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Geodiversity: A Theoretical Analysis and Present Status

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ABSTRACT: Geodiversity is the variety of earth materials, forms and processes that constitute and shape the Earth, either the whole or a specific part of it.^[1] Relevant materials include minerals, rocks, sediments, fossils, soils and water.^{[2][3]} Forms may comprise folds, faults, landforms and other expressions of morphology or relations between units of earth material. Any natural process that continues to act upon, maintain or modify either material or form (for example tectonics, sediment transport, pedogenesis) represents another aspect of geodiversity. However geodiversity is not normally defined to include the likes of landscaping, concrete or other significant human influence.^[2]

KEYWORDS-geodiversity, earth, human, pedogenesis, landscape

I. INTRODUCTION

Geodiversity is neither homogeneously distributed nor studied across the planet. The identification of geodiversity hotspots (e.g. the islands of Great Britain and Tasmania) may be indicative not simply of the distribution of geodiversity but also of the status of geoconservation initiatives. In this regard it is worth noting that the biodiversity of an ecosystem stems at least in part from its underlying geology. With the majority of biological species remaining undescribed the classification and quantification of geodiversity is not an abstract exercise in geotaxonomy but a necessary part of mature nature conservation efforts, which also requires a geoethical approach.^[4]

According to Ponciano et al^[5] geoheritage may be in situ (important geosites bearing any exceptional value, such as scientific, cultural, educational, touristic, etc) and ex situ (minerals, fossils, minerals and rocks that were extracted from their origin site and housed in scientific collections and have notable scientific, cultural, educational, touristic or any other value. These authors also consider any extremely valuable reference to these geodiversity elements as ex situ geoheritage, including therefore field notebooks, papers, photographs, maps, dissertations, books, etc. These references often bear historical and scientific value as, for instance, paleontologist Kenneth Caster's field notebooks which provided informations on unknown fossil localities^[6]). Later (2016), José Brilha argues geodiversity may be of scientific value or valued for other aspects. Geodiversity of scientific value can be either geosites or geoheritage elements that are ex situ (not encompassing references to these elements such as dissertations, letters and field notebooks as geoheritage). [1,2] Similarly geodiversity that is of little or no scientific value may be categorized as sites of geodiversity or geodiversity elements that are ex situ.

Geodiversity also constitutes an important part of developing nature-based solutions to global environmental challenges and demands for natural resources. For example, a recent study argued that the acute lack of considering geodiversity in international conventions and monitoring frameworks poses a threat to achieving the UN Sustainable Development Goals.^[7]

Landscape ecology is the science of studying and improving relationships between ecological processes in the environment and particular ecosystems. This is done within a variety of landscape scales, development spatial patterns, and organizational levels of research and policy.^{[1][2][3]} Concisely, landscape ecology can be described as the science of "landscape diversity" as the synergetic result of biodiversity and geodiversity.^[4]

As a highly interdisciplinary field in systems science, landscape ecology integrates biophysical and analytical approaches with humanistic and holistic perspectives across the natural sciences and social sciences. Landscapes are spatially heterogeneous geographic areas characterized by diverse interacting patches or ecosystems, ranging from relatively natural terrestrial and aquatic systems such as forests, grasslands, and lakes to human-dominated environments including agricultural and urban settings.^{[2][5][6]}

The most salient characteristics of landscape ecology are its emphasis on the relationship among pattern, process and scales, and its focus on broad-scale ecological and environmental issues. These necessitate the coupling between

biophysical and socioeconomic sciences. Key research topics in landscape ecology include ecological flows in landscape mosaics, land use and land cover change, scaling, relating landscape pattern analysis with ecological processes, and landscape conservation and sustainability.^[7] Landscape ecology also studies the role of human impacts on landscape diversity in the development and spreading of new human pathogens that could trigger epidemics.^{[8][9]}

Terminology

The German term Landschaftsökologie – thus landscape ecology – was coined by German geographer Carl Troll in 1939.^[10] He developed this terminology and many early concepts of landscape ecology as part of his early work, which consisted of applying aerial photograph interpretation to studies of interactions between environment and vegetation.

Explanation

Heterogeneity is the measure of how parts of a landscape differ from one another. [2,3]Landscape ecology looks at how this spatial structure affects organism abundance at the landscape level, as well as the behavior and functioning of the landscape as a whole. This includes studying the influence of pattern, or the internal order of a landscape, on process, or the continuous operation of functions of organisms.^[11] Landscape ecology also includes geomorphology as applied to the design and architecture of landscapes.^[12] Geomorphology is the study of how geological formations are responsible for the structure of a landscape.

History

Evolution of theory

One central landscape ecology theory originated from MacArthur & Wilson's The Theory of Island Biogeography. This work considered the biodiversity on islands as the result of competing forces of colonization from a mainland stock and stochastic extinction. The concepts of island biogeography were generalized from physical islands to abstract patches of habitat by Levins' metapopulation model (which can be applied e.g. to forest islands in the agricultural landscape^[13]). This generalization spurred the growth of landscape ecology by providing conservation biologists a new tool to assess how habitat fragmentation affects population viability. Recent growth of landscape ecology owes much to the development of geographic information systems (GIS)^[14] and the availability of large-extent habitat data (e.g. remotely sensed datasets).[3,4]

Development as a discipline

Landscape ecology developed in Europe from historical planning on human-dominated landscapes. Concepts from general ecology theory were integrated in North America.^[when?] While general ecology theory and its sub-disciplines focused on the study of more homogenous, discrete community units organized in a hierarchical structure (typically as ecosystems, populations, species, and communities), landscape ecology built upon heterogeneity in space and time. It frequently included human-caused landscape changes in theory and application of concepts.^[15]

By 1980, landscape ecology was a discrete, established discipline. It was marked by the organization of the International Association for Landscape Ecology (IALE) in 1982. Landmark book publications defined the scope and goals of the discipline, including Naveh and Lieberman^[16] and Forman and Godron.^{[17][18]} Forman^[6] wrote that although study of "the ecology of spatial configuration at the human scale" was barely a decade old, there was strong potential for theory development and application of the conceptual framework.

Today, theory and application of landscape ecology continues to develop through a need for innovative applications in a changing landscape and environment. Landscape ecology relies on advanced technologies such as remote sensing, GIS, and models. There has been associated development of powerful quantitative methods to examine the interactions of patterns and processes.^[5] An example would be determining the amount of carbon present in the soil based on landform over a landscape, derived from GIS maps, vegetation types, and rainfall data for a region. Remote sensing work has been used to extend landscape ecology to the field of predictive vegetation mapping, for instance by Janet Franklin.[4,5]

Definitions/conceptions of landscape ecology

Nowadays, at least six different conceptions of landscape ecology can be identified: one group tending toward the more disciplinary concept of ecology (subdiscipline of biology; in conceptions 2, 3, and 4) and another group—characterized

by the interdisciplinary study of relations between human societies and their environment—inclined toward the integrated view of geography (in conceptions 1, 5, and 6):^[19]

