

THE DEVELOPMENT HISTORY OF BIOGEOGRAPHY

S.N. Wickramaratne

Department of Geography, University of Peradeniya, Peradeniya.

Abstract

Biogeography is a major branch of geography, often considered a sub-division of physical geography. This paper is a qualitative review of the historical perspective of its development.

Although there is no conspicuous beginning to this subject it is clear that ideas pertaining to the geography of biota have a history running back to the pre-Christina era. This paper identifies five periods in the history of emergence of biogeography; early historic period, classical period, late modern to early modern period, modern period and the beginning of the 21st century.

In the earliest days the subject was not a distinct discipline, but had gradually acquired a natural history tradition with accumulating knowledge on the distribution of plants and animals. It was with the great conditions of Alexander von Humboldt that biogeography became a clear branch of geography. Since then, it grew based on evolutionary and ecological theories.

Since the late-middle of the 20th century, biogeography became prominent within the main discipline of geography due advancements in geosciences and the growing environmental awareness.

At the onset of the 21st century is has become a subject of immense breadth and remains a strong branch of geography, ecology and earth sciences in the developed countries. Although currently it is a minor sub-division of geography in Sri Lanka, a growth in the subject can be expected in the forthcoming years due to the revival of geography in the curricula.

Introduction

'The science of geography is likely the oldest of all sciences' (Rosenberg 2006). It was the Greek scholar Eratosthenes who in the 3rd century BC first used the term *geography* to denote that branch of knowledge concerned with the description of the Earth. Geography is the causal interpretation of the earth's spatial diversity. According to Richard Hartshorne it is not either

a natural or social science, but a study of intimately mixed phenomena. Thus, geography stands as a 'holistic' discipline.

There is a number of sub-fields in geography that conventionally stand out in relation to the inappropriate physical-human dichotomy. Those sub-fields exemplified by geomorphology, climatology, soil geography etc. are considered areas of physical geography whereas economic geography, population geography, urban geography etc. falls into the human geography stream.

This paper is a qualitative review of the historical perspective in the development of biogeography, that branch of geography primarily dealing with biota. It attempts to identify in the chronological order some of the innumerable seminal works that have shaped the subject, although there is no definite beginning to the subject.

Early Historic Period

Although it is extremely difficult to trace the earliest records of plants and animals, it is believed that Emperor Huang-di or Huang-ti (2697-2599 BC) of China who made many inventions and investigated natural phenomena identified minerals and plants (Agatucci 1998). Clay tablets of the *Mohendojaro* civilization that flourished 2600-1900 BC have documented many species of now locally extinct wildlife including the Rhinoceros and the Elephant while the *Vedas* of India (1500-500 BC) are known to have documented birds and other fauna and flora (*Wikipedia Encyclopedia*).

Classical Period

However, the emergence of ideas directly pertinent to biogeography can be traced back to Greek philosophers who pioneered the subject of natural history. Aristotle (384-322 BC) for instance, attempted classifying organisms. He divided living organisms into the kingdoms of plants and animals, whereas micro organisms were unknown then. He further divided animals into two categories; those with blood and those without blood. These two categories approximately correspond to the vertebrates and invertebrates in modern classifications (*Microsoft Encarta Encyclopaedia* 2004). Another contribution he made is the classification of the earth into three principal latitudinal climatic zones; Torrid Zone (between 23.5 N and S and Temperate Zone between 23.5 and 66.5 and Frigid Zone beyond 66.5 in each hemisphere (Rosenberg - undated). Later, Theophrastus (372-287 BC), a pupil of Aristotle who studied the vegetation of eastern Mediterranean, for example, had some important ideas bearing on biogeography. He categorized plants as 'trees', 'shrubs', and 'herbs' (thus providing the first 'physiognomic' classification of plant life-forms) and

even described the interrelationships between organisms and their abiotic environment. Moreover, he has some vision on the use of trees to study past environmental conditions (which was to emerge as 'dendrochronology' in the early 20th century as explained later in this article). According to Szafer (1975) he is even considered the founder of plant geography. Another important work was *De Materia Medica*, published by Pedanius Dioscorides (77 A.D.) who included botanical information that he had gathered during travels with the Roman armies.

Late Middle to Early Modern Period

Albertus Magnus (1200-1280) who studied plants identified the dichotomy of *monocots* and *dicots* in the plant kingdom. However, it was English naturalist John Ray's (1627-1705) systematic study of plants that marked the beginning of modern plant sciences. Ray also classified birds based on the shape and size of beaks. He was followed by French botanist J.P. de Tournefort (1656-1708) who studied the 'vertical zonation of vegetation' on Mt. Ararat in Eastern Turkey. His work was posthumously published in 1717. Tournefort also developed a system of classifying plants based on flower characteristics and distinguished between the *Genus* and *Species* in plant classification. Carl von Linnaeus (1707-1778) made great contributions. Among his many works, in the book *Systema Naturae* (1735) he devised the presently used hierarchical system of classification of plants. Later, in 1753 he published *Species Plantarum*, which presented his 'binomial classification system' for plants and animals which is presently used. Therefore, he is considered the father of modern plant taxonomy.

Comte de Buffon (Georges-Louis Leclerc)'s (1761) natural history of animals (*Histoire Naturelle*) contributed much to the development of biogeographic thought. It included information of distribution patterns, adaptation and migration of wildlife. Jeffries (1997) has identified Buffon's *Histoire Naturelle* an early assessment of global biodiversity. According to Myers and Giller (1988) 'the origins of biogeography ...is attributed to Buffon' who perceived the biogeographic dissimilarities of the earth. Another outstanding figure of the 18th century was C.L. Willdenow who contributed to historical plant geography. His 1792 book *Grundriß der Kräuterkunde* (Eng: *Principles of Botany* -1805) was a study of the effects of climate on the distribution of vegetation. He showed that plants in different areas with similar climatic conditions had common characteristics. Moreover, he also worked in the area of plant taxonomy.

Another great contribution of this age was Malthus' (1798) theory of population growth. However, with accumulating pertinent knowledge biogeography remained as natural history at this stage.

