they have been isolated since the most recent common ancestor of the lungfishes).

2. If lungfishes achieved their present distribution by vicariance, then
  - a. they should form a monophyletic taxon
  - b. the common ancestor should have occurred in all three disjunct areas.
  - c. the common ancestor should pre-date the formation of the modern Atlantic, Pacific, and Indian Oceans.
  - d. Australia, South America, and Africa should have been connected during the evolution of the Ceratodimorpha.

We can make these predictions and address their implications even before we have the phylogenetic, fossil, and historic patterns to test them. Both the dispersal and vicariance models predict that the lungfishes form a natural group, so the outcome of any phylogenetic analysis including *Neoceratodus*, *Protopterus*, and/or *Lepidosiren* will be uninformative for testing these hypotheses. However, if they are not monophyletic, then we are not even dealing with a disjunction. In that case, the lungfishes would be like the “porcupine” example described above, and each “lungfish” presumably evolved from the indigenous fish fauna of its respective continent. This is by no means a rare occurrence, and many unrelated fishes have evolved the ability to breath air.

A dispersal model assumes that the oceans surrounding the continents are not perfect barriers and that lungfish can, however infrequently, get across them. Several *ad hoc* scenarios can account for long-distance dispersal. Maybe the eggs of the ancestor got stuck in the mud on the feet of a duck, and that duck flew across the oceans before the eggs dried up. When the duck landed in a pond on one of the other continents, the eggs fell off, developed into adult lungfish, and a new, isolated population was founded. Or, maybe the common ancestor of these three genera was not limited to freshwater and a few individuals swam all that way. These may not sound like very likely occurrences, but that is not necessarily grounds to reject the hypothesis. Over evolutionary time scales (*i.e.*, millions of years) events that happen once every ten million years can actually happen (but see the discussion below).

The vicariance model predicts that at sometime during the evolution of the Ceratodimorpha, there was suitable lungfish habit connecting the now-disjunct continents. This could mean that the ocean barriers did not always exist or that the oceans were not, in fact, always a barrier. The model, though, is very explicit in that the common ancestor of the lungfishes must pre-date the formation of those three oceans as barriers. If the common ancestor is younger than the barrier, a vicariance hypothesis is rejected.

So how do the known phylogenetic, fossil, and historic patterns conform to our predictions?

- a. The Ceratodimorpha is monophyletic.

- b. The fossil record of the lungfishes extends as far back as the Devonian (at least 360 millions years ago), and fossil lungfishes, similar to *Neoceratodus*, have been found on all continents.
- c. Gondwanaland, the land-mass composed of the southern continents, did not begin to disintegrate until the early Cretaceous (144 million years ago) (Figure 5).

Review these data in light of the above alternative predictions. These patterns support the vicariance model while rejecting the dispersal model as we have stated it.

There are two important caveats<sup>†</sup> regarding our conclusion that the present distribution of the Ceratodimorpha is due to vicariance caused by the late Mesozoic break-up of Gondwanaland. The first is that our conclusion is only a corroborated biogeographic hypothesis, not the “Truth.” This hypothesis (and all hypotheses) are in need of further testing. Since we can’t prove our hypothesis, we can raise our confidence in it by not only rejecting all the alternatives, but also by *not* rejecting the vicariance model under further testing. In fact, the next step in our lungfish study should be to try to find the evidence that rejects the vicariance model. What would that entail?

This brings us to the second caveat. Whereas a vicariance hypothesis is rejectable, dispersal hypotheses are not except under certain circumstances. Even though we showed our dispersal predictions to be false, we can always come up with some complicated wrinkle that leaves dispersal as an option. This is especially the case when data regarding the pattern of the fossil record and/or historical geology are missing. Since a dispersal hypothesis counts on some infrequent, freak events, there will be as many dispersal hypothesis to reject as there are conceivable freak events. Is that also true of vicariance hypotheses?

The examples above demonstrate that the Scientific Method can be applied to historical problems like hypotheses of biogeographic process. Many scientists feel that the Scientific Method does not apply to historical problems — How can you do experiments? How can you make “predictions” about the past? While these issues do complicate approaching biogeography (and other historical biological disciplines, like phylogenetics) from a scientific perspective, the hypotheses and predictions (*post-dictions*?) of the various process models can be rejected. It is by overstepping what is rejectable that we revert to biogeographic ‘Just-So’ stories.