1. Interdisciplinary analysis of subjectively defined landscape units (e.g. Neef School^{[20][21]}): Landscapes are defined in terms of uniformity in land use. Landscape ecology explores the landscape's natural potential in terms of functional utility for human societies. To analyse this potential, it is necessary to draw on several natural sciences.
2. Topological ecology at the landscape scale^{[22][23]} 'Landscape' is defined as a heterogeneous land area composed of a cluster of interacting ecosystems (woods, meadows, marshes, villages, etc.) that is repeated in similar form throughout. It is explicitly stated that landscapes are areas at a kilometres wide human scale of perception, modification, etc. Landscape ecology describes and explains the landscapes' characteristic patterns of ecosystems and investigates the flux of energy, mineral nutrients, and species among their component ecosystems, providing important knowledge for addressing land-use issues.
3. Organism-centered, multi-scale topological ecology (e.g. John A. Wiens^{[24][25]}): Explicitly rejecting views expounded by Troll, Zonneveld, Naveh, Forman & Godron, etc., landscape and landscape ecology are defined independently of human perceptions, interests, and modifications of nature. 'Landscape' is defined – regardless of scale – as the 'template' on which spatial patterns influence ecological processes. Not humans, but rather the respective species being studied is the point of reference for what constitutes a landscape.
4. Topological ecology at the landscape level of biological organisation (e.g. Urban et al.^[26]): On the basis of ecological hierarchy theory, it is presupposed that nature is working at multiple scales and has different levels of organisation which are part of a rate-structured, nested hierarchy. Specifically, it is claimed that, above the ecosystem level, a landscape level exists which is generated and identifiable by high interaction intensity between ecosystems, a specific interaction frequency and, typically, a corresponding spatial scale. Landscape ecology is defined as ecology that focuses on the influence exerted by spatial and temporal patterns on the organisation of, and interaction among, functionally integrated multispecies ecosystems.
5. Analysis of social-ecological systems using the natural and social sciences and humanities (e.g. Leser,^[27] Naveh,^{[28][29]} Zonneveld^[30]): Landscape ecology is defined as an interdisciplinary super-science that explores the relationship between human societies and their specific environment, making use of not only various natural sciences, but also social sciences and humanities. This conception is grounded in the assumption that social systems are linked to their specific ambient ecological system in such a way that both systems together form a co-evolutionary, self-organising unity called 'landscape'. Societies' cultural, social and economic dimensions are regarded as an integral part of the global ecological hierarchy, and landscapes are claimed to be the manifest systems of the 'total human ecosystem' (Naveh) which encompasses both the physical ('geospheric') and mental ('noospheric') spheres.
6. Ecology guided by cultural meanings of lifeworldly landscapes (frequently pursued in practice^[31] but not defined, but see, e.g., Hard;^[32] Trepl^[19]): Landscape ecology is defined as ecology that is guided by an external aim, namely, to maintain and develop lifeworldly landscapes. It provides the ecological knowledge necessary to achieve these goals. It investigates how to sustain and develop those populations and ecosystems which (i) are the material 'vehicles' of lifeworldly, aesthetic and symbolic landscapes and, at the same time, (ii) meet societies' functional requirements, including provisioning, regulating, and supporting ecosystem services. Thus landscape ecology is concerned mainly with the populations and ecosystems which have resulted from traditional, regionally specific forms of land use.

Relationship to ecological theory

Some research programmes of landscape ecology theory, namely those standing in the European tradition, may be slightly outside of the "classical and preferred domain of scientific disciplines" because of the large, heterogeneous areas of study. However, general ecology theory is central to landscape ecology theory in many aspects. Landscape ecology consists of four main principles: the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity. The main difference from traditional ecological studies, which frequently assume that systems are spatially homogenous, is the consideration of spatial patterns^[5,6]

II. DISCUSSION

Landscape ecology not only created new terms, but also incorporated existing ecological terms in new ways. Many of the terms used in landscape ecology are as interconnected and interrelated as the discipline itself.

Landscape

Certainly, 'landscape' is a central concept in landscape ecology. It is, however, defined in quite different ways. For example:^[19] Carl Troll conceives of landscape not as a mental construct but as an objectively given 'organic entity', a harmonic individual of space.^[34] Ernst Neef^{[20][21]} defines landscapes as sections within the uninterrupted earth-wide interconnection of geofactors which are defined as such on the basis of their uniformity in terms of a specific land use, and are thus defined in an anthropocentric and relativistic way. According to Richard Forman and Michel Godron,^[22] a landscape is a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout, whereby they list woods, meadows, marshes and villages as examples of a landscape's ecosystems, and state that a landscape is an area at least a few kilometres wide. John A. Wiens^{[24][25]} opposes the traditional view expounded by Carl Troll, Isaak S. Zonneveld, Zev Naveh, Richard T. T. Forman/Michel Godron and others that landscapes are arenas in which humans interact with their environments on a kilometre-wide scale; instead, he defines 'landscape'—regardless of scale—as "the template on which spatial patterns influence ecological processes".^{[25][35]} Some define 'landscape' as an area containing two or more ecosystems in close proximity.^[15]

Scale and heterogeneity (incorporating composition, structure, and function)

A main concept in landscape ecology is scale. Scale represents the real world as translated onto a map, relating distance on a map image and the corresponding distance on earth.^[36] Scale is also the spatial or temporal measure of an object or a process,^[33] or amount of spatial resolution.^[6] Components of scale include composition, structure, and function, which are all important ecological concepts. Applied to landscape ecology, composition refers to the number of patch types (see below) represented on a landscape and their relative abundance. For example, the amount of forest or wetland, the length of forest edge, or the density of roads can be aspects of landscape composition. Structure is determined by the composition, the configuration, and the proportion of different patches across the landscape, while function refers to how each element in the landscape interacts based on its life cycle events.^[33] Pattern is the term for the contents and internal order of a heterogeneous area of land.^[17]

A landscape with structure and pattern implies that it has spatial heterogeneity, or the uneven distribution of objects across the landscape.^[6] Heterogeneity is a key element of landscape ecology that separates this discipline from other branches of ecology. Landscape heterogeneity is able to quantify with agent-based methods as well.^[37]

Patch and mosaic

Patch, a term fundamental to landscape ecology, is defined as a relatively homogeneous area that differs from its surroundings.^[6] Patches are the basic unit of the landscape that change and fluctuate, a process called patch dynamics. Patches have a definite shape and spatial configuration, and can be described compositionally by internal variables such as number of trees, number of tree species, height of trees, or other similar measurements.^[6]

Matrix is the "background ecological system" of a landscape with a high degree of connectivity. Connectivity is the measure of how connected or spatially continuous a corridor, network, or matrix is.^[6] For example, a forested landscape (matrix) with fewer gaps in forest cover (open patches) will have higher connectivity. Corridors have important functions as strips of a particular type of landscape differing from adjacent land on both sides.^[6] A network is an interconnected system of corridors while mosaic describes the pattern of patches, corridors, and matrix that form a landscape in its entirety.^[6]

Boundary and edge

Landscape patches have a boundary between them which can be defined or fuzzy.^[15] The zone composed of the edges of adjacent ecosystems is the boundary.^[6] Edge means the portion of an ecosystem near its perimeter, where influences of the adjacent patches can cause an environmental difference between the interior of the patch and its edge. This edge effect includes a distinctive species composition or abundance.^[6] For example, when a landscape is a mosaic of perceptibly different types, such as a forest adjacent to a grassland, the edge is the location where the two types adjoin. In a continuous landscape, such as a forest giving way to open woodland, the exact edge location is fuzzy and is sometimes determined by a local gradient exceeding a threshold, such as the point where the tree cover falls below thirty-five percent.^[33]

Ecotones, ecoclines, and ecotopes

A type of boundary is the ecotone, or the transitional zone between two communities.^[12] Ecotones can arise naturally, such as a lakeshore, or can be human-created, such as a cleared agricultural field from a forest.^[12] The ecotonal community retains characteristics of each bordering community and often contains species not found in the adjacent communities. Classic examples of ecotones include fencerows, forest to marshlands transitions, forest to grassland transitions, or land-water interfaces such as riparian zones in forests. Characteristics of ecotones include vegetational sharpness, physiognomic change, occurrence of a spatial community mosaic, many exotic species, ecotonal species, spatial mass effect, and species richness higher or lower than either side of the ecotone.^[38]

An ecocline is another type of landscape boundary, but it is a gradual and continuous change in environmental conditions of an ecosystem or community. Ecoclines help explain the distribution and diversity of organisms within a landscape because certain organisms survive better under certain conditions, which change along the ecocline. They contain heterogeneous communities which are considered more environmentally stable than those of ecotones.^[39] An ecotope is a spatial term representing the smallest ecologically distinct unit in mapping and classification of landscapes.^[6] Relatively homogeneous, they are spatially explicit landscape units used to stratify landscapes into ecologically distinct features. They are useful for the measurement and mapping of landscape structure, function, and change over time, and to examine the effects of disturbance and fragmentation.

