The SAGE Handbook of Biogeography

Edited by
Andrew Milllington,
Mark Blumler and
Udo Schickhoff

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List of Contributors

Thomas P. Albright is an Assistant Professor in Geography and is affiliated with the program in Ecology, Evolution, and Conservation Biology at the University of Nevada, Reno. His background includes training in geography (B.S. University of Wisconsin-Madison, MA University of California at Santa Barbara) and biology (PhD and postdoctoral scholarship at UW-Madison) and works at the US Geological Survey's Earth Resources and Observation Science Center. At UNR, he directs the Laboratory for Conservation Biogeography, where research is focused on applying geospatial, statistical, and computational tools to understand biotic responses to climate and environmental change.

Yves Bergeron is Professor at the Université du Québec à Montréal and at the Université du Québec en Abitibi-Témiscamingue. A specialist in forest ecology, he has dedicated his career to studying the dynamics of the Canadian boreal forest and has shown how Canada's boreal forest is controlled by fire and insect epidemics. His work has helped develop new forest management approaches that are inspired by natural dynamics.

Carl Beierkuhnlein holds the Chair of Biogeography at the University of Bayreuth where he directs the Global Change Ecology graduate program within the Elite Network of Bavaria. The research interests of the chair of Biogeography spread over a broad range of biogeographic research areas including the biotic and functional diversity of ecosystems; the spatial organisation of plant species and communities; bioindication; island biogeography focussing on endemic species as well as climate change effects on isolated systems; nature conservation that addresses questions concerning applied ecology. Within the context of climate change, research is conducted for the German Federal Agency for Nature Conservation on the impacts of climate changes on species and biotopes, and within the framework of the Bavarian Climate Program 2020 the concentration is on two projects examining the impacts of climate change on ecosystems. This research is integrated in FORKAST (Climatic Impacts on Ecosystems and Climatic Adaptation Strategies) funded by the Bavarian State Ministry of Sciences, Research and the Arts. Continuing the climate change theme, research is also conducted on vector-borne infectious diseases in climate change for the Bavarian State Ministry of the Environment and Public Health. In collaboration with the chair of disturbance ecology at Bayreuth, experimental research is being conducted on the impacts of extreme weather events on the vegetation.

Shonil A. Bhagwat is a Senior Research Fellow at the School of Geography and the Environment at the University of Oxford. His research interests focus on three areas of investigation: conservation beyond protected-area boundaries; the cultural and spiritual values in conservation; and climate change and conservation.

Mark A. Blumler is Associate Professor in Geography at SUNY-Binghamton in upstate New York. He has wide ranging research and teaching interests in biogeography (life-form and distribution; mediterranean-type ecosystems; invasions; geogenetics; conservation-biogeographical aspects; climate change and ecosystems); plant ecology (succession theory; seed ecology; species-diversity; plant strategies); environmental history (agricultural origins; the Columbian exchange; desertification; history of environmental thought; California; the Middle East) and social theory (diffusion vs. independent invention and cultural

change; environmental vs. social factors in cultural change; Western influences on critical social theory; Carl Barks) which befits somebody trained in the wake of Carl Sauer.

Daniel G. Brown is a Professor in the School of Natural Resources and Environment and faculty associate in the Center for the Study of Complex Systems, Program in the Environment, and the Population Studies Center at the University of Michigan. He has been on the editorial board of *Landscape Ecology*, currently sits on the editorial board of *Journal of Land Use Science*, and has served as guest editor for issues of the *International Journal of Geographical Information Science*, *Computers Environment and Urban Systems*, *Ecological Applications*, *Plant Ecology*, and *GeoCarto International*. A member of the NASA's Land Cover and Land Use Change Science Team since 1997, he also chairs the Land Use and Land Cover Change Steering Group for the US Climate Change Science Program. His research focuses on linking observable landscape patterns and dynamics, obtained through remote sensing, ecological mapping, and digital terrain analysis, with ecological and social processes.

Niall G. Burnside is a Senior Lecturer in Biogeography at the University of Brighton, and is currently Secretary of the Biogeography Research Group of the Royal Geographical Society (UK). Niall has research interests in grassland and woodland ecology, the use of GIS for environmental management and predictive modeling. His expertise covers the development and use of Geographical Information Systems for broad-scale biogeographical and ecological evaluation, and the combination of field-based surveys techniques, remotely sensed data and habitat classification. His PhD and much of his subsequent research has centered on grassland systems and the restoration and management of these under agricultural intensification and climate change.

Jeffrey Cardille is an Assistant Professor at the Université de Montréal. He has a PhD and MS in Environmental Studies (University of Wisconsin-Madison), an MS in Operations Research (Georgia Institute of Technology), and a BS in Applied Mathematics and Computer Science (Carnegie Mellon). He is interested in a wide array of terrestrial and aquatic systems from a landscape ecology perspective, frequently employing landscape metrics, remote sensing, and spatial statistics to solve real-world research questions.

Anthony Cole is a Research Scientist at the New Zealand Centre for Ecological Economics, Palmerston North., New Zealand; and an adjunct Associate Professor in the School of People, Environment and Planning at Massey University.

Mary E. Edwards is Professor of Physical Geography at the University of Southampton. Her interests are centred on global environmental change: understanding climate-driven changes in landscape, vegetation, and ecosystem processes over a range of timescales through palaeoenvironmental records and data-model comparisons. Her main geographic area of interest is the boreal-arctic region, and recent work relates to boreal forest dynamics, including fire disturbance and hydrological regimes, and thermokarst dynamics in relation to biogeochemical processes. Recent collaborative work involves the estimation of past and present plant diversity using novel molecular techniques. A second area of research is concerned with vegetation ecology, biodiversity conservation and land management in both Europe and Madagascar.

Neal J. Enright is Professor of Plant Ecology in the School of Environmental Science at Murdoch University in Perth, Western Australia. He is particularly interested in fire ecology and management, plant species co-existence in high diversity ecosystems, and the demography of woody plants. He has published more than 100 papers and book chapters in the ecological sciences and has co-authored/edited several monographs including *Ecology of the Southern Conifers* (Melbourne University Press/Smithsonian Press 1995).

John Flenley is Professor Emeritus at Massey University, New Zealand, having moved there from Hull University in the late 1970s. He gained his PhD from Australian National University and has had a long

and distinguished career using palynological techniques to unravel questions of archaeology, palaeobotany and palaeoenvironmental science. His field work has mainly been in the Pacific Basin, and his dossier of research includes pioneering research on Easter Island.