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<sup>†</sup> Since most people don’t know Latin, “caveat” sounds much less problematical than “warning.”

## Discussion Questions

If several unrelated taxa share the same basic pattern of endemism (or disjunction), it is reasonable to hypothesize that they share the same historical cause for their distributions? In other words, of what value are the distributions of unrelated taxa to specific biogeographic hypotheses?

Philosophically, how does the testing of vicariance and dispersal hypotheses differ?

*Felis concolor* ( depending on where you are from, it can otherwise be known as a mountain lion, cougar, puma, etc.) has a disjunct distribution. It ranges widely from Mexico through the Rocky Mountain states into Canada and east to Louisiana. There is also an isolated population in southern, peninsular Florida. What biogeographic processes could account for this distribution?

Imagine no fossil or geological data are available for the Galapagos Islands. What alternative predictions can you make regarding the relationships of island finches to those on the mainland? Draw the alternative cladograms you might expect from a phylogenetic analysis.

More than 100 species of fruit flies occur on the Hawaiian Islands. What sorts of biogeographic processes could account for such a pattern? What predictions can be made to test your hypotheses?

Several hundred species of cichlid fishes are endemic to Lake Victoria in eastern Africa. What sorts of biogeographic processes could account for such a pattern?

After discussing the last two questions, consider how the biogeographical and nautical definitions of an island might differ.



Table 1. Predictions of Biogeographic Hypotheses.

**High Provincial Diversity: High Speciation Rate vs. Low Extinction Rate**

<i>Pattern</i>	<i>High Speciation</i>	<i>Low Extinction</i>
Phylogeny	The provincial species in question are more closely related to each other than species outside the province (i.e., they form a monophyletic group).	The provincial species in question are more closely related to species outside the province (i.e., they do not form a monophyletic group).
Fossil Record	The common ancestor(s) of the species in question occurred only in the same endemic province.	The common ancestor(s) of the species in question occurred more widely than the endemic province.
Historical Geology	(no prediction)	The “environment” outside the area of the province was previously more similar to the area within the province.

**Disjunction: Dispersal vs. Vicariance**

<i>Pattern</i>	<i>Dispersal</i>	<i>Vicariance</i>
Phylogeny	The disjunct taxa are more closely related to each other than they are to taxa on their same side of the barrier.	Same as for Dispersal.
Fossil Record	The common ancestor of the disjunct taxa only occurred on one side of the barrier.  The common ancestor of the disjunct taxa is younger than the barrier.	The common ancestor of the disjunct taxa occurred on both sides of the barrier.  The common ancestor of the disjunct taxa is older than the barrier.
Historical Geology	The disjunct regions were never connected.	The disjunct regions were historically connected.

## Figure Captions

Figure 1. Range map of the spotted skunk, *Spilogale putorius*.

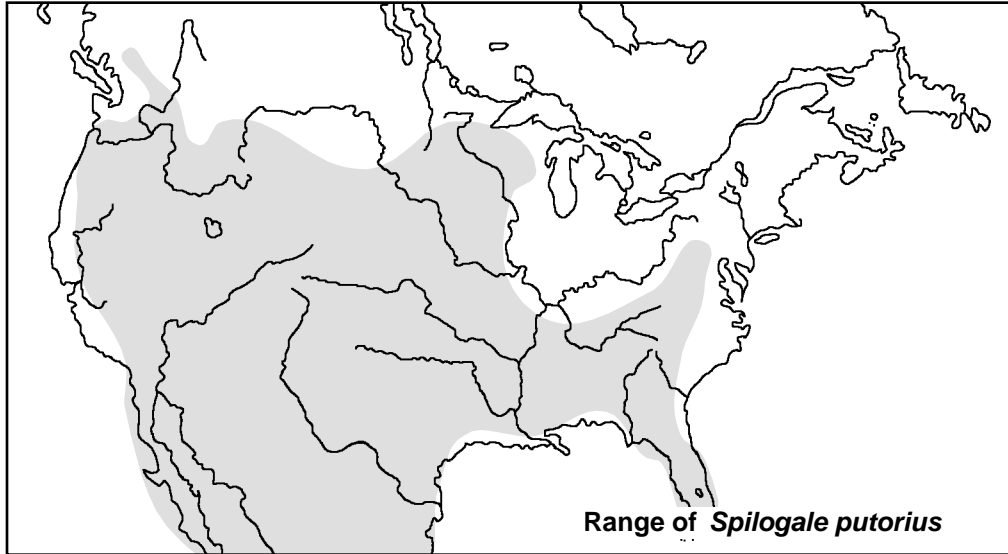
Figure 2. Freshwater mussel provinces of North America. There are about 280 species of freshwater mussels in North America. Some of these are widespread (occurring in more than one mussel province), but most show a high degree of endemism. The figure shows seven freshwater mussel provinces of North America, they are as follows: (A) Atlantic, (C) Cumberland Plateau, (E) Eastern Gulf Coastal, (I) Interior Basin, (O) Ozark Plateau, (P) Pacific, and (W) Western Gulf Coastal. The numbers after the letter-symbols are: # of spp. in the province (# of spp. endemic to the province).