Disturbance and fragmentation

Disturbance is an event that significantly alters the pattern of variation in the structure or function of a system. Fragmentation is the breaking up of a habitat, ecosystem, or land-use type into smaller parcels.^[6] Disturbance is generally considered a natural process. Fragmentation causes land transformation, an important process in landscapes as development occurs.^[6,7]

An important consequence of repeated, random clearing (whether by natural disturbance or human activity) is that contiguous cover can break down into isolated patches. This happens when the area cleared exceeds a critical level, which means that landscapes exhibit two phases: connected and disconnected.^[40]

Theory

Landscape ecology theory stresses the role of human impacts on landscape structures and functions. It also proposes ways for restoring degraded landscapes.^[16] Landscape ecology explicitly includes humans as entities that cause functional changes on the landscape.^[15] Landscape ecology theory includes the landscape stability principle, which emphasizes the importance of landscape structural heterogeneity in developing resistance to disturbances, recovery from disturbances, and promoting total system stability.^[17] This principle is a major contribution to general ecological theories which highlight the importance of relationships among the various components of the landscape.

Integrity of landscape components helps maintain resistance to external threats, including development and land transformation by human activity.^[5] Analysis of land use change has included a strongly geographical approach which has led to the acceptance of the idea of multifunctional properties of landscapes.^[18] There are still calls for a more unified theory of landscape ecology due to differences in professional opinion among ecologists and its interdisciplinary approach (Bastian 2001).

An important related theory is hierarchy theory, which refers to how systems of discrete functional elements operate when linked at two or more scales. For example, a forested landscape might be hierarchically composed of drainage basins, which in turn are composed of local ecosystems, which are in turn composed of individual trees and gaps.^[6] Recent theoretical developments in landscape ecology have emphasized the relationship between pattern and process, as well as the effect that changes in spatial scale has on the potential to extrapolate information across scales.^[33] Several studies suggest that the landscape has critical thresholds at which ecological processes will show dramatic changes, such as the complete transformation of a landscape by an invasive species due to small changes in temperature characteristics which favor the invasive's habitat requirements.^[33]

Application

Research directions

Developments in landscape ecology illustrate the important relationships between spatial patterns and ecological processes. These developments incorporate quantitative methods that link spatial patterns and ecological processes at

broad spatial and temporal scales. This linkage of time, space, and environmental change can assist managers in applying plans to solve environmental problems.^[5] The increased attention in recent years on spatial dynamics has highlighted the need for new quantitative methods that can analyze patterns, determine the importance of spatially explicit processes, and develop reliable models.^[33] Multivariate analysis techniques are frequently used to examine landscape level vegetation patterns. Studies use statistical techniques, such as cluster analysis, canonical correspondence analysis (CCA), or detrended correspondence analysis (DCA), for classifying vegetation. Gradient analysis is another way to determine the vegetation structure across a landscape or to help delineate critical wetland habitat for conservation or mitigation purposes (Choesin and Boerner 2002).^[41]

Climate change is another major component in structuring current research in landscape ecology.^[42] Ecotones, as a basic unit in landscape studies, may have significance for management under climate change scenarios, since change effects are likely to be seen at ecotones first because of the unstable nature of a fringe habitat.^[38] Research in northern regions has examined landscape ecological processes, such as the accumulation of snow, melting, freeze-thaw action, percolation, soil moisture variation, and temperature regimes through long-term measurements in Norway.^[43] The study analyzes gradients across space and time between ecosystems of the central high mountains to determine relationships between distribution patterns of animals in their environment. Looking at where animals live, and how vegetation shifts over time, may provide insight into changes in snow and ice over long periods of time across the landscape as a whole.

Other landscape-scale studies maintain that human impact is likely the main determinant of landscape pattern over much of the globe.^{[44][45]} Landscapes may become substitutes for biodiversity measures because plant and animal composition differs between samples taken from sites within different landscape categories. Taxa, or different species, can "leak" from one habitat into another, which has implications for landscape ecology. As human land use practices expand and continue to increase the proportion of edges in landscapes, the effects of this leakage across edges on assemblage integrity may become more significant in conservation. This is because taxa may be conserved across landscape levels, if not at local levels.^[46]

Land change modeling

Land change modeling is an application of landscape ecology designed to predict future changes in land use. Land change models are used in urban planning, geography, GIS, and other disciplines to gain a clear understanding of the course of a landscape.^[47] In recent years, much of the Earth's land cover has changed rapidly, whether from deforestation or the expansion of urban areas.^[48]

Relationship to other disciplines[5,6]

Landscape ecology has been incorporated into a variety of ecological subdisciplines. For example, it is closely linked to land change science, the interdisciplinary of land use and land cover change and their effects on surrounding ecology. Another recent development has been the more explicit consideration of spatial concepts and principles applied to the study of lakes, streams, and wetlands in the field of landscape limnology. Seascape ecology is a marine and coastal application of landscape ecology.^[49] In addition, landscape ecology has important links to application-oriented disciplines such as agriculture and forestry. In agriculture, landscape ecology has introduced new options for the management of environmental threats brought about by the intensification of agricultural practices. Agriculture has always been a strong human impact on ecosystems.^[18]

In forestry, from structuring stands for fuelwood and timber to ordering stands across landscapes to enhance aesthetics, consumer needs have affected conservation and use of forested landscapes. Landscape forestry provides methods, concepts, and analytic procedures for landscape forestry.^[50] Landscape ecology has been cited as a contributor to the development of fisheries biology as a distinct biological science discipline,^[51] and is frequently incorporated in study design for wetland delineation in hydrology.^[39] It has helped shape integrated landscape management.^[52] Lastly, landscape ecology has been very influential for progressing sustainability science and sustainable development planning. For example, a recent study assessed sustainable urbanization across Europe using evaluation indices, country-landscapes, and landscape ecology tools and methods.^[53]

Landscape ecology has also been combined with population genetics to form the field of landscape genetics, which addresses how landscape features influence the population structure and gene flow of plant and animal populations across space and time^[54] and on how the quality of intervening landscape, known as "matrix", influences spatial variation.^[55] After the term was coined in 2003, the field of landscape genetics had expanded to over 655 studies by 2010,^[56] and continues to grow today. As genetic data has become more readily accessible, it is increasingly being used

by ecologists to answer novel evolutionary and ecological questions,^[57] many with regard to how landscapes effect evolutionary processes, especially in human-modified landscapes, which are experiencing biodiversity loss.^[58]

III. RESULTS

Biogeography is the study of the distribution of species and ecosystems in geographic space and through geological time. Organisms and biological communities often vary in a regular fashion along geographic gradients of latitude, elevation, isolation and habitat area.^[1] Phytogeography is the branch of biogeography that studies the distribution of plants. Zoogeography is the branch that studies distribution of animals. Mycogeography is the branch that studies distribution of fungi, such as mushrooms.

Knowledge of spatial variation in the numbers and types of organisms is as vital to us today as it was to our early human ancestors, as we adapt to heterogeneous but geographically predictable environments. Biogeography is an integrative field of inquiry that unites concepts and information from ecology, evolutionary biology, taxonomy, geology, physical geography, palaeontology, and climatology.^{[2][3]}

Modern biogeographic research combines information and ideas from many fields, from the physiological and ecological constraints on organismal dispersal to geological and climatological phenomena operating at global spatial scales and evolutionary time frames.

The short-term interactions within a habitat and species of organisms describe the ecological application of biogeography. Historical biogeography describes the long-term, evolutionary periods of time for broader classifications of organisms.^[4] Early scientists, beginning with Carl Linnaeus, contributed to the development of biogeography as a science.