Giles M. Foody is Professor of Geographical Information Science at the University of Nottingham, and has a PhD from the University of Sheffield. He applies remote sensing and spatial science to biogeographical and land use issues. He has published over 150 refereed journal articles, 8 books and >175 other publications (book chapters, conference papers etc). He currently serves as Editor-in-chief of International Journal of Remote Sensing (Letters editor 2001-8; EiC 2007–) Editor-in-chief Remote Sensing Letters (Founding editor-in-chief, 2010–) 'Co-ordinating' editor Landscape Ecology (2005–) Associate editor Ecological Informatics & guest editor, vol 2(2), (2005–) Editorial boards (6): Geocarto International (1996–); Remote Sensing of Environment (2005–); International Journal of Applied Remote Sensing (2006–); International Journal of Applied Earth Observation and Geoinformation (2007–); Remote Sensing (2009–); Scottish Geographical Journal (2010–).

Claire Freeman is Associate Professor in Geography and Director of the Planning Programme at the University of Otago, Dunedin New Zealand. Claire came to Otago via lecturing posts at Massey University, Leeds Metropolitan University and the University of the North West in South Africa and has been a planner for the Urban Wildlife Trust in Birmingham, England. Her research interests are in planning for nature, children's environments and community planning. She has undertaken substantial research looking at planning for nature in the city and the need to rethink ecological values when addressing the urban context. Together with colleagues she has recently been involved with a major project to develop a detailed GIS habitat data base for Dunedin city to enhance ecological protection and planning for the city.

Duane A. Griffin is Associate Professor of Geography at Bucknell University in Pennsylvannia. He is actively involved in a number of research projects including fine-scale habitat structure and plant diversity, mapping upland vernal pools of the ridge-and-valley province which is linked a collaborative research on landscape spatial structure and amphibian diversity and development, and a global wildlands project. He also professes an interest in 'The Hollow Earth'.

Geoffrey Griffiths is a Senior Lecturer in Physical Geography at the University of Reading. His research interests cover landscape and biodiversity, GIS and habitat restoration, biodiversity of tropical forests, GIS/remote sensing techniques for predictive vegetation mapping in Brazil and the Mediterranean, understanding the relationship between landscape character and biodiversity, and methods for evaluating ecological quality.

Michael J. Hill is a Professor in Earth System Science and Policy at the University of North Dakota. His research interests include remote sensing, biogeochemical processes and land-use change in savanna and grassland ecosystems, and analysis of coupled human-environment systems using spatial multi-criteria analysis.

Anke V. Jentsch is Professor of Disturbance Ecology and Vegetation Dynamics at the Helmholtz Centre for Environmental Research in the Department of Conservation Biology at the University of Leipzig. Her research includes the response of vegetation to extreme weather events in central Europe (research conducted with the University of Bayreuth); the roles of disturbance in the creation, maintenance and loss of biodiversity; changing land use and biodiversity in cultural landscapes; natural hazards, fire ecology and extreme events; ecosystem dynamics in dry acidic grasslands; and *Corynephorus canescens* as decision support for a habitat connectivity programme in German dry acidic grasslands.

Daniel Kneeshaw is member of the Centre for Forest Studies and a Professor at the Université du Québec à Montréal. He has been active in studying the response of boreal forests to natural disturbances;

primarily disturbances that partially affect the forest canopy such as gaps, windthrow and insect outbreaks. He uses both field techniques and landscape modeling to explore forest responses, to confront public perceptions on different scenarios and to develop forest management and conservation strategies. He is currently editor of *Canadian Journal of Forest Research*.

Anselm Kratochwil is Professor of Ecology at the University of Osnabrück, Germany in the Faculty of Biology and Chemistry. He studied zoology, geobotany, limnology and pedology at the University of Freiburg where he got his Diploma and PhD in Biology. Since 1992 he has been the chair of the Ecology Department and member of the directory board of the Institute of Environmental Systems Research of the University of Osnabrück. He has held lectures, seminars, practical courses and ecological excursions in the field of general ecology, animal ecology, plant ecology, vegetation science and biocenology. His research interest currently focuses on flower-visitor communities of different types of ecosystems, the structure and dynamics of wild-bee communities in different landscapes and the restoration of alluvial landscapes and inland sand-dune communities. Together with Angelika Schwabe he published the textbook *Ökologie der Lebensgemeinschaften* (Ecology of Communities).

John A. Kupfer is a Professor in the Department of Geography at the University of South Carolina. His research examines the manner by which spatial patterns of ecological phenomena interact with and constrain ecological processes. Much of his work stresses vegetation dynamics in human-modified systems, and his projects regularly incorporate quantitative methods and computer techniques, including ecosystem modeling, GIS, remote sensing and geostatistics. Much of his work has focused on the effects of forest fragmentation, and his paper (co-authored by George Malanson and Scott Franklin) 'Not seeing the ocean for the islands: The influence of matrix-based processes on forest fragmentation effects' was awarded the 2007 Henry Cowles Award for Excellence in Publication by the Biogeography Specialty Group of the Association of American Geographers. He received his BA from Valparaiso University and his MA and PhD from the University of Iowa.

Timo Kuuluvainen is an Associate Professor in the Department of Forest Sciences at the University of Helsinki. His research has focused on the fundamental interactions between structure, dynamics and biodiversity of the boreal forest, using both empirical and modeling approaches. He has published more than 100 peer-reviewed papers and text-book chapters. His current research is centered on using ecological understanding to develop methods of restoration and ecosystem management of the boreal forest.

Pedro J. Leitão is a Postdoctoral Researcher at the Geomatics Laboratory of the Humboldt-Universität zu Berlin. Pedro's main research interest is on spatial data analysis in ecology and biogeography. He is particularly interested in the use of spatial and remotely sensed data for ecological research and biodiversity and ecosystem monitoring. He is experienced with most remote sensing data products (optical, thermal, hyperspectral, laser scanning, etc.), and he has a strong focus both on methods development for information extraction and data analysis and on their application for addressing specific research questions. Amongst other things, he has done extensive research on steppe and farmland birds, from regional to global scales, studying their patterns of distribution and habitat selection, and respective effects of climatic and resource availability changes.

George P. Malanson is the Coleman-Miller Professor in the Department of Geography at the University of Iowa. His research is primarily in biogeography, addressing how spatial patterns and processes affect vegetation dynamics in response to human-induced changes such as climatic change and altered disturbance regimes. His research integrates fieldwork, computer simulations, and statistical analyses. Much of the fieldwork is based in the northern Rocky Mountains. Recently, he has directed more attention toward aspects of land-use and land-cover change. He is Editor-for-Biogeography of *Physical Geography*, Associate Editor of *Arctic, Antarctic, and Alpine Research* and is on the editorial boards of *Annals of the Association of American Geographers* and *Geography Compass*.

