Plate tectonics in biogeography

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Plate tectonics deals with the motions of the Earth•s rocky shell, or lithosphere, which cause the gradual shift of continents and are also responsible for mountain building, volcanic islands, and thermal vents. These geological processes have in uenced the distribution of biodiversity. Prior to the identi cation of a geophysical mechanism that could drive movement at the Earth•s surface, its e ects had been predicted. The concept of •continental driftŽ is usually attributed to Alfred Wegener, who presented his ideas on the origin of continents and oceans in 1915. However, in the 1500s the Belgian mapmaker Abraham Ortelius had noted that the coincidence of the coastal outlines of the Americas, Africa, and Europe implied former juxtaposition. In the 1800s, the •father of biogeographnotable failure of twentieth-century scienti c method. The claim that consideration of the theory required demonstration of a geophysical mechanism was unjusti ed, but was nevertheless assuaged in the 1950s and 1960s when a tectonic model was presented. Today, paleomagnetism, radiometric dating, stratigraphy, and spatial information allow detailed interpretation and paleogeographic reconstruction.

One type of evidence presented in support of continental drift by Wegener and others was (paleo)biogeographic: the widespread distribution of certain fossil animals and plants across landscapes that are now disconnected (Figure 1). However, although widely reiterated even today, the occurrence of fossils did not in truth inform on the process of continental isolation. An alternative idea (land bridging) resolves the spatial discontinuity of biota problem equally well and makes the same biological assumptions. As with continental drift, land bridging assumes that the organisms of interest were unlikely to disperse between patches of suitable habitat. Thus both hypotheses require habitat continuity if species (or their lineages) are to be shared among areas. In biogeography, distribution patterns are often taken as evidence of past processes but they provide only the basis for formulating alternative hypotheses about the processes that might explain them. This is a subtle but vital distinction that underpins scienti c method; a proposition cannot be simultaneously proposed and tested using the same observations.

In later editions of his book, Wegener recognized that his continental drift hypothesis was not to be tested with fossils, or for that matter a coincidence of continental crust outline. Rather, the best approach to testing the hypothesis was geodetics (Earth measurement), because the hypothesis that continents had moved in the past generated the prediction that continents would still be moving. Wegener died in his tent during a trip to Greenland to con rm longitudinal drift,

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side by side with plate tectonic theory. The founding concept of continental drift was that most of the Earth•s land had formerly been connected in a single supercontinent (Pangea). Fossils of Permian age indicate that Pangea existed more than 250 mya, and modern evidence supports this (see Figure 1). In fact the key fossils occur primarily across the southern part of this continent, a region usually referred to as Gondwana (or Gondwanaland), and it is noteworthy that this term was also used by land-bridgers who also envisaged a former extensive continent, parts of which subsequently disappeared. Although the geophysical evidence for a supercontinent is very clear, we now know that it did not include all continental areas at any one time. The idea that past breakup of a supercontinent (up to 200 million years later) could result in the establishment of biotas that are visible today makes many assumptions, among them that a supercontinent would have a homogeneous environment with continuous distributions of plants and animals, that other global events did not cause local changes in biotic assemblages, and that dispersal between continents had little in uence on biological assemblages. In fact, paleoecological evidence indicates diverse and sometimes extreme environmental conditions existed across Pangea. Continental drift itself resulted in changes in climatic conditions so that natural selection on the biota would change, an extreme case being the wholesal0 T* [(edf0.6(,)-329g)20(eme9,)]Tet3 6gntiT* [(r)cclima30. bio07(

