

## RESEARCH UPDATE

## Ancestral ranges and historical biogeography

The Earth's biodiversity is not distributed evenly across its surface. To understand biogeographic patterns, it is necessary not only to consider current conditions (of climate, ecology, etc.), but also to view them in their historical context, as outcomes of both biotic (for example, speciation or adaptation) and abiotic (for example, geological) evolutionary processes. The field of historical biogeography is grounded in the principle that histories of Earth and life are intimately linked, such that knowledge about one may inform scientific inquiries about the other. One such line of inquiry is focused on unraveling the geographic history of species and their ancestors: where did species occur in the past, and how did biogeographic processes such as dispersal, extinction, and speciation cause their ranges to change over time (that is, evolve), giving rise to what we observe today? Recent developments of new statistical models for how geographic ranges evolve as species descend from common ancestors are allowing this question to be addressed with increasing sophistication.

### Research

For many years, historical biogeographers were not in fact much interested in the ancestral ranges of species per se, preferring instead to focus on discovering common geological causes for biogeographic patterns. Of particular influence was the idea of area vicariance, the splitting of one contiguous area into two spatially separate (disjunct) areas. For example, a series of vicariance events characterized the breakup of supercontinents (Pangaea, Gondwana, Laurasia) since the Late Triassic, resulting in the present configuration of continents. Because vicariance can divide entire communities, affecting different kinds of organisms (birds, plants, and so on) in the same way, it came to be viewed as a kind of null model for historical biogeography, in providing a common cause for current biological similarities between disjunct areas. By contrast, other kinds of events, most notably long-distance dispersal (the rare movement of organisms or propagules, such as seeds, across barriers to normal range expansion), were viewed as having relatively little explanatory power in this context. The primary goal of "vicariance" biogeography thus became to reconstruct the sequence of past vicariance events that best explained current biotic distributions—in so doing, focusing on historical area relationships and not the geographic histories of individual species.

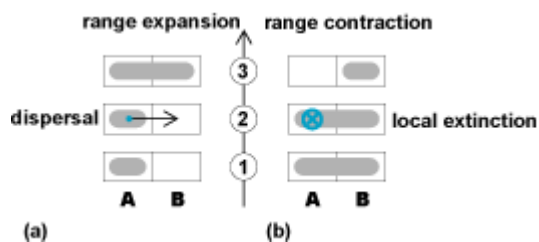
Recently, interest has been revived in the historical biogeography of individual species and their close relatives, particularly in the development of new models and statistical inference methods that allow a variety of biotic and abiotic information sources to be brought to bear on the reconstruction of ancestral species ranges and geographic patterns of speciation. For this purpose, the most important biological data come from two sources. One is the fossil record, which preserves direct (if often incomplete) observations of species in time and space. The other is phylogeny, the treelike genealogy that connects all species to their common ancestors. For extant (currently living) species, phylogeny is most commonly estimated by the analysis of DNA sequence data. A phylogenetic tree depicts past speciation events as lineage branching points or nodes. Lengths of branches connecting nodes can be estimated by using DNA sequences as "molecular clocks," calibrated to geological time by placement on the tree fossils of known age.

The phylogenetic tree is a powerful concept for making inferences about evolution. Darwin's revolutionary idea of "descent with modification" compels us to determine how, along the branches of the tree connecting ancestors to their descendants, hypothetical sequences of evolutionary events—in this context, events of

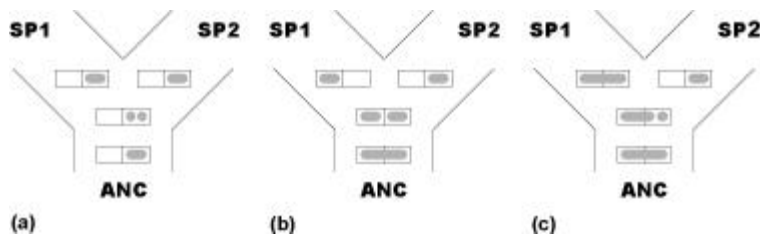
biogeographic history, including geographic patterns of past speciation events at nodes—can be arrayed and evaluated with respect to observed data for extant species at branch tips, or “leaves.”