Rob Marchant has been a Senior Lecturer in the Environment Department, University of York, UK since 2005. Previously he held posts at the University of Leicester; Trinity College, Dublin; and the University of Amsterdam. His PhD was on the Late Quaternary montane vegetation dynamics in Bwindi-Impenetrable Forest, southwest Uganda. His research continues to focus on vegetation dynamics and ecosystem change. In particular, he uses ecological modelling, archaeological and biogeographical data to determine the role of past events in shaping the present day composition of vegetation, especially in the tropics.

Carlos F. Mena is an Ecuadorian doctoral student in the Department of Geography and a pre-doctoral trainee in the NSF IGERT Program at the Carolina Population Center, University of North Carolina at Chapel Hill. He is also the recipient of a NASA Fellowship (2004-2007) from the Land Cover/Land Use Change Program. His research involves the study of land-use and land-cover change in the Northern Ecuadorian Amazon, and biocomplexity in coupled human-natural systems. Specifically, his research deals with the relationships among socioeconomic factors, and demographic variables, and forest and agricultural transitions in frontier environments. He has an undergraduate degree in Geographic Engineering from Escuela Politecnica del Ejercito, Quito, Ecuador and a graduate degree in Environmental Sciences from Florida International University, Florida, USA.

Annette Menzel has been Professor of Ecological Cimatology at the Techncial University of Munich since 2007. She studied forest science at Ludwig Maximilians University Munich and worked in the Bavarian state forest administration. Her research interests focus on plant phenology and climate change.

Joseph P. Messina is a Professor of Geography at Michigan State University. He holds a joint appointment with the Department of Geography and the Center for Global Change and Earth Observations. He is also a faculty member of the Environmental Science and Policy Program, and the Center for Water Sciences. He completed his PhD in Geography at the University of North Carolina at Chapel Hill in 2001 focusing on land-use and land-cover change in the Ecuadorian Amazon. His current research includes continuing work in Ecuador and Northeast Thailand, new work in northern China, and basic GIScience research on spatial error models, simulation models, and software interface development.

Andrew C. Millington is Dean of the School of the Environment at Flinders University, Adelaide. His current research focuses on land-use change and incorporates both its drivers, and its consequences for various types of ecosystems: he relies on remote sensing as a major research tool. He has worked in a diverse array of biomes covering the tropics and sub-tropics of South America, Africa, western Asia and Australia. He has worked for the World Bank, UN and EU; and has held academic positions at Texas A&M, Leicester, Reading and Sierra Leone Universities, and obtained an MA from the University of Colorado and a DPhil from the University of Sussex. He edited *The Geographical Journal* and is currently on the editorial boards of *Journal of Land Use Science,* and *Arid Land Restoration and Rehabilitation*. He was formerly chair of the IGU Commission on Biogeography and Biodiversity.

Jayalaxshmi Mistry is Senior Lecturer of Geography at Royal Holloway, University of London. Her main research interests are in natural resource and land management. Her current work is looking at ways of linking local livelihoods with biodiversity conservation in the Rupununi savannas of Guyana and in the use of participatory video for empowering local communities to take action about their natural resource management issues. She is also concerned with fire management in tropical savannas, particularly decision-making for fire use and indigenous and traditional fire management in the cerrado of Brazil. She is the author of two books on tropical savannas; a student textbook '*World Savannas*' and an edited volume '*Savannas and dry forests: linking people with nature*'.

Ingo Möller studied geography, botany, soil science and geology. His PhD thesis covers the plant sociology and vegetation ecology of north-western Svalbard. He held a couple of positions in German universities and research institutions, and is presently as Senior Scientist at the Federal Institute of Geosciences and Natural Resources, Hannover. Particular research interests are in arctic and tropical vegetation and ecology as well as carbon budgets and cycles on local to regional scales. Field work has led him several times to Svalbard and the Canadian Arctic.

Jens Mutke is Curator (Akademischer Oberrat) at the Nees Institute for Biodiversity of Plants at the University of Bonn. He is a member of the German National Scientific Committee of DIVERSITAS within the Earth System Science Partnership. He holds a Diploma in Biology and a PhD in Botany. His main research interests are macroecology, conservation biogeography, and tropical ecology. Current research projects focus on continental to global patterns of land plant diversity and their implications for nature conservation. He did field studies on the ecology of tropical montane forests and on the vegetation of rock outcrops (inselbergs) in South America.

Joanne M. Nightingale currently works at NASA's Goddard Space Flight Center, and is responsible for coordinating EOS global land product validation activities and currently chairs the CEOS Working Group on Calibration and Validation, sub-group for Land Product Validation. Joanne obtained her Ph.D. in geography from the University of Queensland in Australia and has completed two post-doctoral research positions at universities within the United States. Her research interests center on remote sensing and ecosystem/biogeochemical modeling with emphasis on incorporating remotely sensed information into regional ecosystem models that assess seasonal inter- and intra-annual trends in carbon storage and terrestrial productivity in addition to fostering validation efforts for improving the accuracy of satellite-derived land products.

Patrick E. Osborne is a Senior Lecturer in the School of Civil Engineering and the Environment at the University of Southampton. His recent research focuses on applied ecological issues, especially in relation to spatial ecology and the conservation of agricultural birds. In the last decade he has worked on a multi-scale study of habitat selection by steppe birds using remote sensing and GIS, and is currently starting work on modelling the distributions of steppe birds at the global scale. He is also training Russian researchers to survey bustards using Distance Sampling and to build a spatial model of the bustard's distribution in Saratov Oblast, Russia.

Josep Peñuelas is a Research Professor of the National Research Council of Spain (CSIC), and Director of the Global Ecology Unit CREAF-CEAB-CSIC located at CREAF (Center for Ecological Research and Forestry Applications)-Universitat Autònoma de Barcelona. He works on plant ecophysiology and atmosphere-biosphere interactions; and has recently investigated global change, climate change, atmospheric pollution, biogenic VOC emissions, remote sensing, and functioning and structure of Mediterranean terrestrial plants and ecosystems. Alongside his academic publications he tries to popularize science issues in journals and Spanish newspapers. He has been a visiting professor at over 20 universities in North and Central America, Europe, Asia and Australia. He has received national (Conde de Barcelona 1990, Medi Ambient Institut d'Estudis Catalans-Caixa Sabadell 2008, I Premi Recerca de Catalunya 2010) and international (NASA 1993, Science Ministry of Japan 1998) awards. He has been president of Institució Catalana d'Història Natural and adviser of the Consell Asessor per al Desenvolupament Sostenible of the Generalitat of Catalonia.