The scientific theory of biogeography grows out of the work of Alexander von Humboldt (1769–1859),^[5] Francisco Jose de Caldas (1768–1816),^[6] Hewett Cottrell Watson (1804–1881),^[7] Alphonse de Candolle (1806–1893),^[8] Alfred Russel Wallace (1823–1913),^[9] Philip Lutley Sclater (1829–1913) and other biologists and explorers.^[10]

Introduction

The patterns of species distribution across geographical areas can usually be explained through a combination of historical factors such as: speciation, extinction, continental drift, and glaciation. Through observing the geographic distribution of species, we can see associated variations in sea level, river routes, habitat, and river capture. Additionally, this science considers the geographic constraints of landmass areas and isolation, as well as the available ecosystem energy supplies.

Over periods of ecological changes, biogeography includes the study of plant and animal species in: their past and/or present living refugium habitat; their interim living sites; and/or their survival locales.^[11] As writer David Quammen put it, "...biogeography does more than ask Which species? and Where. It also asks Why? and, what is sometimes more crucial, Why not?".^[12]

Modern biogeography often employs the use of Geographic Information Systems (GIS), to understand the factors affecting organism distribution, and to predict future trends in organism distribution.^[13] Often mathematical models and GIS are employed to solve ecological problems that have a spatial aspect to them.^[14]

Biogeography is most keenly observed on the world's islands. These habitats are often much more manageable areas of study because they are more condensed than larger ecosystems on the mainland.^[15] Islands are also ideal locations because they allow scientists to look at habitats that new invasive species have only recently colonized and can observe how they disperse throughout the island and change it. They can then apply their understanding to similar but more complex mainland habitats. Islands are very diverse in their biomes, ranging from the tropical to arctic climates. This diversity in habitat allows for a wide range of species study in different parts of the world.

One scientist who recognized the importance of these geographic locations was Charles Darwin, who remarked in his journal "The Zoology of Archipelagoes will be well worth examination".^[15] Two chapters in *On the Origin of Species* were devoted to geographical distribution.^[3,4]

History

18th century

The first discoveries that contributed to the development of biogeography as a science began in the mid-18th century, as Europeans explored the world and described the biodiversity of life. During the 18th century most views on the world were shaped around religion and for many natural theologians, the bible. Carl Linnaeus, in the mid-18th century, improved our classifications of organisms through the exploration of undiscovered territories by his students and disciples. When he noticed that species were not as perpetual as he believed, he developed the Mountain Explanation to explain the distribution of biodiversity; when Noah's ark landed on Mount Ararat and the waters receded, the animals dispersed throughout different elevations on the mountain. This showed different species in different climates proving species were not constant.^[4] Linnaeus' findings set a basis for ecological biogeography. Through his strong beliefs in Christianity, he was inspired to classify the living world, which then gave way to additional accounts of secular views on geographical distribution.^[10] He argued that the structure of an animal was very closely related to its physical surroundings. This was important to a George Louis Buffon's rival theory of distribution.^[10]

Closely after Linnaeus, Georges-Louis Leclerc, Comte de Buffon observed shifts in climate and how species spread across the globe as a result. He was the first to see different groups of organisms in different regions of the world. Buffon saw similarities between some regions which led him to believe that at one point continents were connected and then water separated them and caused differences in species. His hypotheses were described in his work, the 36 volume *Histoire Naturelle, générale et particulière*, in which he argued that varying geographical regions would have different forms of life. This was inspired by his observations comparing the Old and New World, as he determined distinct variations of species from the two regions. Buffon believed there was a single species creation event, and that different regions of the world were homes for varying species, which is an alternate view than that of Linnaeus. Buffon's law eventually became a principle of biogeography by explaining how similar environments were habitats for comparable types of organisms.^[10] Buffon also studied fossils which led him to believe that the earth was over tens of thousands of years old, and that humans had not lived there long in comparison to the age of the earth.^[4]

19th century

Following the period of exploration came the Age of Enlightenment in Europe, which attempted to explain the patterns of biodiversity observed by Buffon and Linnaeus. At the birth of the 19th century, Alexander von Humboldt, known as the "founder of plant geography",^[4] developed the concept of *physique generale* to demonstrate the unity of science and how species fit together. As one of the first to contribute empirical data to the science of biogeography through his travel as an explorer, he observed differences in climate and vegetation. The earth was divided into regions which he defined as tropical, temperate, and arctic and within these regions there were similar forms of vegetation.^[4] This ultimately enabled him to create the isotherm, which allowed scientists to see patterns of life within different climates.^[4] He contributed his observations to findings of botanical geography by previous scientists, and sketched this description of both the biotic and abiotic features of the earth in his book, *Cosmos*.^[10]

Augustin de Candolle contributed to the field of biogeography as he observed species competition and the several differences that influenced the discovery of the diversity of life. He was a Swiss botanist and created the first Laws of Botanical Nomenclature in his work, *Prodromus*.^[16] He discussed plant distribution and his theories eventually had a great impact on Charles Darwin, who was inspired to consider species adaptations and evolution after learning about botanical geography[2,3]. De Candolle was the first to describe the differences between the small-scale and large-scale distribution patterns of organisms around the globe.^[10]

Several additional scientists contributed new theories to further develop the concept of biogeography. Charles Lyell developed the Theory of Uniformitarianism after studying fossils. This theory explained how the world was not created by one sole catastrophic event, but instead from numerous creation events and locations.^[17] Uniformitarianism also introduced the idea that the Earth was actually significantly older than was previously accepted. Using this knowledge, Lyell concluded that it was possible for species to go extinct.^[18] Since he noted that earth's climate changes, he realized that species distribution must also change accordingly. Lyell argued that climate changes complemented vegetation changes, thus connecting the environmental surroundings to varying species. This largely influenced Charles Darwin in his development of the theory of evolution.^[10]

Charles Darwin was a natural theologian who studied around the world, and most importantly in the Galapagos Islands. Darwin introduced the idea of natural selection, as he theorized against previously accepted ideas that species were static or unchanging. His contributions to biogeography and the theory of evolution were different from those of other

explorers of his time, because he developed a mechanism to describe the ways that species changed. His influential ideas include the development of theories regarding the struggle for existence and natural selection. Darwin's theories started a biological segment to biogeography and empirical studies, which enabled future scientists to develop ideas about the geographical distribution of organisms around the globe.^[10]

Alfred Russel Wallace studied the distribution of flora and fauna in the Amazon Basin and the Malay Archipelago in the mid-19th century. His research was essential to the further development of biogeography, and he was later nicknamed the "father of Biogeography". Wallace conducted fieldwork researching the habits, breeding and migration tendencies, and feeding behavior of thousands of species. He studied butterfly and bird distributions in comparison to the presence or absence of geographical barriers. His observations led him to conclude that the number of organisms present in a community was dependent on the amount of food resources in the particular habitat.^[10] Wallace believed species were dynamic by responding to biotic and abiotic factors. He and Philip Sclater saw biogeography as a source of support for the theory of evolution as they used Darwin's conclusion to explain how biogeography was similar to a record of species inheritance.^[10] Key findings, such as the sharp difference in fauna either side of the Wallace Line, and the sharp difference that existed between North and South America prior to their relatively recent faunal interchange, can only be understood in this light. Otherwise, the field of biogeography would be seen as a purely descriptive one.^[4]

20th and 21st century

Moving on to the 20th century, Alfred Wegener introduced the Theory of Continental Drift in 1912, though it was not widely accepted until the 1960s.^[4] This theory was revolutionary because it changed the way that everyone thought about species and their distribution around the globe. The theory explained how continents were formerly joined in one large landmass, Pangea, and slowly drifted apart due to the movement of the plates below Earth's surface. The evidence for this theory is in the geological similarities between varying locations around the globe, the geographic distribution of some fossils (including the mesosaurs) on various continents, and the jigsaw puzzle shape of the landmasses on Earth. Though Wegener did not know the mechanism of this concept of Continental Drift, this contribution to the study of biogeography was significant in the way that it shed light on the importance of environmental and geographic similarities or differences as a result of climate and other pressures on the planet. Importantly, late in his career Wegener recognised that testing his theory required measurement of continental movement rather than inference from fossils species distributions.^[19]