Alexander von Humboldt (1769-1859) who is often regarded as 'the father of modern plant geography' deviated from the natural history tradition and contributed much to develop biogeography as a distinct branch of geography. He perceived climatic and vegetation zones and searched for patterns and causes. Moreover, he looked upon the earth as a single entity with interdependent parts and this view led to the concept of holism. Thus he and his followers elaborated the geographical aspects of biota, away from purely biological views. Nevertheless, at this stage biogeography was a descriptive and catalogue-styled subject, whereas, geography itself was considered as exploration and the description of the earth's surface. Plant geography and animal geography became two divisions of geography and the discipline lacked a clear conceptual basis.

Several of Humboldt's contemporaries also contributed to plant geography. Augustine P. de Candolle's (1820) geographical botany book *Théorie élémentaire de la botanique*, among his many other works was a very important contribution to plant geography. Actually it was he who invented the term 'taxonomy' and contributed to the development of plant taxonomy. In later years he also introduced the term 'heliotropism' to describe the movement of plants toward or away from the sun. Then, J.F. Schouw (1822) in a book published in Danish classified the 'floristic regions of the earth' (of which the German edition followed in the next year under the name *Grundzüge einer allgemeinen Pflanzengeographie*) from a view point of historical plant geography. He was also one of the editors of *Flora Danica*. Gloger's Rule (1833) applies to animals and hence to zoogeography which states that endothermic (i.e. warm-blooded) animal species in warm humid regions tend to have darker skin colours than their counterparts living in cooler and drier regions. Likewise, animals found in low altitudes are darker than those at higher altitudes. Pierre-Francois Verhulst's (1838) 'Logistic Model' (also known as Logistic Equation) had a tremendous impact on population biology and demography as well as biogeography. It has been even referred to as Verhulst's Law recently (see Haemig 2006)

Carl Bergmann (1847) showed a relationship between the body size (and hence mass) of endothermic animals and environmental temperature. As he explained larger animals have a lower surface area-to-volume ratio (specific surface) than smaller ones and thus radiate less body heat. This is advantageous in colder climates as opposed to thin and small animals living in warmer parts that have to radiate more heat to avoid hyperthermia. This relationship is now referred to as Bergmann's Rule. Another important figure in the 19th century was Louise Agassiz, who received credit for his '*Continental Glaciation Theory*'. But, he made a greater contribution by recognizing three main provinces of animal distribution; the Arctic Province (with the Antarctic Province being a special one due to greater

maritime influence), the Temperate zone and the Tropical Zone (Agassiz 1850). Each of these zones had been subdivided, too.

Alphonse de Candolle (1855) published a plant geography book in two volumes (*Geographic Botanique Raisonnee*). Another outstanding work was George Perkins Marsh's (1801-1882) book; *Man and Nature or Physical Geography as Modified by Human Action* which was published in 1864. This book shows his foresight on the problems of deforestation, water pollution etc. although people then had hardly noticed his warnings. He is often considered the first modern environmentalist of the United States and his great contribution to biogeography and environmental geography is obvious. A. Grisebach (1872) wrote in German a book on vegetation of the earth (*Die Vegetation der Erde nach Ihrer Klimatischen Anordnung*) which became a very important plant geography book. It was Grisebach who invented the term *geobotany*. Grisebach's works became the basis of the 'Three Schools of biogeography/plant ecology of the 20th century; Northern European, Southern European and Anglo-American.

All these authors emphasized the close relationship between climate and vegetation, thus, contributing to the development '*ecological biogeography*'.

J.D. Hooker published several plant geography books (e.g.1851, 1853, 1855, 1862 and 1866). He is considered the first to study 'the development and interrelations of floras of the entire globe' (Wulff 1950). The English ornithologist P.L.Sclater (1858) made a great contribution as the first to identify 'biogeographic regions' of the Earth. His six biogeographic regions (Palaeartic, Aethiopian, Indian, and Australasian, Nearctic and Neotropical) were actually avifaunal regions based on taxonomic and phylogenetic relationships of birds. (It was Sclater who named the mythical or hypothetical missing continent of South Asia as *Lemuria*).

In 1859 Charles Darwin's 'theory of evolution' became a major breakthrough for the development of sciences which greatly influenced biogeography as well. Darwin theorized that evolution is a gradual, progressive process which operates over a long time frame of thousands to millions of years, of which the main mechanism is natural selection. In 1860 H.D. Thoreau coined the word 'succession' especially in relation to forest trees and it has been a key concept in the study of vegetation dynamics.

A.R.Wallace in his book *The Geographical Distribution of Animals* (1876) conceptualized 'zoogeographical realms' (or *Wallace's Realms*) based on Darwinian Theory and thus, modified Sclater's scheme by considering the distribution of all vertebrates. His six realms are; Palaeartic, Ethiopian,

Oriental, Australian, Nearctic and Neotropical. Wallace, who studied animal geography in relation to the theory of evolution, is regarded as the father of zoogeography and was a co-founder of the theory of evolution. Thus, biogeography by this stage had acquired an evolutionary tradition. Wallace is also highly recognized for his contributions to the '*Theory of Evolution*'.

Earnst Haeckle (1866) presented a classification of organisms into three kingdoms; *Protista*, *Plantae* and *Animalia* based on evolutionary relationships, and propounded the '*biogenetic law*' (which is not considered absolutely true now). In 1869 he coined the term *ecology* and is given credit for enrichment of biogeography with ecological ideas. J.A. Allen's contributions were manifold. In 1871 he delineated eight '*ecogeographic realms*' of the Earth on the basis of mean annual isotherms. He presented 'Allen's Rule' of biogeography which states that endothermic animals living in cold areas tend to have shorter limbs and other exposed parts than those living in warmer climates. This is an adaptation to conserve body heat by reducing specific surface of bodies of animals in cold areas. Alexander Supan (1879) introduced the '*timberline*' concept. British scientist Burdon Sanderson in 1893 considered ecology as a division of biology (with physiology and morphology) and defined it as 'the philosophy of nature'. Another important contribution was made by S.A. Forbes (1887) of the US, who identified the *ecosystem concept* in his article entitled *The Lake as a Microcosm*. The same study also founded modern *limnology*, the ecological study of freshwater bodies.