Stuart R. Phinn is a Professor of Geography in the School of Geography, Planning and Environmental Management at the University of Queensland. He is currently the Director of Australia's Terrestrial Ecosystem Research Network (www.tern.org.au). He also directs the Centre for Spatial Environmental Research (www.gpem.uq.edu.au/cser), which focuses on collaborative research and training in all areas of geographic information science. His own work develops remote sensing solutions for environmental monitoring and management applications by combining field and image data sets.

Brett R. Riddle is a Professor in the School of Life Sciences at the University of Nevada, Las Vegas, and has a PhD from the University of New Mexico. His research focuses primarily on the history of biodiversity in western North America, with ongoing projects including: historical assembly of the warm desert biotas; phylogeography of Great Basin montane island biotas; and molecular systematics and biogeography of diverse North American rodent groups. He is co-founder and past President of the International Biogeography Society, an editor of the Journal of Biogeography, and an associate editor of Systematic Biology.

Udo Schickhoff has been Professor of Biogeography in the Institute of Geography at the University of Hamburg since 2004, prior to which he held professorial positions in geography at the University of Bonn, landscape ecology at the University of Rostock, and was foundation professor in the Institute of Botany at the University of Griefswald. He is currently working on two research projects funded by the Volkswagen-Stiftung Research Foundation, in one he coordinates a project on the impact of the transformation process on human-environmental interactions in southern Kyrgyzstan for the universities of Hamburg, Berlin, Bonn and several institutions in Kyrgyzstan. He also works on a project on changing pastoral ecosystems in western Mongolia (Khovd Aimag) using a landscape-ecological approach for assessing grazing land degradation and grazing capacity. He has previously worked on research projects in Germany and the Karakoram. He is currently chair of the IGU Commission on Biogeography and Biodiversity.

Angelika Schwabe is Professor of Botany with main emphasis on vegetation ecology and geobotany at Darmstadt University of Technology, Germany. She studied biology and geography and carried out her PhD in Geobotany at the University of Freiburg, Germany. After her habilitation in Freiburg she was awarded a Heisenberg Grant by the German Research Foundation (DFG). Her research focuses on vegetation complexes, scale-dependent processes and plant-animal interactions. She has experience both in phytosociological classification approaches as well as in ecological field experiments. She studied vegetation complexes of extensive grassland, running waters and alpine dry grassland. Presently she is especially involved in projects dealing with strategies for the protection of endangered sandy grassland, e.g., by extensive livestock grazing, and in restoring endangered habitats. She is a member of the Advisory Council of the International Association for Vegetation Science.

Tim H. Sparks is a Research Fellow in the Institute of Advanced Studies at the Technical University of Munich. Until 1991 he worked in agricultural research switching to ecological research at the Monks Wood Research Station until 2009. In 1998 he founded the UK Phenology Network and has represented the UK in collaborative research programmes in phenology. Tim is a visiting professor at the Poznań University of Life Sciences, and at the University of Liverpool and was a contributing author to the last IPCC report. He is an editor of *Climate Research*, and on the editorial boards of five other journals. Immediately prior to starting his fellowship he was working on biodiversity indicators at the University of Cambridge.

Chris Stoate is Head of Research at the Game and Wildlife Conservation Trust's 'Allerton Project', a research and demonstration farm in Leicestershire, England. He has contributed to numerous UK government and EU-funded research projects and is the author of more than eighty research papers, and a book, '*Exploring a Productive Landscape'*. He has researched the ecology and management of farming systems in West Africa and southern Europe, as well as in England and is a farmer in his own right.

David M. Taylor is currently University Professor of Geography at Trinity College, University of Dublin, a position he has held since January 2001. Prior to his appointment at Trinity College, David was a member of faculty at the National University of Singapore (1997-2001) and at the University of Hull, UK (1989-1997). David's DPhil is on the dynamics of tropical vegetation in central Africa during the Late Quaternary (entitled The vegetation history of southwestern Uganda over the last 40,000 years). His main research interest continues to be the dynamics of ecosystems at low latitudes over the last few thousands of years.

Dietbert Thannheiser studied geography, biology and geology. His PhD thesis is on the vegetation of northern Norway. Afterwards he focused on coastal vegetation and arctic environments. From 1970 to 1982 he was Associate Professor at the University of Münster, and in 1983 he was appointed as Professor at the Institute of Geography of the University of Hamburg, He has gained extensive polar field experience in the Canadian Arctic, Svalbard, Iceland, and Greenland.

Piotr Tryjanowski is Director of the Zoological Institute at the University of Poznan, and one of the most active avian ecologists and researchers in Poland. He was previously a Trustee of Birdlife Poland and is an advisor to EcoFund. His research interests cover a wide spectrum of behavioural ecological and evolution issues. He leads research on different ecological groups and taxa, though birds of agricultural environments are undoubtedly closest to his heart. In particular he works on population ecology; synchronization phenomenon; environmental effects, and the influence climate on behavioural ecology.

Monica G. Turner is the Eugene P. Odum Professor of Ecology in the Department of Zoology, University of Wisconsin-Madison. She obtained her PhD in ecology in 1985 from the University of Georgia, spent seven years as a research scientist at Oak Ridge National Laboratory, and joined the faculty of UW-Madison in 1994. She has published over 190 scientific papers and has authored or edited six books, and she is co-editor in chief of the journal, *Ecosystems*. She was elected to the National Academy of Sciences in 2004. Her research emphasizes the causes and consequences of spatial heterogeneity in ecological systems, focusing largely on ecosystem and landscape ecology in forested systems. Research areas include: interactions of disturbance regimes (fire and insects), vegetation dynamics, and nutrient cycling in the Greater Yellowstone Ecosystem; effects of historic and contemporary land-use patterns on southern Appalachian landscapes; and land-water interactions in north temperate landscapes.

Yordan Uzunov is Associate Professor of Hydrobiology and Head of the Department of Bio-Indication and Environmental Risk Assessment of the Central Laboratory of General Ecology at the Bulgarian Academy of Sciences. He is an aquatic ecologist devoted to study and implement knowledge about the structure and functions of riverine and lacustrine ecosystems, in particular bottom invertebrates, in environmental monitoring, stream/river typology and classification of ecological status of water bodies. He has introduced modern approaches within hydrobiological studies of Bulgarian rivers, lakes and swamps/wetlands, and developed the methodology and methods for the national bio-monitoring of rivers. He was formerly Deputy Minister of the Environment (1992-1997); since 2004 has been a member of the UN Secretary General's Advisory Board on Water and Sanitation.