In 1958 paleontologist Paul S. Martin published *A Biogeography of Reptiles and Amphibians in the Gómez Farias Region, Tamaulipas, Mexico*, which has been described as "ground-breaking"^{[20]:35 p.} and "a classic treatise in historical biogeography".^{[21]:311 p.} Martin applied several disciplines including ecology, botany, climatology, geology, and Pleistocene dispersal routes to examine the herpetofauna of a relatively small and largely undisturbed area, but ecologically complex, situated on the threshold of temperate – tropical (nearctic and neotropical) regions, including semiarid lowlands at 70 meters elevation and the northernmost cloud forest in the western hemisphere at over 2200 meters.^{[20][21][22]}

The publication of *The Theory of Island Biogeography* by Robert MacArthur and E.O. Wilson in 1967^[23] showed that the species richness of an area could be predicted in terms of such factors as habitat area, immigration rate and extinction rate. This added to the long-standing interest in island biogeography. The application of island biogeography theory to habitat fragments spurred the development of the fields of conservation biology and landscape ecology.^[24]

Classic biogeography has been expanded by the development of molecular systematics, creating a new discipline known as phylogeography. This development allowed scientists to test theories about the origin and dispersal of populations, such as island endemics. For example, while classic biogeographers were able to speculate about the origins of species in the Hawaiian Islands, phylogeography allows them to test theories of relatedness between these populations and putative source populations on various continents, notably in Asia and North America.^[15]

Biogeography continues as a point of study for many life sciences and geography students worldwide, however it may be under different broader titles within institutions such as ecology or evolutionary biology.

In recent years, one of the most important and consequential developments in biogeography has been to show how multiple organisms, including mammals like monkeys and reptiles like squamates, overcame barriers such as large oceans that many biogeographers formerly believed were impossible to cross.^[25] See also Oceanic dispersal.

Modern applications

Biogeography now incorporates many different fields including but not limited to physical geography, geology, botany and plant biology, zoology, general biology, and modelling. A biogeographer's main focus is on how the environment and humans affect the distribution of species as well as other manifestations of Life such as species or genetic diversity. Biogeography is being applied to biodiversity conservation and planning, projecting global environmental changes on species and biomes, projecting the spread of infectious diseases, invasive species, and for supporting planning for the establishment of crops. Technological evolving and advances have allowed for generating a whole suite of predictor variables for biogeographic analysis, including satellite imaging and processing of the Earth.^[26] Two main types of satellite imaging that are important within modern biogeography are Global Production Efficiency Model (GLO-PEM) and Geographic Information Systems (GIS). GLO-PEM uses satellite-imaging gives "repetitive, spatially contiguous, and time specific observations of vegetation". These observations are on a global scale.^[27] GIS can show certain processes on the earth's surface like whale locations, sea surface temperatures, and bathymetry.^[28] Current scientists also use coral reefs to delve into the history of biogeography through the fossilized reefs.^[1,2]

Two global information systems are either dedicated to, or have strong focus on, biogeography (in the form of the spatial location of observations of organisms), namely the Global Biodiversity Information Facility (GBIF: 2.57 billion species occurrence records reported as at August 2022)^[29] and, for marine species only, the Ocean Biodiversity Information System (OBIS, originally the Ocean Biogeographic Information System: 116 million species occurrence records reported as at August 2022),^[30] while at a national scale, similar compilations of species occurrence records also exist such as the U.K. National Biodiversity Network, the Atlas of Living Australia, and many others. In the case of the oceans, in 2017 Costello et al. analyzed the distribution of 65,000 species of marine animals and plants as then documented in OBIS, and used the results to distinguish 30 distinct marine realms, split between continental-shelf and offshore deep-sea areas.^[31]

Since it is self evident that compilations of species occurrence records cannot cover with any completeness, areas that have received either limited or no sampling, a number of methods have been developed to produce arguably more complete "predictive" or "modelled" distributions for species based on their associated environmental or other preferences (such as availability of food or other habitat requirements); this approach is known as either Environmental niche modelling (ENM) or Species distribution modelling (SDM). Depending on the reliability of the source data and the nature of the models employed (including the scales for which data are available), maps generated from such models may then provide better representations of the "real" biogeographic distributions of either individual species, groups of species, or biodiversity as a whole, however it should also be borne in mind that historic or recent human activities (such as hunting of great whales, or other human-induced exterminations) may have altered present-day species distributions from their potential "full" ecological footprint. Examples of predictive maps produced by niche modelling methods based on either GBIF (terrestrial) or OBIS (marine, plus some freshwater) data are the former Lifemapper project at the University of Kansas (now continued as a part of BiotaPhy^[32]) and AquaMaps, which as at 2022 contain modelled distributions for around 200,000 terrestrial, and 33,000 species of teleosts, marine mammals and invertebrates, respectively.^{[32][33]} One advantage of ENM/SDM is that in addition to showing current (or even past) modelled distributions, insertion of changed parameters such as the anticipated effects of climate change can also be used to show potential changes in species distributions that may occur in the future based on such scenarios.^[34]

Paleobiogeography

Paleobiogeography goes one step further to include paleogeographic data and considerations of plate tectonics. Using molecular analyses and corroborated by fossils, it has been possible to demonstrate that perching birds evolved first in the region of Australia or the adjacent Antarctic (which at that time lay somewhat further north and had a temperate climate). From there, they spread to the other Gondwanan continents and Southeast Asia – the part of Laurasia then closest to their origin of dispersal – in the late Paleogene, before achieving a global distribution in the early Neogene.^[35] Not knowing that at the time of dispersal, the Indian Ocean was much narrower than it is today, and that South America was closer to the Antarctic, one would be hard pressed to explain the presence of many "ancient" lineages of perching birds in Africa, as well as the mainly South American distribution of the suboscines.

Paleobiogeography also helps constrain hypotheses on the timing of biogeographic events such as vicariance and geodispersal, and provides unique information on the formation of regional biotas. For example, data from species-level phylogenetic and biogeographic studies tell us that the Amazonian teleost fauna accumulated in

increments over a period of tens of millions of years, principally by means of allopatric speciation, and in an arena extending over most of the area of tropical South America (Albert & Reis 2011). In other words, unlike some of the well-known insular faunas (Galapagos finches, Hawaiian drosophilid flies, African rift lake cichlids), the species-rich Amazonian ichthyofauna is not the result of recent adaptive radiations.^[36]

For freshwater organisms, landscapes are divided naturally into discrete drainage basins by watersheds, episodically isolated and reunited by erosional processes. In regions like the Amazon Basin (or more generally Greater Amazonia, the Amazon basin, Orinoco basin, and Guianas) with an exceptionally low (flat) topographic relief, the many waterways have had a highly reticulated history over geological time. In such a context, stream capture is an important factor affecting the evolution and distribution of freshwater organisms. Stream capture occurs when an upstream portion of one river drainage is diverted to the downstream portion of an adjacent basin. This can happen as a result of tectonic uplift (or subsidence), natural damming created by a landslide, or headward or lateral erosion of the watershed between adjacent basins.^[36]

Concepts and fields

Biogeography is a synthetic science, related to geography, biology, soil science, geology, climatology, ecology and evolution.

Some fundamental concepts in biogeography include:

- allopatric speciation – the splitting of a species by evolution of geographically isolated populations
- evolution – change in genetic composition of a population
- extinction – disappearance of a species
- dispersal – movement of populations away from their point of origin, related to migration
- endemic areas
- geodispersal – the erosion of barriers to biotic dispersal and gene flow, that permit range expansion and the merging of previously isolated biotas
- range and distribution
- vicariance – the formation of barriers to biotic dispersal and gene flow, that tend to subdivide species and biotas, leading to speciation and extinction; vicariance biogeography is the field that studies these patterns

Comparative biogeography[4,5]

The study of comparative biogeography can follow two main lines of investigation:^[37]

- Systematic biogeography, the study of biotic area relationships, their distribution, and hierarchical classification
- Evolutionary biogeography, the proposal of evolutionary mechanisms responsible for organismal distributions. Possible mechanisms include widespread taxa disrupted by continental break-up or individual episodes of long-distance movement.