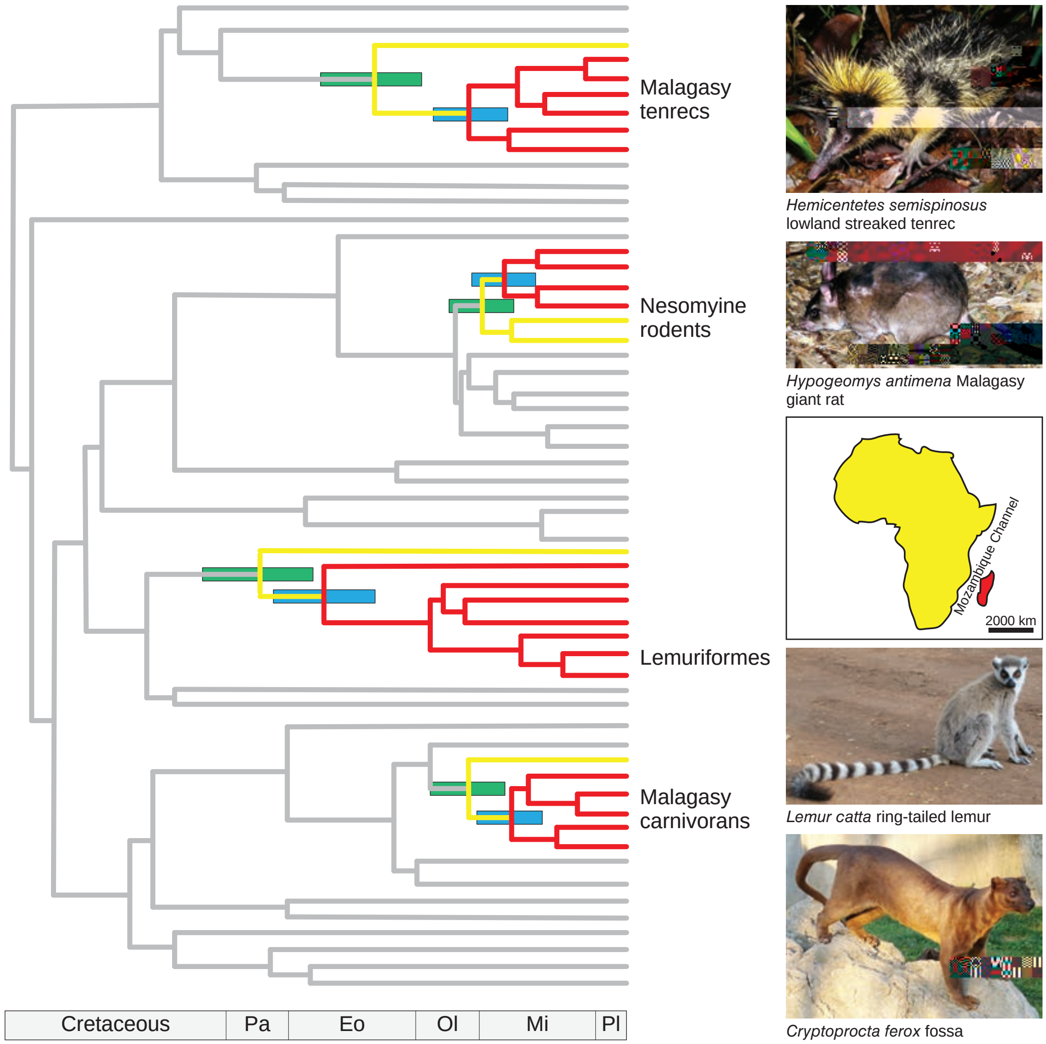

Figure 2 Dated phylogenetic analysis of four Madagascan mammal lineages using multiple nuclear DNA gene sequences and fossil calibrations. Origins and diversi cation of the Madagascan mammal fauna substantially postdate the pre-Cretaceous plate tectonic separation of Madagascar (red) from Africa (yellow). Very di erent dates for each of the mammal groups suggest no single mechanism for their arrival in Madagascar is supported. Tectonic crustal movements may have resulted in some parts of the Mozambique Channel being raised above sea level in the upper Eocene. Although there is no evidence for a continuous land bridge, islands might

populations of marine creatures (and even seabirds that are reluctant to y over land) were split between western Atlantic and eastern Paci c communities. On land, the isthmus led to changes in rainfall and climate patterns and facilitated the exchange of land creatures (a.k.a. the Great American Biotic Interchange). Many animals are inferred to have moved between continents and contributed to biotic mixing and thus elevated biodiversity in Central America.

The late Pliocene formation of the Panama Isthmus demonstrates a way that plate tectonics in uences biogeography, which is counter to the e ects of continental drift vicariance. This geologically, ecologically, and phylogenetically well-studied phenomenon is precisely the type of land bridge proposed by Charles Schuchert and others to explain exchange of biota between continents in past times. Their ideas replaced earlier, simplistic land bridge models that required special, unknown, processes to destroy large parts of continents. Systems similar to the Panama Isthmus might be geologically short-lived and thus hard to detect after the passage of time. Clearly, however, small and short-lived geophysical phenomena can have a profound in uence on biogeography.