Robert Voeks is a Professor of Geography at California State University—Fullerton and Chair of the Environmental Studies Graduate Program. His research focuses on tropical ethnobotany and cultural ecology—especially medicinal plants and healing systems—in Brazil and Borneo. He is currently vice-president of the California Geographical Society, and serves on the editorial board for the *International Journal of Environmental Science and Technology*.

Ioannis Vogiatzakis is a Research Fellow in the Centre for Agri-Environmental Studies at the Univeristy of Reading and has research interests in plant ecology and biogeography of Mediterranean islands and mountains, GIS and remote sensing for vegetation and habitat modeling, landscape character assessment and habitat restoration, the effects of landscape structure and habitat quality on biodiversity, and the integration of species and habitat data for nature conservation evaluation.

Stephen Waite is a Principal Lecturer in Ecology at the University of Brighton. He has a BSc Hon. in Biology and a DPhil in plant population ecology from the University of Sussex and a BA in mathematics from the Open University. He has written an advanced text on the statistical analysis of environmental data and has published extensively on various aspects of applied ecology. He has particular research interests in the relationships between plant reproductive strategies, germination ecology and species distribution and population viability at a local and landscape scale. Current research interests include the biogeography of fragmented woodland and chalk-heath plant communities.

Stephen J. Walsh is a Professor of Geography, member of the Ecology Curriculum, and Research Fellow of the Carolina Population Center at the University of North Carolina – Chapel Hill, USA. He is on the editorial boards of *Plant Ecology, GeoCarto International*, and the *Annals of the Association of American Geographers*, he has co-edited special issues in the *Journal of Vegetation Science, Geomorphology*, and *Photogrammetric Engineering and Remote Sensing*. Since 2001, he has co-edited a series of books for Kluwer Academic Publishers—*GIS and Remote Sensing Applications in Biogeography and Ecology* (2001, Millington, Walsh, Osborne); *Linking People, Place, and Policy: A GIScience Approach* (2002, Walsh and Crews-Meyer); and *People and the Environment: Approaches for Linking Household and Community Surveys to Remote Sensing and GIS* (2003, Fox, Rindfuss, Walsh, Mishra); and in 2003 for Elsevier, *Mountain Geomorphology – Integrated Earth Systems* (Butler, Walsh, Malanson). Specific research foci are on pattern and process at the alpine treeline, biocomplexity in coupled human-natural systems, scale dependence and information scaling, and land-use and land-cover dynamics using spatial simulation models, GIS, and remote sensing.

Katherine J. Willis works at Oxford University where she holds the Tasso Leventis Chair of Biodiversity and is Director of the Biodiversity Institute in the Zoology Department. She established the Oxford Long-term Ecology Laboratory in 2002 and was made a Professor of Long-term Ecology in 2008. She moved to her current position in Zoology in October 2010. She is an Adjunct Professor (Professor II) in the Department of Biology, University of Bergen, Norway. She has recently been elected to the position of Director-at-Large of the International Biogeography Society; was awarded the Lyell Fund for 2008 by the Geological Society of London, elected as a Fellow of the Royal Geological Society in 2009, and made a Foreign Member of the Norwegian Academy of Sciences and Letters in 2010. Her research interests focus on the relationship between long-term (>50 years) ecosystem dynamics and environmental change.

Kenneth R. Young has traveled in and researched the tropics of Central and South America since the 1970s. Currently, he is focusing his research on the dynamism of tropical landscapes, the alterations caused by climate change, and the challenges in carrying out biodiversity conservation. He is currently Professor and Head of the Department of Geography and the Environment of the University of Texas at Austin.

Foreword

Imagine the scene. Four biogeographers – an American, two Germans and the fourth British – on a field excursion, bumping through the wilds of the Caucasus in a minibus accompanied by Armenian geographers and biologists. Between stops, with dust billowing from under the bus, talk turned to what our undergraduates were being taught in upstate New York, the English Midlands and two German universities – one in the former East, the other in the former West. As the afternoon heat became increasingly stifling, talk shifted effortlessly to contemporary biogeographical research and (post)graduate training in those three countries, and the differences in what we had presented at the pre-field course symposium in Yerevan State University a few days earlier compared to the talks of our Armenian colleagues who had been trained in the Soviet School of Geography. The differences between our biogeographies appeared as distant as the political doctrines in the Soviet Republic of Armenia and East Germany were from those in West Germany, the UK and the USA a decade earlier. It was June 2000.

Such conversations are commonplace when academics gather – the small talk between stops on field trips, or tales of academia told and retold in bars at conferences the world over. Such conversations, we tell our graduate students, are "…the real business of conferences". Conversations they remain, to be recalled, embellished and rehearsed again the next time old friends meet. But not always.

In this case the conversation took on a life of its own when the British biogeographer was approached not long afterwards by Robert Rojek who was developing a series of physical geography titles for Sage Publication's Handbook Series.

It's spring in New York City. Sitting in a bar in the Avenue of the Americas during the annual conference of the Association of American Geographers are the four biogeographers who had met in Armenia, two other German biogeographers, and Robert Rojek and David Mainwearing from Sage. The heated topic of conversation was the *Handbook of Biogeography*. Why the heat? Simple, we were a group of academics discussing the chapters that each of us felt *had* to be included in the *Handbook of Biogeography*. Our experiences were so different and our feelings so strong, that the list of chapters was well over fifty. Scrawled on Andrew Millington's notes from this discussion is "70?" and "Can we publish a two-volume handbook?" It was April 2001.

Left to the academics the debate would probably never have been resolved. Business sense prevailed. Discussions continued for months. "Around 40 chapters" was the strong advice from Robert Rojek. An editorial team was established. Glenn MacDonald was consulted over matters palaeoecological. We set about finalizing topics and potential authors. It was 2004 when authors were first approached and up to two years before we had our final list. As we write this introduction years later we understand the enormity of the task that that field trip conversation a decade ago in Armenia led prompted. Should it have remained one of the conversations that would be recalled, embellished and rehearsed again the next time we met? We think not. We hope you agree as you continue reading.

Andrew Millington, Mark Blumler and Udo Schickhoff
Adelaide, Binghamton, College Station and Hamburg.