Biogeographic regionalisations

There are many types of biogeographic units used in biogeographic regionalisation schemes,^{[38][39][40]} as there are many criteria (species composition, physiognomy, ecological aspects) and hierarchization schemes: biogeographic realms (ecozones), bioregions (sensu stricto), ecoregions, zoogeographical regions, floristic regions, vegetation types, biomes, etc.

The terms biogeographic unit,^[41] biogeographic area^[42] or bioregion sensu lato,^[43] can be used for these categories, regardless of rank.

In 2008, an International Code of Area Nomenclature was proposed for biogeography.^{[44][45][46]} It achieved limited success; some studies commented favorably on it, but others were much more critical,^[47] and it "has not yet gained a significant following".^[48] Similarly, a set of rules for paleobiogeography^[49] has achieved limited success.^{[48][50]} In 2000, Westermann suggested that the difficulties in getting formal nomenclatural rules established in this field might be related to "the curious fact that neither paleo- nor neobiogeographers are organized in any formal groupings or societies, nationally (so far as I know) or internationally — an exception among active disciplines."^[51]

IV. CONCLUSION

Geobiology is a field of scientific research that explores the interactions between the physical Earth and the biosphere. It is a relatively young field, and its borders are fluid. There is considerable overlap with the fields of ecology, evolutionary biology, microbiology, paleontology, and particularly soil science and biogeochemistry. Geobiology applies the principles and methods of biology, geology, and soil science to the study of the ancient history of the co-evolution of life and Earth as well as the role of life in the modern world.^[2] Geobiologic studies tend to be focused on microorganisms, and on the role that life plays in altering the chemical and physical environment of the pedosphere, which exists at the intersection of the lithosphere, atmosphere, hydrosphere and/or cryosphere. It differs from biogeochemistry in that the focus is on processes and organisms over space and time rather than on global chemical cycles.

Geobiological research synthesizes the geologic record with modern biologic studies. It deals with process - how organisms affect the Earth and vice versa - as well as history - how the Earth and life have changed together. Much research is grounded in the search for fundamental understanding, but geobiology can also be applied, as in the case of microbes that clean up oil spills.^[3]

Geobiology employs molecular biology, environmental microbiology, organic geochemistry, and the geologic record to investigate the evolutionary interconnectedness of life and Earth. It attempts to understand how the Earth has changed since the origin of life and what it might have been like along the way. Some definitions of geobiology even push the boundaries of this time frame - to understanding the origin of life and to the role that humans have played and will continue to play in shaping the Earth in the Anthropocene.^[3]

History

The term geobiology was coined by Lourens Baas Becking in 1934. In his words, geobiology "is an attempt to describe the relationship between organisms and the Earth," for "the organism is part of the Earth and its lot is interwoven with that of the Earth." Baas Becking's definition of geobiology was born of a desire to unify environmental biology with laboratory biology. The way he practiced it aligns closely with modern environmental microbial ecology, though his definition remains applicable to all of geobiology. In his book, *Geobiology*, Baas Becking stated that he had no intention of inventing a new field of study.^[4] Baas Becking's understanding of geobiology was heavily influenced by his predecessors, including Martinus Beijerinck, his teacher from the Dutch School of Microbiology. Others included Vladimir Vernadsky, who argued that life changes the surface environment of Earth in *The Biosphere*, his 1926 book,^[5] and Sergei Vinogradsky, famous for discovering lithotrophic bacteria.^[6]

The first laboratory officially dedicated to the study of geobiology was the Baas Becking Geobiological Laboratory in Australia, which opened its doors in 1965.^[4] However, it took another 40 or so years for geobiology to become a firmly rooted scientific discipline, thanks in part to advances in geochemistry and genetics that enabled scientists to begin to synthesize the study of life and planet.

In the 1930s, Alfred Treibs discovered chlorophyll-like porphyrins in petroleum, confirming its biological origin,^[7] thereby founding organic geochemistry and establishing the notion of biomarkers, a critical aspect of geobiology. But several decades passed before the tools were available to begin to search in earnest for chemical marks of life in the rocks. In the 1970s and '80s, scientists like Geoffrey Eglington and Roger Summons began to find lipid biomarkers in the rock record using equipment like GCMS.^[8]

On the biology side of things, in 1977, Carl Woese and George Fox published a phylogeny of life on Earth, including a new domain - the Archaea.^[9] And in the 1990s, genetics and genomics studies became possible, broadening the scope of investigation of the interaction of life and planet.

Today, geobiology has its own journals, such as *Geobiology*, established in 2003,^[10] and *Biogeosciences*, established in 2004,^[11] as well as recognition at major scientific conferences. It got its own Gordon Research Conference in 2011,^[12] a number of geobiology textbooks have been published,^{[3][13]} and many universities around the world offer degree programs in geobiology (see External links).

Major geobiological events

The geologic timescale overlain with major geobiologic events and occurrences. The oxygenation of the atmosphere is shown in blue starting 2.4 Ga, although the exact dating of the Great Oxygenation Event is debated.^[14]

Perhaps the most profound geobiological event is the introduction of oxygen into the atmosphere by photosynthetic bacteria. This oxygenation of Earth's primordial atmosphere (the so-called oxygen catastrophe or Great Oxygenation Event) and the oxygenation of the oceans altered surface biogeochemical cycles and the types of organisms that have been evolutionarily selected for.

A subsequent major change was the advent of multicellularity. The presence of oxygen allowed eukaryotes and, later, multicellular life to evolve.

More anthropocentric geobiologic events include the origin of animals and the establishment of terrestrial plant life, which affected continental erosion and nutrient cycling, and likely changed the types of rivers observed, allowing channelization of what were previously predominantly braided rivers.

More subtle geobiological events include the role of termites in overturning sediments, coral reefs in depositing calcium carbonate and breaking waves, sponges in absorbing dissolved marine silica, the role of dinosaurs in breaching river levees and promoting flooding, and the role of large mammal dung in distributing nutrients.^{[15][16]}

Important concepts

Geobiology is founded upon a few core concepts that unite the study of Earth and life. While there are many aspects of studying past and present interactions between life and Earth that are unclear, several important ideas and concepts provide a basis of knowledge in geobiology that serve as a platform for posing researchable questions, including the evolution of life and planet and the co-evolution of the two, genetics - from both a historical and functional standpoint, the metabolic diversity of all life, the sedimentological preservation of past life, and the origin of life.

Co-evolution of life and Earth

A core concept in geobiology is that life changes over time through evolution. The theory of evolution postulates that unique populations of organisms or species arose from genetic modifications in the ancestral population which were passed down by drift and natural selection.^[17]

Along with standard biological evolution, life and planet co-evolve. Since the best adaptations are those that suit the ecological niche that the organism lives in, the physical and chemical characteristics of the environment drive the evolution of life by natural selection, but the opposite can also be true: with every advent of evolution, the environment changes.