Intriguingly, while many mammals appear to have walked between continents once the Panama Isthmus formed, molecular and fossil data indicate that habitat connectivity is not essential for exchange. For example, the best explanation for the initial presence in South America of several mammal lineages involves oversea dispersal from Africa. This includes some that were subsequent North American colonists (e.g., porcupine). The marsupials, for instance, are represented by just one species in

PLATE TECTONICS IN BIOGEOGRAPHY

lowered sea level resulting from water being locked into polar ice caps created land connection in many parts of the world. Habitable continents were linked as recently as 13 000 years ago through features such as the Bering land bridge between Siberia and Alaska that enabled the migration of many plants and animals, including humans.

Mountains

Linear mountain ranges form when continental plates collide, and it is routinely suggested that the formation of mountain ranges is a likely driver of allopatric speciation in terrestrial ecosystems. Populations sundered by geophysical barriers such as mountain ranges could evolve independently of one another if gene ow between them was su ciently impeded. Mountain formation provides an appealing scenario for terrestrial vicariance because it generates abrupt environmental discontinuity (similar to land bridges dividing marine environments). Abrupt changes in environmental conditions are expected to in uence population density, range sizes, and natural selection, but proven examples of the emergence of mountains causing speciation through vicariance are few. Cases where related species occupy habitat either side of mountains provide the expected distribution patterns but might also have resulted from occupation of habitat patches after mountains formed. They might also be the remnants of species distributions that predate mountain formation.

Mountain building contributes to biogeography in another way. The steep environmental gradients and habitat mosaics that mountain ranges produce appear to have stimulated adaptive radiations in many taxa. Examples include alpine buttercups in New Zealand, paper daisies in South Africa, and Andean hummingbirds in South America. Species that evolve to use alpine conditions in one location may also be successful on other ranges where similar ecological opportunities exist even though these are island-like, and this can result in disjunct distributions that are suggestive of vicariance.

Numerous studies in Europe and elsewhere show that plants and animals responded to Pleistocene climate cycling by range shifting, and this is contrary to the idea that mountains (and other geophysical features) routinely make biological barriers. The distribution across Europe of genetic variation within species and species groups shows that only in some cases do some mountain ranges correspond with species limits. In these cases, of course, the mountains are already present but the climate zones and species move. Distinguishing between mountains (and similar features) as drivers of lineage splitting and their longer-term in uence on environmental gradients and ecosystem processes is challenging and exposes a general problem for biogeography. Mountains may come to be correlated with the limits of species and assemblage ranges or they might provide convenient landscape markers that constitute the only major biological systems that do not draw their energy from the sun. Secondary production from Archaea and chemosynthetic bacteria supports faunas that include giant worms, shrimps, clams, and limpets, at depths of 1…4 km below the sea•s surface. The habitat of hydrothermal vent faunas is dictated almost entirely by tectonic processes that result in a patchy distribution around the globe. These islands have histories tens of millions of years long but their biological isolation appears to be in uenced by their chemistry and the ecology of their fauna. Gene ow between invertebrate populations living around widely spaced geothermal vents is mediated by planktonic larvae. Plate tectonic activity may be implicated in the origins of life in the ancient seas of Earth as it has been proposed that the thermal, chemical (e.g., acidity), and physical (e.g., high pressure) conditions around hydrothermal vents could have supplied the environment suitable for initial emergence of replicating organic molecules and protocells. There is evidence for hydrothermal vents in the Earth•s oceans in the appropriate time frame more than 3 billion years ago.

Volcanoes

Oceanic volcanoes create virgin land that is physically separate from existing, inhabited land areas. Although separated froms41ebise many of the details of how this happens remain to be thoroughly tested. A traditional focus on spatial e ects (vicariance) is gradually being replaced by more in-depth analysis of the way geophysical attributes of the planet in uence evolutionary ecology.

SEE ALSO: Biodiversity; Biogeography: history; Mountain biogeography; Ocean biogeography; Zoogeography

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