1

Situating Contemporary Biogeography

Andrew C. Millington, Mark A. Blumler, and Udo Schickhoff

1.1 A SHARED ENDEAVOR

Biogeography is shared between three globally recognized and broad disciplines: biology, geography, and geology. Though all biogeographers share a common, natural history or ancestry dating back to the eighteenth and nineteenth centuries, the twentieth century has witnessed divergence as its practitioners have evolved to populate different niches within each of their three disciplinary homes. While we do not go as far as Mike Meadows, who opens his 1997 review of the subdiscipline with "Biogeography is as diverse as the organisms that form its subject matter" (583), we agree with the biogeographical analogy alluded to in the title of his article—there has been adaptive radiation of biogeography.

Biogeography's history has been partly written (e.g., Cox and Moore, 2005; Ebach and Tangey, 2007; Lomolino et al., 2004), but a truly comprehensive analysis of how it has evolved from its common origin to something distinctive in each of the three disciplines from a global perspective still eludes us. This book, with its aim of reflecting on contemporary biogeographical trends within geography, is not the place for such an analysis. Nonetheless in the following chapter (Blumler et al., this volume), we review how biogeographical thought has evolved (with a geographical emphasis) and in this chapter we offer an analysis of contemporary 'difference' in biogeography. By this, we mean the differences between styles of biogeography within geography in different parts of the academy. Having identified these, we suggest how they have evolved and what the divergence they have fostered may mean for the future of biogeography.

The aim of this chapter is primarily to define what contemporary biogeography is within its 'geographical niche'. We do not attempt to do this for the 'geological' and 'biological' niches because we are introducing a book on a sub-discipline of geography, as interesting as comparing these other niches might be. In writing it this way, we acknowledge this does provide a highly biased perspective. First, we describe the main differences in the teaching of biogeography in geography departments around the world. We then look at the main contemporary biogeographical research themes in geography before providing a preliminary analysis as to how these patterns have emerged. Next, we consider what the apparent fragmentation within biogeography might mean for the sub-discipline within geography. In this, we pay particular attention to the challenges and opportunities it might pose for the future of geographical biogeography. We conclude by outlining the structure of this book and considering the rationale behind it.

1.2 BIOGEOGRAPHY IS THRIVING—BUT NOT EVERYWHERE

Biogeography is recognised, but is it thriving? Were it not recognised as a valid subdivision of our subject, it is unlikely that SAGE would have included it in its handbook survey of geography's

sub-disciplines. However, this has not always been the case in Anglo-American academia (see, for example, Gregory, 2000). The status of biogeography in English-speaking geography departments dramatically increased from the mid-1960s to the early 1980s (e.g., Tivy, 1982; Watts' comment on its status in the United Kingdom (1978); for North America, see Rogers, 1983). Before then it was generally weakly developed and non-existent in most departments. However, the English-speaking world is but one geographical arena in which biogeography is taught and researched. The common ancestry of biogeography lies in the geographical borders of modern-day Germany. Biogeography is currently a strong sub-discipline in German geography departments and has been so throughout the twentieth century. The influence of German-speaking natural historians, geologists, biologists, and geographers is fundamental to the story of biogeography (see, for example, the following chapter; Cox and Moore, 2005; Ebach and Tangey, 2007; Lomolino et al., 2010). The 'Continental School' of biogeography, which evolved mainly in German-speaking Europe, remains strong in Central and Eastern Europe and in the countries of the former Soviet Union. It is a diversion at this point to speculate that if SAGE had launched a geography handbook series in 1965—when it was founded—it is unlikely it would have included biogeography. By contrast, it is very likely that a German academic publisher would have included something that we would recognize today as a biogeography handbook.

A global survey of undergraduate and graduate biogeography teaching (in geography departments) carried out for the International Geographical Union between 1998 and 2002 and a mid-1990s survey of biogeography in British geography departments (Table 1.1) revealed the following:

- Biogeography was well established and actively pursued in the majority of the geography departments in Canada, Germany, the United Kingdom, and the United States.
- It was also well developed in Australian and New Zealand geography departments. Many of these departments had added biogeography to their

Table 1.1 Summary of IGU survey of biogeography teaching, 1998–2002

Area	*Proportion of people teaching biogeography who declare themselves primarily biogeographers (%)*	*Countries with > three geography departments teaching biogeography*	*Notes*
Europe	66	Germany, United Kingdom[1]	Little[2] biogeography in geography departments in Scandinavia, Netherlands, Belgium, France, Italy, Portugal, Spain
Asia	48	India, Russia, China	China, Japan, and Russia are underrepresented in the returns. Little biogeography in geography departments in western Asia
Africa	36	South Africa	Almost no biogeography taught in geography departments in francophone and lusophone African universities, or in North Africa
North America	55	Canada, United States	
South and Central America	36	Argentina, Chile	Brazil and Mexico are underrepresented in the returns
Pacific	54	Australia, New Zealand	

1 The United Kingdom was not included in the IGU survey as the BSG (see Table 1.2) had surveyed the status of biogeography in U.K. universities a few years previously.

2 The qualitative descriptor is used in relation to the number of geography departments in each country.

curricula around the same time as the expansion in Great Britain and North America in the 1960s and 1970s. Biogeography was a core element of most curricula at the time of the survey; often more than one person was active in teaching biogeography.