C.H. Merriam (1894) perceived that altitudinal zonation of vegetation is generally similar to latitudinal zonation in response to variations of temperature and precipitation and thus, proposed the 'life zone' concept. Thus, on the basis of the mean temperature of the warmest six months of the year and indicator plants and animals he identified 13 life zones of North America. Danish scientist E. Warming (1895) wrote *Plantensamfund* in Danish (which was translated to German and English respectively in 1896 and 1909).

This book is considered the first strictly ecological book- which established the above mentioned term *ecology* coined by Haeckle and provided a theoretical basis for the discipline and also introduced the concept of '*plant community*'. This book gave biogeography an ecological perspective. Warming also is credited for formulating the 'theory of ecological succession' (Goldsmith 1985). The year 1898 was important for biogeography, for two significant works appeared in that year. One was by A.F.W. Schimper (1898) who studied the geographical distribution of plants in relation to physical environmental factors (and the English translation of his original German book was published in 1903 under the

name *Plant-geography Upon a Physical Basis*). He had adopted an ecological approach and it was he who coined the term '*tropical rainforest*'. The next was the joint work of R. Pound and F.E. Clements of America; *The Phytogeography of Nebraska* which was a pioneer study on plant succession. These works were followed in the next year (1899) by Henry C. Cowles's study of the succession of sand dune vegetation of Lake Michigan.

By about this time two different schools of thought - European and American - had emerged emphasizing two different aspects of vegetation communities; the European school studied the composition, structure and distribution of plant communities. The American school paid more attention to the succession of communities.

Modern Period: Developments in the 20th Century

Among the events of biogeographic importance of the early 20th Century were: A.G. Tansley's (1911) publication of *Types of British Vegetation* and the first *International Phytogeographic Excursion* which was held in the same year guided by the same book. American zoologist and conservationist Victor E. Shelford in 1913 wrote *Animal Communities in Temperate America* which became a great contribution to zoogeography as well as physiological animal ecology. It was Shelford who developed the '*Law of Tolerance*' which states that the distribution of a species will be limited by its range of tolerance for local environmental factors.

In the same year Marion Newbegin published her book *Animal Geography* (Newbegin 1913). According to Smith (2005) this is considered an important contribution to the early development of the field of geography and it demonstrated the '*relation of biology--and the scientific method--to the subject*'.

In the subsequent year A.K. Douglas (1914) propounded '*dendrochronology*', the scientific study of annual tree rings to determine past environmental conditions and events. Wegener's (1915) theory of continental drift had a tremendous impact on biogeography. Although many scientists rejected his theory for the lack of an acceptable mechanism to explain continental movements, the fossil evidence he had gathered were substantial to palaeobiogeography. This is evidenced by a number of studies that followed on the evolution and distribution of biota due to the drifting of continents. In 1916 F.E. Clements formalized the concepts of plant succession and climax vegetation. In 1920, American entomologist A.D. Hopkins studied phenological changes in relation to latitude and elevation. He found that events in spring occur 4 days later for every degree of latitude northward or 400 feet of elevation. This led to the formulation of

'Hopkins' Bioclimatic Law' (or Hopkins' Law) which states that 305m (i.e. 1000 feet) of elevation is approximately equivalent to 160km (100miles) of latitudinal variation. He is also 'referred to as the father of forest entomology' (*The Hopkins U.S. System Index-HUSSI-undated*)

Thus, by the end of the first quarter of the 20th century biogeography had embraced evolutionary, ecological and spatial (distributional) aspects of biota.

However, hard ecological ideas enriched biogeography only since the second quarter of the 20th century. This was especially due to several seminal works. First, August Thienemann of Germany forwarded the concept of 'trophic levels' in ecosystems in 1920 (*Encyclopaedia Britannica*). He is also known for his many contributions to *limnology*. In the same year Raymond Pearl applied mathematics to the study of biological populations and put into use the '*logistic growth*' concept which had been forwarded by Verhulst in 1838. Pearl also pioneered the application of principles of population biology to study human populations by studying the growth of the population of the United States. Next, Alfred Lotka's (1925) *Elements of Physical Biology* introduced the application of quantitative methods in biological sciences. Moreover, Lotka had perceived the ecosphere as a whole, where the living and non-living components are co-evolving and inseparable. His concepts of population biology were followed by V. Volterra (1926). Today Lotka-Volterra 'predator-prey' and 'competition' models remain very important foundations of modern population biology and demography. It is noteworthy that these developments took place before the 'quantitative revolution of geography' that took place toward the early 1950s.

Then, in 1926 Russian mineralogist V. I. Vernadsky put into use the term '*biosphere*' (*Biosphera*) in the present context of use which had been originally conceptualized by Jean-Baptiste Lamarck (1744-1829) to define the domain of life on earth. With his mineralogical background he showed how elements are recycled through the biosphere via 'biogeochemical cycles'.

In the same year H.A. Gleason of America proposed the '*individualistic concept*' of vegetation (Gleason 1926) -as opposed to community approach - to the study of organisms. In this concept Gleason identified a plant community as an assemblage of individual species with similar (abiotic) environmental requirements, which became one of the alternative explanations to the community structure. English scientist C. S. Elton wrote *Animal Ecology* (1927) -and *Animal Ecology and Evolution* (1930) - examined the geographical distribution of animals from an ecological view-point. He moreover identified ecological niches and conceptualized

ecological pyramids (referred to as 'Eltonian Pyramids') and food chains. Braun-Blanquet's (1928) German plant sociology book *Pflanzensoziologie* was published (which was translated into English as *Plant Sociology; The Study of Plant Communities* in 1932). He initiated the '*floristic approach*' to study vegetation in which he identified different plant communities based on their floristic composition. He also laid the foundation to the 'Zurich-Montpellier (Southern European) Tradition' mentioned earlier in this article. Another important development was E. V. Wulff's (1932) *Vvedenie v Istoricheskuiu Geografiiu Rastenii* (which was translated into English as *An Introduction to Historical Plant Geography* in 1943).

One of the next important developments was the '*plant life forms*' of Raunkiaer (1934). In his system known as the '*Raunkiaer Sytem*' he identified six life forms of plants according to their way of survival of drought and cold or '*perennation*'. He moreover, established the concept of '*phytoclimate*' and recognized four basic phytoclimates; (1) the hot, humid tropics, (2) arid regions, (3) high latitude and altitude areas, (4) and the moderately humid temperate zones.

