I. Classical Biogeography

Biogeography concerns the study of biological patterns and processes on broad, geographical scales and time scales.

The formalization of biogeography dates from the work of Alfred R. Wallace, who studied the distribution of the flora and fauna in the Malay Archipelago in the mid 1800s. These studies figured prominently in the formulation of Wallace’s Line – the beginning of the separation of Asiatic and Australian taxa – first noted in 1521.

Biogeography remained a primarily historical and descriptive field until the publication of *The Theory of Island Biogeography* by Robert MacArthur and E. O. Wilson in 1967. Their work focused on the species richness of an area of an area, and argued that the number of species present could be predicted by the factors such as island size (habitat area), distance from source populations and immigration and extinction rates.

Biogeography differs from studies of spatial patterns and processes that concentrate on fine-scale phenomena (e.g., phylogeography) and instead focuses on broad-scale phenomena. The former approach is more related to ecology, where one looks in the opposite direction, i.e. from local through geographical to global scales. However, the distinction between biogeography and ecology is simply one of scale over which a phenomenon occurs, together with the direction in which one looks. Although the immediate aim of biogeography is to describe and explain spatial patterns and processes of taxa, its ultimate goal is to aid our understanding of evolutionary processes.

Because the processes that are thought to produce patterns of spatial distributions operated at evolutionary and geological time one has to ask the question of why a particular taxon isn’t everywhere rather than restricted to a specific area or region. The null model is: *Everything is everywhere* (Ball, 1975 – Systematic Zoology 24: 407-430).

Ball argued that the formulation of biogeographical hypotheses must have a phylogenetic framework for the taxa under consideration and the hypotheses must have "explanatory power, internal consistency, predictive power, and potential for falsification."

For a long part of its history biogeography was considered to be a subsidiary to taxonomic classifications. From the viewpoint distributions and ranges were considered merely as taxonomic characters. For example, ‘widely distributed taxa’ vs. ‘endemic taxa’ - of feeding vs. non-feeding larvae, wind-dispersed seeds, etc. Hennig suggested both biogeography and ecology could be used to augment outgroup analysis in determining
character polarity. Hennig suggested that the older, more basal taxa would be found at the center of the range with the more derived taxa advancing into new regions form this center of origin. Ecological specialization followed a similar pattern.

Center of origin assumptions are as flawed as the commonality principle (common = primitive) that assumes that a character state that occurs in the largest number of taxa within the ingroup is plesiomorphic.

The dynamic and complex nature of interactions between organisms and a varying environment also makes recognizing biotic interchange in the fossil record problematic, especially when regional extinction has occurred.

The bivalve mollusc *Mya arenaria*, for example, has a broad geographical range occurring on both coasts of the Atlantic Ocean and along the east coast of the Pacific Ocean. However, fossils indicate that *M. arenaria* first appeared in the Miocene of the Pacific and invaded the Atlantic during the Pliocene.

Regional extinction of *M. arenaria* along the east coasts of the Pacific and Atlantic Oceans during the Pleistocene left the taxon present only in the western Atlantic. From here, it was reintroduced by human activity into the eastern Pacific and Atlantic Oceans and the Black Sea. An incomplete fossil record or lack of knowledge regarding human introductions could produce a very different interpretation of the biogeographical history of *Mya arenaria* in the northern hemisphere.

Biogeographical studies are complicated by these patterns of biotic interchange, which are some of the most temporally and spatially fluid of all phenomena in organismal biology.

The term biotic interchange has been used to describe the almost instantaneous transfer of a plant virus from a natural forest to an adjacent agricultural field or the wholesale movement of a fauna or flora between continents over millions of years. With such broad usage and scalability it is not surprising that the mechanisms and implications of biotic interchange are often controversial. Biotic interchange begins with the arrival of an individual in a region outside of the taxon’s existing distribution.
Palaeontological studies of biotic interchange document changing distributions of animals and plants through time and correlate these changes with physical and biotic events and perturbations. These patterns may involve species or genera (e.g. the introduction of *Astarte* spp. into the North Pacific), or substantially higher taxonomic categories (e.g. the stampede of Amniota between the Americas). Incomplete biostratigraphy can obviously complicate interpretation, but a much greater danger is the use of taxonomy as a surrogate for phylogeny for recognition and comparison of disjunct biotic patterns.

Whether a taxon has rafted into a new region *via* crustal plate segments or the water column, the "smoking gun" of such an event is the recognition of a relationship between the disjunct taxa. However, most taxa lack a modern phylogenetic treatment and sister taxa status has not been established for many of the classical examples cited in the literature. Hence most workers use ranks within the Linnean classification as a proxy for relatedness in the absence of phylogenetic hypotheses.

Given the danger of confusing common ancestry with convergence, all putative patterns require independent assessment and demonstration of the phyletic relationships amongst the organisms before biotic interchange is invoked.

Modern biogeography also requires the incorporation of knowledge about species' habitat preferences, geographical and population genetical patterns, and their physiological and anatomical basis into this perspective.

The consider of differences or similarities between closely or distantly related species in relation to such properties can be used to explain differences or similarities in geographical distribution or range dynamics.

The consideration of patterns in climatic fluctuation, either over short or long time periods to explain shifts in distribution or changes in range size.

The statistical characteristics of ranges, such as size, location, internal structure, and dynamics are different expressions of the biology of great numbers of living individuals considered together.

Thus, when conditions deteriorate, individuals or their descendants will emigrate to other, more favorable locations, resulting either in local shifts in density, or shifts in the entire range. When conditions change over great expanses of the earth, some ranges may expand, whereas others may contract or vanish. The result of
continuous changes in environmental conditions at different spatial and temporal scales from fine, temporary, and local scales to broad, long-lasting, and global ones, is a “permanent amoeboid creeping of species” over the earth, and this in turn results in “kaleidoscopic changes” in patterns of species ranges relative to each other.

*The study of this endless movement, described in terms of ever-changing environmental conditions, is the heart of biogeography.*