- The situation in continental Europe (outside Germany) was split between two camps at least. In eastern and central Europe (e.g., Austria, Romania, Poland, and German-speaking Swiss universities), biogeography was taught in a number of geography departments. They generally tended to have one biogeographer, whereas some departments in Germany had two or more: for example, Bayreuth, Erlangen, Münster, and Bonn, as did many departments in Canada, the United Kingdom, and the United States. By contrast, very little biogeography was taught in geography departments in France and in French-speaking departments in Belgium and Switzerland and many of the countries of the Mediterranean littoral. For example, no biogeography was taught in Greek geography departments, and there was little taught in Italy, Portugal or Spain.
- In English-speaking universities in the Caribbean, Africa, Asia, and the Pacific, biogeography was considered to be a legitimate and an even important part of curricula, but its inclusion appeared to depend on the efforts of one person in small departments who was not necessarily a biogeographer. This gave it a rather precarious foothold in the education of geographers and, therefore, shaky foundations for research and application to pressing 'development' issues. This was particularly so for countries with only one university, but the general observation applies to countries with many universities (e.g., India, Nigeria, and South Africa). We consider that the place of biogeography in curricula in these universities is due to their establishment by, and close links with, other Commonwealth universities throughout the twentieth century. In fact, some African universities were established as satellite campuses of British universities: for example, Fourah Bay College (part of the University of Sierra Leone) was part of Durham. Additionally, many people teaching in these universities obtained their higher degrees in Australia, Canada, New Zealand, the United Kingdom, and the United States, and then from often a very narrow range of universities in those countries (e.g., Cambridge, Durham, Liverpool, Oxford, and Swansea in Great Britain). Further evidence of the links with Anglo-American biogeography in the developed world is the use of undergraduate textbooks published in the United Kingdom and United States, most notably Cox and Moore's *Biogeography: An Ecological and Evolutionary Approach*'[1], though in India at least two biogeography textbooks have been published in English by Indian geographers (Bhattacharyya, 2003; Methani and Sinha, 2010) for Indian geography undergraduates, and Meadows (1985) has published a textbook in South Africa.
- The lack of biogeography teaching that was reported in French geography was reflected also in an apparent dearth of biogeography in geography departments throughout the francophone zone, though there were exceptions, for example, Universitié Nationale de Bénin. A similar trend was observed in lusophone geography departments in Africa and Asia.
- The situation in Central and South America was the most complex of the developing world regions. Biogeography is well embedded in a number of geography departments in Argentina[2] and Chile, where geography is a strong discipline. This is related to its European (mainly Germanic) roots, and it probably applies to southern Brazil as it is a phenomenon of the southern cone countries of South America (Gade, 2006a, 2006b). However, in the rest of Brazil,[3] where geography in general is also strong, the curriculum is dominated by human geography themes and biogeography is poorly represented. In other Latin American countries where geography is taught at university, biogeography was either not represented (e.g., Colombia, Guatemala) or taught in only one of a number of geography departments (e.g., Costa Rica, Ecuador). There were no geography departments in Bolivia and Paraguay.
- Departments in China, Mongolia, Japan, and the former Soviet Union were not adequately surveyed at the turn of the millennium. Subsequently, we have interviewed geographers and biologists about the status of biogeography in these countries in writing this chapter, and consulted gazetteers of geographers and, in the case of China consulted Leng et al. (2009). Biogeography is weakly developed in Japanese geography departments, in a somewhat dated directory of Japanese geographers only six geographers in 225 departments listed their specialist area as biogeography: four described themselves as vegetation geographers, one a biogeographer and another a palaeobiologist (The Association of Japanese Geographers, 1991). The dearth of Japanese biogeographers is stark when compared to work on vegetation science emanating from Japanese biology departments. This body of work is strongly influenced by German geobotanists, and it is epitomized by Akira Miyawaki (1924–present), who established a school of phytosociology, syntaxonomy, and plant geography at Yokohama National University and who edited the ten-volume *The Vegetation of Japan* (1980–89). Around 1950, phytogeography

and zoogeography courses were launched in geography departments in universities in China, and simultaneously, teaching materials were published. These courses were merged later into biogeography courses that were taught as part of contemporary geography curricula but were also offered in biology, ecology, natural resource management, and environmental science departments. Geographers have responded by publishing biogeography textbooks (e.g., Northeast Normal University, 1989; Yin, 2004; Chen, 2007). In 2007, the Higher Education Press translated the seventh edition of Cox and Moore's textbook. Biogeography in Russia is so well developed that some universities have biogeography departments: for example, Moscow State University. There are also several biogeography textbooks in Russian, but complete information on biogeography teaching in the former Soviet Union still eludes us and is a great lacuna in this handbook.

What we teach is not necessarily what we research, and our teaching may also be contingent on what courses other biogeographers, in biology and geology departments, in our universities are already offering. Notwithstanding this, and the fact that any global survey is likely to suffer from geographical differences in response rates, the >300 responses obtained paint a picture of uneven training in biogeography to undergraduate and graduate students globally. While it was a core element in many departments where the Anglo-American and Continental (German) School traditions hold sway, it was poorly represented elsewhere. A further concern is the low proportion of people actually teaching biogeography who declared their primary (research/scholarship) interest to be biogeography (Table 1.1). This ranged from 66% in Europe to 36% in Africa and Latin America. The high proportion in Europe can be attributed to the long history of the sub-discipline in most European countries and the larger size of many departments, compared to departments in Africa and Latin America. However, even in Europe, these proportions were lower than anticipated. There were (and still are) departments where significant numbers of graduates are being trained and undergraduate programs are buoyant (e.g., Oxford; University College London in the United Kingdom; British Columbia; Tennessee; UCLA; Wisconsin in North America; Bayreuth, Bonn, Erlangen, Münster, and Trier in Germany; Basel in Switzerland). The global unevenness in teaching evident in the survey is mainly an outcome of four things: (a) the strength of physical geography within geography generally within a country—where it is strong, biogeography is more likely to be strong; (b) the perceived importance, relevance, and utility of biogeography to national research and teaching goals; (c) the links between biogeographers in biology, geography, and geology within a country; and (d) the roles that influential biogeographers play or have played in the past in promoting the subject.

The situation with respect to research is more complex. Many biogeographers, perhaps the majority, conduct research in the countries where they teach. But biogeographers' enduring interests in other parts of the world, which we consider date back to the investigations of Darwin, Humboldt, Linneaus, and Wallace, and the expansion of Victorian natural history and science, mean that a significant amount of research has been and still is prosecuted in countries where biogeography's foothold in geography is precarious. For example, this book's editors have conducted research in countries where geography is not a university-level subject (e.g., Bolivia) or where biogeography is poorly represented in geography departments (e.g., Israel, Pakistan, Kyrgyzstan, and Yemen). Biogeographers who reside outside such countries—like the editors—have been able to obtain funds for research and (our own) doctoral training in these countries relatively easily. Yet it appears that in doing so developed world biogeographers have generally neglected to use their influence to ensure that biogeography attains a permanent place in geography curricula in the countries where geography is taught. We are wealthy researchers but poor missionaries: biogeographers appear to neglect the reproduction of our subject outside their own countries.

Progressing beyond the 1990's survey has been possible because of detailed reviews carried out by Young et al. (2004) and Veblen (1989) for North America, and Joyce (2009) for the United Kingdom. As far as we could ascertain no such reviews exist for other countries. In Germany, biogeography has gained a strong foothold within physical geography during the twentieth century. This can be attributed to influential geographers, such as Carl Troll and Josef Schmithüsen, who developed the concept of landscape ecology out of their biogeographical perspectives. In spite of the decline of geography (including biogeography) at some German universities due to fiscal constraints, biogeography has recently become a thriving sub-discipline and is expanding at universities such as Trier and Bayreuth. The significant upturn in German biogeography is related to the growing importance of research on implications of climate change and land degradation, but it is also due to the change from a more descriptively aligned discipline into a modern environmental science with strong reference to organisms and their spatial patterns. The increasing use of biogeographical experiments, augmenting the

acceptance of biogeography within biology, has also contributed to the 'biogeography boom'. Interestingly, a few years after the establishment of the Working Group Biogeography within the Association of Geographers at German Universities (VGDH) in 1998, a Specialist Group on Macroecology was founded within the Ecological Society of Germany, Austria, and Switzerland (GfÖ). Scrutinizing the program of the macroecology meetings, it is thinly disguised biogeography, although the macroecology proponents who are biologists (mostly zoologists) consider it to be a 'young discipline'. Apparently, Middle European biologists doing biogeography hesitate to call it biogeography and instead prefer to use the term macroecology. Thus, there is recent biogeographical research that is not labeled biogeography, a situation that might hold for other regions as well.