The British scientist A. G. Tansley (1935) propounded the term '*ecosystem*' (which probably had been conceptualized by the Greeks much earlier) giving it a modern definition. This was important as it provided biogeography and ecology with some form of basis that both these areas lacked. In 1937, French marine biologist Edouard Chatton differentiated between *Prokaryotes*, organisms such as bacteria that lack nuclei, and *Eukaryotes*. His understanding became more acceptable with the advancement of biological classification systems in the 1960s. In 1938 Herbert Copeland of the US proposed to include Prokaryotes in a separate kingdom as Kingdom Monera. Lindeman (1942) presented the '*trophic dynamic concept of ecology*' pertinent to the flow of energy in ecosystems. This paper showed how '*all ecosystem functions depend on the movement of energy by way of trophic relationships*' (*Environmental Encyclopedia* 2005-06). L.R. Holdridge (1947) identified vegetation zones of the earth based on what he called '*biotemperature*'. Thinking from a plant physiological viewpoint, he considered all temperatures above freezing point as biotemperature whereas below the freezing point plants are dormant. Thus, he rejected the Merriam's (1894) life zones which were based on temperature and latitude or altitude and used degrees of mean annual biotemperature to develop his own life zone scheme. Another important development is the Physiognomic Vegetation Classification presented by Kuchler (1949). '*Vegetation physiognomy*' generally refers to the vegetation structure (i. e. height, spacing and stratification) and functioning (seasonality, phenology etc.). A very important development of the 1950s is E. P. Odum's energy based approach to ecology which

continued through the latter part of the century. Among his many works the book *Fundamentals of Ecology* (Odum 1951) is noteworthy in a broader context. One of the great books of the mid-20th Century was *Man's Role in Changing the Face of the Earth* edited by W.I. Thomas (1956). It included 53 papers present at a major ecological conference held in 1955, and covered the three main areas of: (1) clearing woodlands, fire, and natural history of urbanization, (2) Ecology of wastes, man's impact on the oceans and coasts and urban and industrial demand for resources, (3) Population and resources, possible limits of resource and energy use. "A pioneering publication in the field of environmental research, the work has steadily contributed to ecological studies, and is now considered a classic" (Binghamton Geomorphology Symposium 2006). In 1956 another contribution was made to biogeography by Professor Reinhold Tuexen of Germany who introduced the concept of 'potential natural vegetation' in addition to his manifold works (Tuexen 1956, cited in: *Profiles of the 2006 Blue Planet Prize Recipients* 2006). Potential natural vegetation (PNV) is the vegetation that would become established in an area if the natural succession was allowed in the absence of all kinds of human interference. However, it is not necessarily climax vegetation. This concept has been applied in a number of subsequent publications e.g. Kuchler (1964) and Gaussen et al. (1968).

Charles Elton mentioned before, whose contributions became important in the early part of the century in 1958 pioneered the field of 'invasion ecology' (Elton 1958) although he did not clearly define the terms *invasion*, *invader* (or *invasive species*). Followed by the works of Jarvis (1969), Williamson (1996) etc. invasion ecology has become an expanding field today especially with increasing awareness on the threat of invasive species (see Richardson et al. 2000).

In 1959 Robert H. Whittaker proposed that fungi should belong to a fifth kingdom of organism and presented the scheme of classifying organisms into the five Kingdoms; *Monera*, *Protista*, *Fungi*, *Plantae* and *Animalia*.

Another great development since the late 1950s is the emergence of textbooks of the *Monographia Biologicae* series. They covered biogeographical and ecological aspects of continents or their parts, islands and special ecosystems such as coral reefs and mangroves. It is noteworthy to mention the *Ecology and Biogeography of Sri Lanka* edited by C.H. Fernando (1984) preceded by *Ecology and Biogeography in India* (Mani ed. 1974). The series continues and the latest *Biogeography and Ecology of Bulgaria* will be published in mid-2007 by Springer.

Since the 1960s a number of new thoughts greatly influenced biogeography. One is the revolutionary theory of 'global plate tectonics'

which explained the mechanism of continental drift that Wegener could not explain. Thus, it revitalized the Wegenerian continental drift theory. Numerous subsequent works on biogeography and plate tectonics have been written.

Also noteworthy is the effect of the environmental movement of the 1960s (that followed Rachel Carson's *Silent Spring*) on biogeography. It gave a new life to geography via biogeography, and biogeography text books written after 1960s reflect this by their emphasis on the impact of human activities on the biosphere.

'*The Theory of Island Biogeography*' written by Robert H. MacArthur and E.O. Wilson (1967) attracted much scientific attention. In spite of the penetration of quantification into biological sciences and geography, biogeography has still been mainly considered a descriptive subject and it was the Theory of Island Biogeography that changed this view (see: *ArticleWorld.org*, and *BiologyDaily.com*.) Since then, many studies have been made on this theory, particularly on its applicability to the design of protected areas. It remains a main part of both theoretical and applied biogeography courses.

The '*refugia theory*' of Haffer (1969) was another important development of this time which states that species survived during the Pleistocene glaciations in fragmented lower elevation habitats with warmer conditions. Despite the fact that this theory has been debated, its importance to explain vicariance and dispersal and adaptation of species with the Pleistocene climate changes is appreciated.

James Lovelock's 'Gaia Hypothesis' of 1969, (1972 and 1979) was a very important contribution as it helped perceive the Earth's biotic and abiotic systems together as a whole. Working since mid-1960s Lovelock developed this hypothesis to view the earth as an intricately related, mutually evolving single system which is self-regulated. The Earth is analogous to a single organism that regulates its conditions for survival. The hypothesis, though controversial, has attracted much attention in view of the human-induced environmental problems. According to Richard (2006) "*Lovelock's ideas are the basis of our current understanding of global warming and the need to cut carbon emissions*".

Since the late 1970s the use of computers and remote sensing techniques in geography contributed especially to the study of biogeographic dynamics as well. The effects of these techniques became more visible from the later years of the 20th to the present century. The 1972 book of Robert H. MacArthur, *Geographical Ecology* was a seminal work for biogeography as well as ecology and used a mathematical approach that examined the

patterns in the distribution of species. This book marked the beginning of modern studies of large-scale effects of ecology (and biogeography) (Blackburn and Gaston 2004).