### Processes of range evolution

Before addressing the question of how ancestral ranges and biogeographic events are inferred on a tree, first principles about process are needed. Three kinds of events can cause the geographic range of a species to evolve (that is, change through time): dispersal, local extinction, and speciation. Dispersal is simply successful establishment of a species in a previously unoccupied area, resulting in range expansion (**Fig. 1a**). Local extinction in an area is the converse, causing range contraction (Fig. 1b). Speciation is the event whereby one ancestral species becomes two daughter species, which are each genetically distinct and geographically cohesive (**Fig. 2**). Among the many causes of speciation, genetic divergence due to geographic isolation between areas is commonly regarded as being particularly important and ubiquitous. For example, divergence of populations separated by a geographic barrier divides the ancestral species range into two distinct daughter ranges, both of which differ from the ancestral range (Fig. 2b). Another geographic pattern is peripheral isolate speciation, whereby one daughter species is geographically localized and the other retains the original ancestral range (Fig. 2).



**Fig. 1** Events of range evolution for a single species through time: (a) dispersal, leading to range expansion of a locally distributed ancestor to a widespread descendant, and (b) local extinction, leading to range contraction of a widespread ancestor to a locally distributed descendant. The range of the species is indicated in gray by its presence in areas A and B: (1) before, (2) during, and (3) after each kind of event.



**Fig. 2** Geographic patterns of speciation. At cladogenesis (evolutionary branching) events, the ancestral geographic range (ANC) is subdivided and inherited by two daughter species (SP1 and SP2). The subdivision can occur (a) within the area of a locally distributed ancestor, (b) between areas occupied by a widespread ancestor, or (c) within an area of a widespread ancestor.

These biogeographic processes—dispersal, local extinction, and speciation—can be used to construct an evolutionary model that allows us to estimate ancestral ranges and geographic patterns of speciation events on a phylogenetic tree of the species of interest. In the model, dispersal and local extinction events occur stochastically through time, according to expectations of a Poisson process (a probabilistic model for a sequence of discrete events, with the defining characteristic being that the time intervals between successive events are exponentially distributed). Probabilities of geographic ranges changing from ancestors to descendants are calculated as a function of time: the longer the time interval, the more likely it is that dispersal and extinction events will occur. These probabilities are calculated across all branches of the tree, allowing alternative hypotheses about ancestral ranges and geographic scenarios of speciation to be

compared statistically. Generally speaking, hypotheses requiring fewer dispersal and extinction events (less evolutionary change) on the tree are more likely than those requiring more, assuming that such events are relatively rare.

### **Incorporating fossils and abiotic information**

Observed ranges of species and their phylogeny represent minimum amounts of information needed to estimate ancestral ranges and geographic patterns of past speciation events; in practice, other sources of relevant information are often available. For example, the spatial arrangement of geographic areas leads us to expect dispersal events between distant areas to be relatively rare compared to areas in close proximity. Geological records may indicate the past rise and fall of temperatures, rainfall, and sea levels, timing of mountain building and erosion, shifts in river catchment (drainage basin), and continental movements. These and other kinds of data tell us about the history of habitats through time, specifically with regard to their suitability for species colonization and persistence, and opportunities for dispersal between them.

To incorporate such information into inferences of biogeographic history, one needs to encode it into the model for range evolution as quantitative constraints. A few examples describing this are as follows. We might define the rate of dispersal to be a function of distance between areas, including terms representing factors such as prevailing directions of winds or ocean currents. Knowledge about the timing of land bridge formation, such as the Isthmus of Panama (connecting Central and South America) or Beringia (the Bering land bridge, connecting the northern points of eastern Asia and western North America), could be used to restrict dispersal between the areas involved to a specific period, with probabilities of range evolution adjusted accordingly for the phylogenetic branches spanning that period. A fossil specimen known to represent a particular branch on the tree means that the range of that ancestor must have included the area of the fossil at the time it was preserved, so the model can thus be adjusted to exclude from consideration other ranges (those that do not contain the fossil's area) at that time.

Use of models to infer the past is not new to evolutionary biology; they are commonly applied to reconstructing ancestral changes in morphological, genetic, and other kinds of biological traits on phylogenetic trees. For historical biogeography, however, they represent a new direction, with much potential for theoretical development and empirical applications. Benefits of using such models include well-understood statistical behavior and specification of uncertainty, important factors in any scientific undertaking. They will allow rigorous tests of biogeographic hypotheses, such as whether direction of dispersal has been significantly asymmetric between areas (for example, "stepping-stone" dispersal from older to younger islands along the Hawaiian archipelago) or to what extent dispersal to new areas has driven speciation and lineage diversification. Continued development of evolutionary models for geographic ranges can thus help move historical biogeography from being a primarily descriptive science to a more quantitative one.

For background information See also: Animal systematics; Biodiversity; Biogeography; Extinction (biology); Fossil; Organic evolution; Phylogeny; Population dispersal; Speciation; Supercontinent; Zoogeography in the McGraw-Hill Encyclopedia of Science & Technology

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