A classic example of co-evolution is the evolution of oxygen-producing photosynthetic cyanobacteria which oxygenated Earth's Archean atmosphere. The ancestors of cyanobacteria began using water as an electron source to harness the energy of the sun and expelling oxygen before or during the early Paleoproterozoic. During this time, around 2.4 to 2.1 billion years ago,^[18] geologic data suggests that atmospheric oxygen began to rise in what is termed the Great Oxygenation Event (GOE).^{[19][20]} It is unclear for how long cyanobacteria had been doing oxygenic photosynthesis before the GOE. Some evidence suggests there were geochemical "buffers" or sinks suppressing the rise of oxygen such as volcanism^[21] though cyanobacteria may have been around producing it before the GOE.^[22] Other evidence indicates that the rise of oxygenic photosynthesis was coincident with the GOE.^[23]

The presence of oxygen on Earth from its first production by cyanobacteria to the GOE and through today has drastically impacted the course of evolution of life and planet.^[19] It may have triggered the formation of oxidized minerals^[24] and the disappearance of oxidizable minerals like pyrite from ancient stream beds.^[25] The presence of banded-iron formations (BIFs) have been interpreted as a clue for the rise of oxygen since small amounts of oxygen could have reacted with reduced ferrous iron (Fe(II)) in the oceans, resulting in the deposition of sediments containing Fe(III) oxide in places like Western Australia.^[26] However, any oxidizing environment, including that provided by microbes such as the iron-oxidizing photoautotroph *Rhodospirillum rubrum*,^[27] can trigger iron oxide formation and thus BIF deposition.^{[28][29][30]} Other mechanisms include oxidation by UV light.^[31] Indeed, BIFs occur across large swaths of Earth's history and may not correlate with only one event.^[30]

Other changes correlated with the rise of oxygen include the appearance of rust-red ancient paleosols,^[19] different isotope fractionation of elements such as sulfur,^[32] and global glaciations and Snowball Earth events,^[33] perhaps caused by the oxidation of methane by oxygen, not to mention an overhaul of the types of organisms and metabolisms on Earth. Whereas organisms prior to the rise of oxygen were likely poisoned by oxygen gas as many anaerobes are today,^[34] those that evolved ways to harness the electron-accepting and energy-giving power of oxygen were poised to thrive and colonize the aerobic environment.

The Earth has changed

Earth has not remained the same since its planetary formation 4.5 billion years ago.^{[35][36]} Continents have formed, broken up, and collided, offering new opportunities for and barriers to the dispersal of life. The redox state of the atmosphere and the oceans has changed, as indicated by isotope data. Fluctuating quantities of inorganic compounds such as carbon dioxide, nitrogen, methane, and oxygen have been driven by life evolving new biological metabolisms to make these chemicals and have driven the evolution of new metabolisms to use those chemicals. Earth acquired a magnetic field about 3.4 Ga^[37] that has undergone a series of geomagnetic reversals on the order of millions of years.^[38] The surface temperature is in constant fluctuation, falling in glaciations and Snowball Earth events due to ice–albedo feedback,^[39] rising and melting due to volcanic outgassing, and stabilizing due to silicate weathering feedback.^[40]

And the Earth is not the only one that changed - the luminosity of the sun has increased over time. Because rocks record a history of relatively constant temperatures since Earth's beginnings, there must have been more greenhouse gasses to keep the temperatures up in the Archean when the sun was younger and fainter.^[41] All these major differences in the environment of the Earth placed very different constraints on the evolution of life throughout our planet's history. Moreover, more subtle changes in the habitat of life are always occurring, shaping the organisms and traces that we observe today and in the rock record.

Genes encode geobiological function and history

The genetic code is key to observing the history of evolution and understanding the capabilities of organisms. Genes are the basic unit of inheritance and function and, as such, they are the basic unit of evolution and the means behind metabolism.^[42]

Phylogeny predicts evolutionary history

Phylogeny takes genetic sequences from living organisms and compares them to each other to reveal evolutionary relationships, much like a family tree reveals how individuals are connected to their distant cousins.^[43] It allows us to decipher modern relationships and infer how evolution happened in the past.

Phylogeny can give some sense of history when combined with a little bit more information. Each difference in the DNA indicates divergence between one species and another.^[43] This divergence, whether via drift or natural selection, is representative of some lapse of time.^[43] Comparing DNA sequences alone gives a record of the history of evolution with an arbitrary measure of phylogenetic distance “dating” that last common ancestor. However, if information about the rate of genetic mutation is available or geologic markers are present to calibrate evolutionary divergence (i.e. fossils), we have a timeline of evolution.^[44] From there, with an idea about other contemporaneous changes in life and environment, we can begin to speculate why certain evolutionary paths might have been selected for.^[45]

Genes encode metabolism

Molecular biology allows scientists to understand a gene's function using microbial culturing and mutagenesis. Searching for similar genes in other organisms and in metagenomic and metatranscriptomic data allows us to understand what processes could be relevant and important in a given ecosystem, providing insight into the biogeochemical cycles in that environment.

For example, an intriguing problem in geobiology is the role of organisms in the global cycling of methane. Genetics has revealed that the methane monooxygenase gene (pmo) is used for oxidizing methane and is present in all aerobic methane-oxidizers, or methanotrophs.^[46] The presence of DNA sequences of the pmo gene in the environment can be used as a proxy for methanotrophy.^{[47][48]} A more generalizable tool is the 16S ribosomal RNA gene, which is found in bacteria and archaea. This gene evolves very slowly over time and is not usually horizontally transferred, and so it is often used to distinguish different taxonomic units of organisms in the environment.^{[9][49]} In this way, genes are clues to organismal metabolism and identity. Genetics enables us to ask 'who is there?' and 'what are they doing?' This approach is called metagenomics.^[49]

Metabolic diversity influences the environment

Life harnesses chemical reactions to generate energy, perform biosynthesis, and eliminate waste.^[52] Different organisms use very different metabolic approaches to meet these basic needs.^[53] While animals such as ourselves are limited to aerobic respiration, other organisms can "breathe" sulfate (SO₄²⁻), nitrate (NO₃⁻), ferric iron (Fe(III)), and uranium (U(VI)), or live off energy from fermentation.^[53] Some organisms, like plants, are autotrophs, meaning

that they can fix carbon dioxide for biosynthesis. Plants are photoautotrophs, in that they use the energy of light to fix carbon. Microorganisms employ oxygenic and anoxygenic photoautotrophy, as well as chemoautotrophy. Microbial communities can coordinate in syntrophic metabolisms to shift reaction kinetics in their favor. Many organisms can perform multiple metabolisms to achieve the same end goal; these are called mixotrophs.^[53]

Biotic metabolism is directly tied to the global cycling of elements and compounds on Earth. The geochemical environment fuels life, which then produces different molecules that go into the external environment. (This is directly relevant to biogeochemistry.) In addition, biochemical reactions are catalyzed by enzymes which sometimes prefer one isotope over others. For example, oxygenic photosynthesis is catalyzed by RuBisCO, which prefers carbon-12 over carbon-13, resulting in carbon isotope fractionation in the rock record.^[54]

Sedimentary rocks tell a story

Sedimentary rocks preserve remnants of the history of life on Earth in the form of fossils, biomarkers, isotopes, and other traces. The rock record is far from perfect, and the preservation of biosignatures is a rare occurrence. Understanding what factors determine the extent of preservation and the meaning behind what is preserved are important components to detangling the ancient history of the co-evolution of life and Earth.^[8] The sedimentary record allows scientists to observe changes in life and Earth in composition over time and sometimes even date major transitions, like extinction events.

Some classic examples of geobiology in the sedimentary record include stromatolites and banded-iron formations. The role of life in the origin of both of these is a heavily debated topic.^[19]

Life is fundamentally chemistry

The first life arose from abiotic chemical reactions. When this happened, how it happened, and even what planet it happened on are uncertain. However, life follows the rules of and arose from lifeless chemistry and physics. It is constrained by principles such as thermodynamics. This is an important concept in the field because it represents the epitome of the interconnectedness, if not sameness, of life and Earth.^[55]

While often delegated to the field of astrobiology, attempts to understand how and when life arose are relevant to geobiology as well.^[56] The first major strides towards understanding the “how” came with the Miller-Urey experiment, when amino acids formed out of a simulated “primordial soup”. Another theory is that life originated in a system much like the hydrothermal vents at mid-oceanic spreading centers. In the Fischer-Tropsch synthesis, a variety of hydrocarbons form under vent-like conditions. Other ideas include the “RNA World” hypothesis, which postulates that the first biologic molecule was RNA, and the idea that life originated elsewhere in the solar system and was brought to Earth, perhaps via a meteorite.^[55]

Methodology

While geobiology is a diverse and varied field, encompassing ideas and techniques from a wide range of disciplines, there are a number of important methods that are key to the study of the interaction of life and Earth that are highlighted here.^[3]

1. Laboratory culturing of microbes is used to characterize the metabolism and lifestyle of organisms of interest.
2. Gene sequencing allows scientists to study the relationships between extant organisms using phylogenetics.
3. Experimental genetic manipulation or mutagenesis is used to determine the function of genes in living organisms.
4. Microscopy is used to visualize the microbial world. Microscope work ranges from environmental observation to quantitative studies with DNA probes to high-definition visualization of the microbe-mineral interface by electron microscope (EM).
5. Isotope tracers can be used to track biochemical reactions to understand microbial metabolism.
6. Isotope natural abundance in rocks can be measured to look for isotopic fractionation that is consistent with biologic origin.
7. Detailed environmental characterization is important to understanding what about a habitat might be driving life's evolution and, in turn, how life might be changing that niche. It includes and is not limited to, temperature, light, pH, salinity, concentration of specific molecules like oxygen, and the biologic community.