Arne Naess's (1973) '*Deep Ecology Movement*' distinguishes between shallow ecology, which views nature in terms of its value to human beings, and deep ecology, which values nature independently of its usefulness to humanity. It undoubtedly was inspired by the Gaia Hypothesis. While rejecting 'anthropocentrism', deep ecology provided the basis of 'green ideas' of the later years. As an ecological philosophy it moreover, led to the introduction of environmental ethics.

J.P. Grime in 1974 put forward the concept of three plant strategies, of which the textbook was published in 1979. The three strategies; '*ruderal*', '*competitive*' and '*stress-tolerant*' that he identified have been controversial as he tried to fit a given species into one of the three modes of life but, yet influenced much the subjects of plant ecology and biogeography. In the same year the debut of the *Journal of Biogeography* was a year mark which has continued through to the 21st Century. In the next year M.D.F. Udvardy developed a system of eight 'biogeographic realms' (Udvardy 1975).

Norman Myers identified 'Biodiversity Hotspots' in the terrestrial habitats of the world in 1988. The original number was 10 and in 1990 Myers added eight other hotspots. In 2000 the number rose to 25. This finding has tremendously influenced biogeography as it highlighted the adverse human impacts on areas of very high biodiversity and conservation needs. (In 2002, ten 'marine biodiversity hot spots' were identified (Roberts et al. 2002). In February 2005 Conservation International added nine more hotspots and, thus, at present there are 34 land biodiversity hotspots in the world). Another contemporary issue was the concept of '*global warming*' (human-induced) which (despite its roots of the 1930s) became a major concern after the UN Intergovernmental Panel on Climate Change (IPCC) was created in 1988. (The IPCC publishes its assessment reports every five or six years. Having received more scientific and political attention after the IPCC report of 1990, this was especially highlighted in the 1992 'Earth Summit in Rio de Janeiro'). In spite of the fact that 'global warming' has not gained scientific consensus, it has influenced biogeography as well as other branches of earth/environmental sciences, resulting in numerous publications related to the biogeographical aspects of human-induced climatic changes such as the loss of species and the shifts in their geographical ranges, as well as possible changes in biological productivity due to global warming.

With the expansion of environmental concern toward the latter part of 1980s (in particular after the *Brundtland Report*) biogeography expanded to address ecopolitical and biodiversity issues.

Avise et al. (1987) first used the term '*phylogeography*' to the study of geographical distribution of genetic lineages. Since then the subject has become important to evolutionary biology, historical biogeography, paleontology and biological conservation.

Brown and Maurer (1989) formally introduced the '*macroecology*' concept. It has become the branch of biogeography that studies large-scale spatial and temporal patterns and processes of biota based on statistical distributions of variables at the levels of species, populations and communities.

In the same decade the application of GAP analysis in biodiversity protection which also incorporated GIS had a positive effect on biogeography. In 1984 J.H. Brown forwarded the Brown's Principle (Brown 1984) which states that individuals of a species tend to be most abundant near its range centre, showing a declining abundance away from the centre (Also see Gilman 2005).

The latest area of concern of biogeography seems to be the sustainability of the planet, which has given rise to the modeling of biogeographical phenomena.

Also in 1990 Carl Woese proposed the '*Domain Concept*' in biology and divided *monera* organisms into two domains: *Bacteria* and *Archaea*. Further, he included Eukaryotes in the Domain Eukarya. This helped recognize the six kingdoms organisms; *Eubacteria*, *Archaeobacteria*, *Protista*, *Plantae*, *Fungi* and *Animalia*.

The birth of *Global Ecology and Biodiversity Letters* (to become *Biodiversity Letters* in 1993, which is published under the name *Diversity and distributions since 1998*) and *Global Ecology and Biogeography Letters* (continued as *Global Ecology and Biogeography* since 1999) as sister journals of the *Journal of Biogeography* in 1991 is another big step and was a result of the revival of the environmental awareness since 1908s mentioned before.

David Tilman & John A. Downing (1994) showed that biodiversity stabilizes community and ecosystems processes. Until then, the importance of biodiversity for ecosystem stability was theoretically known particularly after Mac Arthur (1955) and Elton 1958 *opp cit* :145-153). Yet, Tilman and Downing based their finding on more than a decade

of experiments done in 207 prairie plant plots to determine that biodiversity stabilizes community and ecosystem process (though not population processes). In other words, they proved that ecosystems with high biodiversity have greater primary production and higher stability and can even better survive perturbations.

Biogeography in the 21st Century

Undoubtedly, the most important event at the onset of the new millennium is the establishment of the '*International Biogeography Society*' (IBS) in the year 2000, followed by its inaugural meeting held in 2003. Since then, it has become the best forum for biogeographers and allied scientists. In 2001, a long-needed book on GIS and remote sensing in biogeography and ecology appeared (Millington et al. 2001). Charles H. Smith (2002, 2003 and 2005) presented three classical works important to biogeography. The first of these is the detailed bibliography entitled; '*Early Classics in Biogeography, Distribution and Diversity Studies: To 1950*' completed in 2002. This was followed by '*Early Classics in Biogeography, Distribution and Diversity Studies: 1951 to 1975*' completed in 2003. His work of 2005 (Smith et al. 2005) is a joint work, with the title '*Some Biogeographers, Evolutionists and Ecologists*'. Lomolino et al. (2003) published an important book covering the main contributions to biogeography from 1700s to 1975 by prominent biogeographers. Another important development that took place towards the end of 2004 is the birth of the first book of the '*Frontiers of Biogeography*' series edited by Lomolino and Heaney (2004). The '*Happy Planet Index*' in 2006 (The New Economics Foundation 2006), although not a biogeographic novelty *per se.*, has some bearing on biogeography as it emphasizes that general life satisfaction and well-being of a people do not necessarily require a high level of consumerism that endangers the sustainability of the planet's resources. According to the 'IPCC Report summary of 2007' released on Feb. 02, 2007, (Intergovernmental Panel on Climate Change 2007) human-induced global warming -especially due to the burning of fossil fuels- is an almost-certain thing. This report has a wider range of indicators such as 'below-the-surface sea temperatures. The biogeographical implications of the global warming could be drastic. For instance, even rapid evolutionary changes (called '*evolution explosion*') can happen in plants with short life-cycles within a few generations due to global warming, as understood in the case of *Brassica rapa*, a close relative of the mustard plant (Franks et al. 2007).