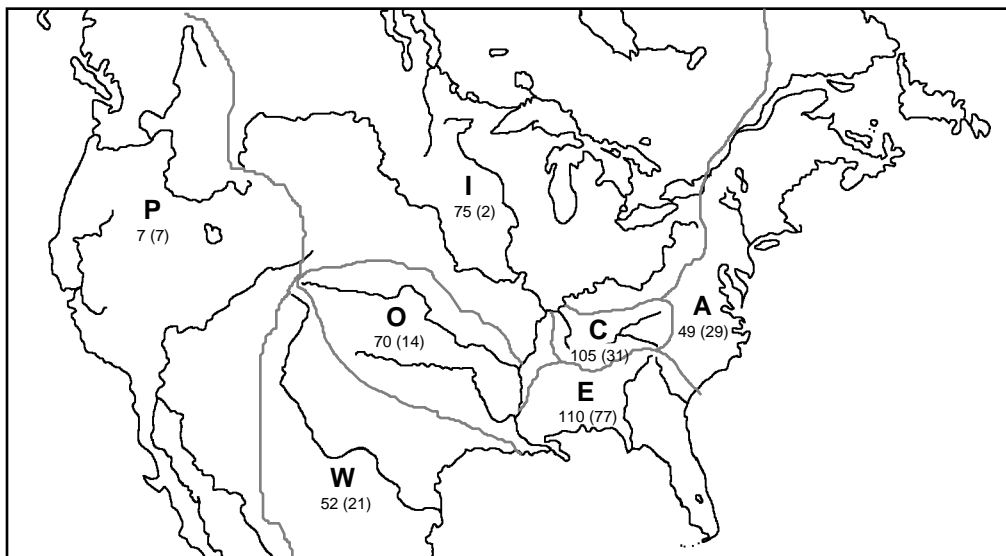
Figure 3. Global distribution of marsupial mammals.

Figure 4. Dispersal vs. Vicariance. The figure shows two different biogeographic processes that result in the same phylogenetic pattern: A evolving into B and C. At Time<sub>0</sub>, the dispersal model shows the Ancestor A occurring in one area. Some time elapses, during which A disperses to another area. These two isolated populations evolve into B and C. The vicariance model shows A occupying a very similar area. However, over the course of time, the area becomes divided. The fragments of A evolve into B and C.

Figure 5. Gondwanaland during the Late Jurassic.

Figure 6. Global distribution of the Ceratodimorpha.

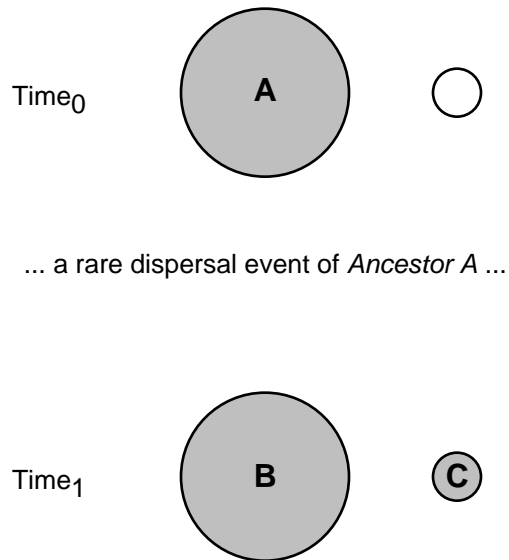






**Distribution of marsupials**

### Dispersal



### Vicariance