8. Sedimentology and stratigraphy are used to read the rocks. The rock record stores a history of geobiologic processes in sediments which can be unearthed through an understanding of deposition, sedimentation, compaction, diagenesis, and deformation.
9. The search for and study of fossils, while often delegated to the separate field of paleontology, is important in geobiology, though the scale of fossils is typically smaller (micropaleontology).
10. The biochemical analysis of biomarkers, which are fossilized or modern molecules that are indicative of the presence of a certain group of organisms or metabolism, is used to answer the evidence for life and metabolic diversity questions.^[8]
11. Paleomagnetism is the study of the planet's ancient magnetic field. It is significant to understanding magnetofossils, biomineralization, and global ecosystem changes.

Sub-disciplines and related fields

As its name suggests, geobiology is closely related to many other fields of study, and does not have clearly defined boundaries or perfect agreement on what exactly they comprise. Some practitioners take a very broad view of its boundaries, encompassing many older, more established fields such as biogeochemistry, paleontology, and microbial ecology. Others take a more narrow view, assigning it to emerging research that falls between these existing fields, such as with geomicrobiology. The following list includes both those that are clearly a part of geobiology, e.g. geomicrobiology, as well as those that share scientific interests but have not historically been considered a sub-discipline of geobiology, e.g. paleontology.

Astrobiology

Astrobiology is an interdisciplinary field that uses a combination of geobiological and planetary science data to establish a context for the search for life on other planets. The origin of life from non-living chemistry and geology, or abiogenesis, is a major topic in astrobiology. Even though it is fundamentally an earth-bound concern, and therefore of great geobiological interest, getting at the origin of life necessitates considering what life requires, what, if anything, is special about Earth, what might have changed to allow life to blossom, what constitutes evidence for life, and even what constitutes life itself. These are the same questions that scientists might ask when searching for alien life. In addition, astrobiologists research the possibility of life based on other metabolisms and elements, the survivability of Earth's organisms on other planets or spacecraft, planetary and solar system evolution, and space geochemistry.^[57]

Biogeochemistry

Biogeochemistry is a systems science that synthesizes the study of biological, geological, and chemical processes to understand the reactions and composition of the natural environment. It is concerned primarily with global elemental cycles, such as that of nitrogen and carbon. The father of biogeochemistry was James Lovelock, whose "Gaia hypothesis" proposed that Earth's biological, chemical, and geologic systems interact to stabilize the conditions on Earth that support life.^[58]

Geobiochemistry

Geobiochemistry is similar to biogeochemistry, but differs by placing emphasis on the effects of geology on the development of life's biochemical processes, as distinct from the role of life on Earth's cycles. Its primary goal is to link biological changes, encompassing evolutionary modifications of genes and changes in the expression of genes and proteins, to changes in the temperature, pressure, and composition of geochemical processes to understand when and how metabolism evolved. Geobiochemistry is founded on the notion that life is a planetary response because metabolic catalysis enables the release of energy trapped by a cooling planet.^[59]

Environmental microbiology

Microbiology is a broad scientific discipline pertaining to the study of that life which is best viewed under a microscope. It encompasses several fields that are of direct relevance to geobiology, and the tools of microbiology all pertain to geobiology. Environmental microbiology is especially entangled in geobiology since it seeks an understanding of the actual organisms and processes that are relevant in nature, as opposed to the traditional lab-based approach to microbiology. Microbial ecology is similar, but tend to focus more on lab studies and the relationships between organisms within a community, as well as within the ecosystem of their chemical and geological physical environment. Both rely on techniques such as sample collection from diverse environments, metagenomics, DNA sequencing, and statistics.

Geomicrobiology and microbial geochemistry

Geomicrobiology traditionally studies the interactions between microbes and minerals. While it is generally reliant on the tools of microbiology, microbial geochemistry uses geological and chemical methods to approach the same topic from the perspective of the rocks. Geomicrobiology and microbial geochemistry (GMG) is a relatively new interdisciplinary field that more broadly takes on the relationship between microbes, Earth, and environmental systems. Billed as a subset of both geobiology and geochemistry, GMG seeks to understand elemental biogeochemical cycles and the evolution of life on Earth. Specifically, it asks questions about where microbes live, their local and global abundance, their structural and functional biochemistry, how they have evolved, biomineralization, and their preservation potential and presence in the rock record. In many ways, GMG appears to be equivalent to geobiology, but differs in scope: geobiology focuses on the role of all life, while GMG is strictly microbial. Regardless, it is these tiniest creatures that dominated to history of life integrated over time and seem to have had the most far-reaching effects.^[60]

Molecular geomicrobiology

Molecular geomicrobiology takes a mechanistic approach to understanding biological processes that are geologically relevant. It can be at the level of DNA, protein, lipids, or any metabolite. One example of Molecular geomicrobiology research is studying how recently created lava fields are colonized by microbes. The University of Helsinki is currently conducting research to determine what specific microbial traits are necessary for successful initial colonization, and how waves of microbial succession can transform the volcanic rock into fertile soil.^[61]

Organic geochemistry

Organic geochemistry is the study of organic molecules that appear in the fossil record in sedimentary rocks. Research in this field concerns molecular fossils that are often lipid biomarkers. Molecules like sterols and hopanoids, membrane lipids found in eukaryotes and bacteria, respectively, can be preserved in the rock record on billion-year timescales. Following the death of the organism they came from and sedimentation, they undergo a process called diagenesis whereby many of the specific functional groups from the lipids are lost, but the hydrocarbon skeleton remains intact. These fossilized lipids are called steranes and hopanes, respectively.^[62] There are also other types of molecular fossils, like porphyrins, the discovery of which in petroleum by Alfred E. Treibs actually led to the invention of the field.^[8] Other aspects of geochemistry that are also pertinent to geobiology include isotope geochemistry, in which scientists search for isotope fractionation in the rock record, and the chemical analysis of biominerals, such as magnetite or microbially-precipitated gold.

Paleontology

Perhaps the oldest of the bunch, paleontology is the study of fossils. It involves the discovery, excavation, dating, and paleoecological understanding of any type of fossil, microbial or dinosaur, trace or body fossil. Micropaleontology is particularly relevant to geobiology. Putative bacterial microfossils and ancient stromatolites are used as evidence for the rise of metabolisms such as oxygenic photosynthesis.^[63] The search for molecular fossils, such as lipid biomarkers like steranes and hopanes, has also played an important role in geobiology and organic geochemistry.^[8] Relevant sub-disciplines include paleoecology and paleobiogeography.

Biogeography

Biogeography is the study of the geographic distribution of life through time. It can look at the present distribution of organisms across continents or between microniches, or the distribution of organisms through time, or in the past, which is called paleobiogeography.

Evolutionary biology

Evolutionary biology is the study of the evolutionary processes that have shaped the diversity of life on Earth. It incorporates genetics, ecology, biogeography, and paleontology to analyze topics including natural selection, variance, adaptation, divergence, genetic drift, and speciation.

Ecohydrology

Ecohydrology is an interdisciplinary field studying the interactions between water and ecosystems. Stable isotopes of water are sometimes used as tracers of water sources and flow paths between the physical environment and the biosphere.^[7]



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