Conclusion

The above review of some of numerous seminal works related to biogeography explained how this discipline has evolved from a

disorganized scattered body of knowledge into a more rigorous, methodological sub-discipline of geography. At this point a brief review of the scope and role of modern biography is worthwhile before concluding.

In order to examine this, it will be necessary to understand the relationship between biogeography and ecology. It is evident that both ecology and biogeography have rapidly grown since the mid-20th century and this development has been mutually beneficial to both disciplines. These subjects are intimately related but, it appears that, until about the 1970s ecology mainly focused on local-scale ecosystems, whereas the scope of biogeography was to study macro-scale ecosystems (see Forsberg 1976). Since the mid 1970s many changes took place in the subject of biogeography with the development of new techniques such as GIS and the emergence of macroecology and phylogeography as discussed before. *'Although biogeography and ecology had previously been considered distinct disciplines, this outlook began to change in the early 1990s'* (Briggs 2007) mainly due to the influence of macroecology. Even in the 1970s the difference between these two areas has been hazy and the distinction between them was never seen by MacArthur (1972 *op.cit.*). Also according to Forsberg (*ibid*) it is trivial (however) to discuss the meanings of such terms as biogeography, ecology and geography because these subjects are closely related.

It is also important to understand the where biogeography stands among the multitude of scientific disciplines. Conventionally, biogeography has been viewed as a specialty within physical geography. Yet, modern environmentalism has brought in human dimensions to this subject. The emergence of *'human biogeography'* the study of the spatio-temporal aspects of the interactions between the biological environment and the humans - is a result of this (e.g. Terrell 2006). Although early global change studies mainly focused on the biophysical environment, since mid-1980s the human dimensions of global change have received attention (Brown 1996). The investigation of the geography of genetic variation within the human species is also within its purview (Tishkoff and Kidd 2004). For these reasons according to the view of Young (2002) *"... biogeographers and biogeography are something apart from other endeavors in geography. Biogeography is a biological science, inspired by and interacting with the physical and social sciences..."* Mathur (2003) perceives biogeography as the vital link between natural and social sciences.

The following excerpt from the IBS Mission Statement helps understand the scope of biogeography: *"Traditionally viewed as the study of geographic distributions, modern biogeography now explores a great*

diversity of patterns in the geographic variation of nature from physiological, morphological and genetic variation among individuals and populations to differences in the diversity and composition of biotas along geographic gradients. Given its interdisciplinary and integrative nature, biogeography is now broadly recognized as a unifying field that provides a holistic understanding of the relationships between the earth and its biota”.

Biogeography is a very complex subject that has become much wider in its scope. It is related to an array of other subject areas such as anthropology, biology, climatology, environmental science, geology, physical geography and systematics. It “*provides a valuable link between traditional single disciplines (such as ecology, taxonomy, geology and conservation biology) and a focus for interdisciplinary studies*” (Spellerberg and Sawyer 1999: Chap 1). As previously discussed, it has become much wider in its scope to possess many main divisions and sub divisions. The main divisions are: conservation biogeography, dynamic biogeography, ecological biogeography, historical biogeography, human biogeography, island biogeography, macroecology, paleobiogeography, phylogeography, plantgeography and zoogeography. Examples of numerous sub divisions of biogeography are regional biogeographies, microbial biogeography, biogeography of extreme environments, biogeography of hydrothermal vents and deep sea communities.

Biogeography today continues to advance as a subject with a strong conceptual basis that tests biogeographic theories. 'Biogeography Specialty Group' of the Association of American Geographers and the 'Biogeography Team' of the National Oceanic and Atmospheric Administration (NOAA) and the National Center for Coastal Ocean Science are only two examples of institutional practical contributions made by biogeographers.

A review will reveal that biogeography is an integral subject in many geography and biology departments of universities in the developed countries where the majority of undergraduates studying these subjects have a natural science background. On the contrary, in Sri Lanka it remains a very minor sub-division of geography in a social science setting, even though a revival of geography can be expected with the re-introduction of geography to the school curricula and this will contribute to a concomitant appreciation of biogeography.

Acknowledgments

The author wishes to thank the Coordinating Editor of this journal, Mr. P. Vidanapathirana for inviting him to write this article. He highly appreciates the opportunity to submit this article to the special volume that felicitates his former teacher Professor M.M. Karunanayake and recalls fun memories of numerous field trips undertaken under Professor Karunanayake's guidance, while an undergraduate at the University of Sri Jayawardenepura, Sri Lanka.

Special thanks are due to Professors Robert E. Frenkel and Gordon E. Matzke of Oregon State University Department of Geosciences for their valuable comments on an early draft of this paper.

References:

Agassiz, Louis (1850) Geographical distribution of Animals. *Christian Examiner and Religious Miscellany* 48:181-204.

Agatucci, Cora (1998) China Timeline | Cultures and Literatures of Asia. Central Oregon Community College.
<http://web.cocc.edu/cagatucci/classes/hum210/tml/chinatml/chinatml1.htm>

Allen, J. A. (1877) The influence of Physical conditions in the genesis of species. *Radical Review* 1: 108-140.

Articleworld.org (no date)
<http://www.articleworld.org/index.php/Category:Biogeography>

Avise, J. C., J. Arnold, R. M. Ball, Jr., E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reed, and N. C. Saunders (1987). Intraspecific Phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18: 489-522

Bergmann, C. (1847) Ueber die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3 (1), 595-708

Binghamton Geomorphology Symposium (2006). Commemorating the 50th anniversary of *Man's Role in Changing the Face of the Earth* (Thomas, 1956). Conference held at the Department of Geography, University of South Carolina, Columbia, South Carolina, Oct 20-22, 2006

- BiologyDaily.com (no date)
<http://www.biologydaily.com/biology/Biogeography>
- Blackburn, Tim M. and Kevin J. Gaston eds.(2004) Introduction: Why Macroecology. Chap 1, pp106 in: *Macroecology: Concepts and Consequences*. 43rd Symposium of the British Ecological Society. Blackburn, Tim M. and Kevin J. Gaston eds. Cambridge University Press.
- Branson, Sir Richard (2006) Making the Skies Green. *Newsweek* Dec. 18, 2006 issue. (Technology and Science).
- Braun-Blanquet, J. (1932). *Plant Sociology*. McGraw Hill. New York.
- Briggs, John C. (2007) Marine biogeography and ecology: invasions and introductions
Journal of Biogeography 34 (2), 193-198.
- Brown, Dwight (1996) Introduction to Biogeography and the Human Dimensions of Global Change:Background Information. Unit I in: Module; *Living in the Biosphere: Production, Pattern, Population, and Diversity*. Association of American Geographers.
<http://www.colorado.edu/geography/virtdept/module/biosphere/units/unit1/html/unit1frame.html>
- Brown, J.H. (1984) On the Relationship between abundance and distribution of Species. *American Naturalist* 124: 255-279.
- and B.A. Maurer. 1989. Macroecology: The division of food and space among species on continents. *Science* 243: 1145-1150
- Copeland, H. F. (1938). "The kingdoms of organisms". *Quarterly Review of Biology* 13: 383-420.
- Cowles, H. C. (1899) The ecological relations of the vegetation of the sand dunes of Lake Michigan. *Botanical Gazette* 27: 95-117, 167-202, 281-308, 361-391.
- Douglas, A.E. (1914) A Method of Estimating Rainfall by the Growth of Trees. *Bulletin of the American Geographical Society*. 46(5):321-335.
- Elton, C. S. (1927) *Animal Ecology*. Sidgwick and Jackson, London.
- (1930) *Animal Ecology and Evolution*. Oxford University Press.

----- (1958) *Ecology of Invasions by Animals and Plants*. Methuen, London.

Encyclopaedia Britannica online Ecology

Environmental Encyclopedia (2005-2006) (ed) Raymond L. Lindeman (1915 - 1942) American Ecologist.

Fernando, C.H. (ed.), 1984. *Ecology and biogeography in Sri Lanka*. Dr. W. Junk Publ., The Hague.

Fosberg, F.R. (1976) Geography, Ecology, and Biogeography. *Annals of the Association of American Geographers* 66 (1):117-123.

Franks, Steven J., Sheina Sim and Arthur E. Weis (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. National Academy of Sciences of the USA* (Jan 23, 2007) 104 (4): 1278-1282.

Gausson, H., Legris, P., Viart, M. & L. Labrou (1968). *Explanatory notes on the Vegetation Map of Ceylon*. Technical & Scientific Section, French Inst. Pondicherry.

Gilman, Sarah (2005) A test of Brown's principle in the intertidal limpet *Collisella scabra* *Journal of Biogeography* 32(9)1583-1589.

Gleason, Henry A. (1926) The Individualistic Concept of the Plant Association. *Bull. Torrey Bot. Club* 53.

Goldsmith, Edward (1985) Ecological succession rehabilitated. *The Ecologist* 15 (3)-Online at:
<http://www.edwardgoldsmith.com/page119.html>

Grime J. P. (1974) Vegetation classification by reference to strategies. *Nature* 250: 26-31.

Grime J.P. (1979) *Plant Strategies and Vegetation Processes*. New York: John Wiley.

Grisebach, A. (1872) *Die Vegetation der Erde nach Ihrer Klimatischen Anordnung*. Verlag von Wilhelm Englemann, Leipzig.

- Haemig P.D. (2006) Laws of Population Ecology. ECOLOGY.INFO 23 online review. <http://www.ecology.info/laws-population-cology.htm> Haemig
- Haffer, Jurgen. 1969. Speciation in Amazonian Forest Birds. *Science*. Vol. 165:131-137.
- Holdridge, Leslie R. (1947) Determination of World Plant Formations from Simple Climatic Data. *Science* 105(2727):367-368.
- Hopkins, A.D. (1920) The bioclimatic law. *Jour. Wash. Acad. Sci.* 10:34-40
- Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: The Physical Science Basis. Summary for Policy Makers*. IPCC Secretariat, WMO, Geneva.
- Jeffries, Michael J. (1997) *Biodiversity and Conservation*. Routledge. London.
- Kuchler, A.W. (1949) A Physiognomic Classification of Vegetation *Annals of the Association of American Geographers*, Vol. 39, No. 3 (Sep., 1949), pp. 201-210.
- Kuchler, A.W. 1964. Potential Natural Vegetation of the Conterminous United States, *American Geographical Society, Special Publication No. 36*.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399-418.
- Lomolino, Mark V. and Lawrence R. Heaney eds. (2004) *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer Associates.
- , Dov F. Sax and James H. Brown eds. (2003) *Foundations of Biogeography*. Univ. of Chicago Press.
- Lotka, Alfred (1925) *Elements of Physical Biology*. Williams and Wilkins, Baltimore.
[Reprinted in 1956: *Elements of mathematical biology*. Dover Publ. New York).
- Lovelock, J. E. *Gaia: A New Look at Life on Earth*. Oxford: Oxford University Press (1979).

MacArthur, R. H (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology* 36: 533-536.

----- and Wilson, E. O. 1967. *The Theory of Island Biogeography*. Princeton, Princeton University Press.

----- (1972) *Geographical Ecology Princeton*. Princeton University Press.

Malthus, Thomas Robert (1798) *An Essay on the Principle of Population, as it affects the Future Improvement of Society*. J. Johnson, Lond.

Mani, M.S. (Ed.) (1974) *Ecology and Biogeography in India*. Springer

Marsh, George Perkins (1864) *Man and Nature - or Physical Geography as Modified by Human Action*. Harvard University Press. (1965 reprint of the original edition).

Mathur, H.S. (2003) *Essentials of Biogeography*. Pointer, Jaipur-India.

Millington, Andrew C.; Walsh, Stephen J.; Osborne, Patrick E. eds. (2001) *GIS and Remote Sensing Applications in Biogeography and Ecology. The International Series in Engineering and Computer Science*, Vol. 626, Springer

Myers, A.A. and Giller, P.S. (1988) *Analytical Biogeography*. Chapman and Hall.

Myers, N. Threatened biotas: 'hotspots' in tropical forests. *Environmentalist* 8, 187-208 (1988).

Naess, Arne. 1973. "The Shallow and the Deep, Long-Range Ecology Movements: A Summary." *Inquiry* (1): 16.

Newbegin, Marion (1936) *Plant and Animal Geography*. Methuen, London.

Odum, E. P. (1951) *Fundamentals of Ecology* (first edition) Saunders, Philadelphia.

Pound, R., and F. E. Clements. (1898) *Phytogeography of Nebraska*. Botanical Seminar, Lincoln, Nebraska, USA.

Profiles of the 2006 Blue Planet Prize Recipients (2006) <http://www.af-info.or.jp/eng/honor/hot/enr-miyawaki.html>

Raunkiaer, C. (1937) *Plant Life Forms*. Oxford University Press, New York.

Richardson, David M., Peter Pysek, Marcel Rejmánek, Michael G. Barbour, F. Dane Panetta, and Carol J. West (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93-107.

Roberts, Callum M., et. al. Colin J. McClean, John E. N. Veron, Julie P. Hawkins, Gerald R. Allen, Don E. McAllister, Cristina G. Mittermeier, Frederick W. Schueler, Mark Spalding, Fred Wells, Carly Vynne, and Timothy B. Werner (2002) Marine Biodiversity Hotspots and Conservation Priorities for Tropical Reefs. *Science* 295 (5558): 1280-1284, 15 Feb. 2004.

Rosenberg, Matt (2006) An Overview of Geography. *Geography* 101. (Nov.10, 2006)
<http://geography.about.com/od/studygeography/a/geog101.htm>

-----_ (undated) Temperate, Torrid, and Frigid Zones: Aristotle's Climate Classification. *About.com*.
<http://geography.about.com/od/physicalgeography/a/torridfrigid.htm>

Science Watch (1996) *University of Sheffield's Philip Grime: Strategic Advances in Plant Ecology*.
http://www.sciencewatch.com/interviews/philip_grime.htm
 (July/August 1996)

Sclater, Philip L (1858) On the general geographical distribution of the members of the class Aves. *Jour. Proc. Linn. Soc.: Zoology* 2: 130-145. A.T.: faunal regions; faunal realms; birds; systematic zoogeography; ornithogeography.

Schaefer, F.K. (1953): Exceptionalism in Geography: A Methodological Examination, *Annals of the Association of American Geographers*, 43, pp. 226-245.

Schimper, A.F.W. (1898) *Pflanzengeographie physiologischer Grundlage*, G. Fischer, Publ.

----- (1903) *Plant Geography upon a Physiological Basis*, Oxford; Clarendon Press

Smith, Charles H. (2002) *Early Classics in Biogeography, Distribution and Diversity Studies: To 1950*.
<http://www.wku.edu/%7Esmithch/biogeog/>

----- (2003) *Early Classics in Biogeography, Distribution and Diversity Studies: 1951 to 1975*.
<http://www.wku.edu/%7Esmithch/biogeog/index2.htm>

----- (2005) Newbigin, Marion Isabel (Scotland 1869-1934), geography, biology. *Some Biogeographers, Evolutionists and Ecologists: Chrono-Biographical Sketches*.
<http://www.wku.edu/~smithch/chronob/NEWB1869.htm>

-----, Joshua Woleben, and Carubie Rodgers (2005) *Some Biogeographers, Evolutionists and Ecologists: Chrono-Biographical Sketches*. <http://www.wku.edu/~smithch/chronob/homelist.htm>

Spellerberg IF and Sawyer JWD. 1999. *An Introduction to Applied Biogeography, Cambridge*. Cambridge University Press. Chap 1. Biogeography: the nature of the subject, its history and its applications.

Tansley, Arthur G. "The Use and Abuse of Vegetational Concepts and Terms." *Ecology* 16 (1935): 284-307.

Terrell, John Edward (2006) Human biogeography: evidence of our place in nature. *Journal of Biogeography* 33 (12): 2088-2098.

The Hopkins U.S. System Index-HUSSI (Undated)
<http://www.fs.fed.us/pnw/bmnri/hussi4.html>

The New Economics Foundation (2006) The Happy Planet Index. an index of human well-being and environmental impact.
<http://www.happyplanetindex.org/>

Thomas Jr., W.I. ed. (1956) *Man's Role in Changing the Face of the Earth*. Chicago, University of Chicago Press.

Thoreau, H. D. (1860) Succession of forest trees. Massachusetts Board of Agriculture - Eighth Annual Report. Wm. White Printer, Boston, Massachusetts, USA.

Tilman, David and Downing, John A. (1994) Biodiversity and stability in grasslands. *Nature* 367:363-365.

- Tillman, David (1996) Biodiversity: Population versus ecosystem stability. *Ecology* 77 (2):350-363.
- Tishkoff, Sarah A and Kidd, Kenneth K (2004) Implications of biogeography of human populations for 'race' and medicine. *Nature Genetics* 36: S21 - S27 (2004)
- Udvardy, M. D. F. (1975). *A classification of the biogeographical provinces of the world*. IUCN Occasional Paper no. 18. Morges, Switzerland: IUCN
- Verhulst, P-F (1838) Notice sur la loi que la population suit dans son accroissement. *Corr. Math. Phys.* 10: 113-121.
- Vernadsky V.I., 1926. *Biosphera (The Biosphere)*, Nauchnoe khimiko-technicheskoye izdatel'stvo (Scientific Chemico-Technical Publishing): Leningrad, 200p.
- Volterra, V. (1926) Variations and the Fluctuations of the Number of Individuals in Animal Species Living Together. in: *Animal Ecology*. R.N.Chapman ed. McGraw-Hill, New York. 1926.
- Wegener, Alfred (1915) *The Origin of Continents and Oceans*. English translation of the original *Die Entstehung der Kontinente und Ozeane* by John Biram (1966 Dover Publ.)
- Whittaker, R. H. (1969). "New concepts of kingdoms of organisms". *Science* 163: 150-160.
- Wikipedia Encyclopedia - Indian Natural History).
- Wulff, E.V. (1950) *An Introduction to Historical Plant Geography*. Chronica Botanica Co., Waltham, Mass, USA
- Young, Kenneth R. Young (2002) Biogeography is neither a social nor a physical science.
- President's Column, *THE BIOGEOGRAPHER*, Newsletter of the Biogeography Specialty Group of the Association of American Geographers (Fall 2002).