Within the United States, the recent growth in biogeography has elevated it to more-or-less equal status with the more traditional branches of physical geography—geomorphology and climatology; the membership of the Association of American Geographers (AAG) biogeography specialty group (441) now exceeds that of the climate and geomorphology groups (411 and 393 respectively, 2010 data). In the United Kingdom, biogeography plays a secondary role to geomorphology within physical geography. In Germany, the number of physical geographers who declare biogeography as their topical specialization (36, 2010 data) ranks fifth after geomorphology (134), climate (79), soils (75), and hydrology/glaciology (55). However, the German biogeography community is increasing and catching up with the other sub-disciplines, reflected inter alia in the establishment of the Working Group Biogeography within the Association of Geographers at German Universities (VGDH). Internationally, the formation of the interdisciplinary International Biogeography Society in 2003 and the Biogeography and Biodiversity Commission of the International Geographical Union (IGU) is raising the profile of biogeography within its three disciplines, though perhaps least so in geography (Table 1.2).

1.3 WHAT IS BIOGEOGRAPHY?

Notwithstanding the exceptions noted above, biogeography is generally well represented in geography departments around the world. It is also practised in biology and geology, but it was beyond our purview to comment on their recent development and global status in this book. Beyond these three disciplines, biogeography is taught and researched in environmental science and environmental studies departments, and in several branches of applied biology such as forestry, range management, horticulture, and pest management. Given these different disciplinary foci, the answer to the fundamental question 'What is biogeography?' will differ according to one's disciplinary home or department. The answer to the same question, asked specifically of geographers, could also vary according to where one has been trained, what teaching and research experiences one has had, where one currently is employed, and the length of one's career. If you were trained in and then spent your career in German geography departments, your biogeographical preoccupations would be different from those of a biogeographer who had trained and worked simultaneously in the United States. Evidence for this observation will be readily apparent as you read this book; compare, for example, the biogeographical emphases evident in the chapters on classification, biodiversity gradients, disturbance, and polar and mountain environments in this book (all written by German biogeographers) and consider how they might have been written by an American or a Canadian biogeographer. Biogeography evolves. So,

Table 1.2 National affinity groups for biogeographers organised by geographers, and other key organisations

National organisation	*Affinity group*	*Year established*
Royal Geographical Society with the Institute of British Geographers	Biogeography Research Group	1974
Association of American Geographers	Biogeography Speciality Group	1981
International Geographical Union	Biogeography and Biodiversity Commission	1996
Association of Geographers at German Universities	Working Group Biogeography	1998
International Biogeography Society		2003

somebody with a recently acquired Ph.D. entering a British geography department as a biogeographer will have a different set of research questions and skills from those of a biogeographer who has been in the same department for 30 years or more. A European- or North American-trained biogeographer who takes up a university position in Australia, New Zealand, or South Africa will find different, as well as similar, biogeographical concerns to those of colleagues they left behind. Geography is a mosaic of geographical and historical contingencies (Livingstone, 1994; Martin, 2005); these maxims can be applied to many, if not all, of geography's sub-disciplines, not just biogeography. In biogeography, historical contingency arises among late-nineteenth century natural historians at which time different subject material gained prominence in different countries due to the establishment of schools of geographical thought; and the presence of biogeographers in other disciplines (especially biology and geology) and the levels of interaction (bio)geographers[4] had with them.

Maybe the fundamental question we should then ask in *this* book is not 'What is biogeography?' but 'What is contemporary biogeography to a geographer?' As already noted, practicing biogeography within geography differs between countries, and there may even be differences in biogeography between geography departments in the same country. But are these differences significant, that is, are there biogeographies (both within geography *and* between disciplines)? If differences exist, are they so great that collaboration is impossible, or are they small enough to suggest the possibility of synergistic opportunities? To use a more biological analogy, is cross-breeding impossible and can we benefit from hybrid vigor?

Take two definitions of biogeography:

> The study of the geographical distribution of plants, animals and other organisms. (Spellerberg and Sawyer, 1999: 1)

> The study of the past and present geographic distributions of plants and animals and other organisms. (MacDonald, 2003: 1)

The first—a typical definition—stresses 'distribution' of all living things. The authors are biologists. The second definition is little different from the first—it also focuses on 'distribution' of all living things but explicitly mentions 'past' and 'present'. It is from a key text written for geographers, by a geographer with a strong historical biogeography interest. What is apparent from these two contemporary definitions (and many other in textbooks over the last three decades) is that they are essentially the same. At one level, we do all agree on what biogeography is.

Is that, however, the reality? We argue there is only partial universal agreement. In geography, there are activities under the name of 'biogeography' that hardly fit either definition. In fact, there are different biogeographies within geography, and there are some biogeographies that (bio)geographers (compared to biological and geological biogeographers) contribute very little to at all. One way we have attempted to define 'biogeography' in geography is to undertake a contextual analysis of key words in section headings and chapters of a series of textbooks that have introduced biogeography to undergraduates since the 1970s from the Anglo-American and 'Continental' schools (Table 1.3). The analysis of the most frequently occurring words (Table 1.4) is revealing. If we omit 'biogeography', a number of tendencies in Anglo-American biogeography are revealed. First, we see the close relationship with ecology. The most frequently occurring word is 'ecosystem'—perhaps the must fundamental concept in ecology (Tansley, 1935)—and words that signal the influences of abiotic factors on (mainly) plant distributions such as 'environment(al)', 'soil', and 'change' (e.g., when used in the context of environmental change). The secondmost frequently occurring word is 'distribution', which, when considered alongside 'realm', 'communities', and 'community', illustrates what many biogeographers (in all three disciplines) would see as their main academic pursuit and which ties in with the definitions above. Further analysis of the use of this word group shows that it is more strongly aligned to spatial patterns of distribution, rather than temporal changes in distributions: this is perhaps not surprising as these books have been written by geographers. The final theme (represented by 'vegetation' and 'plant') to emerge from this analysis is the preoccupation of (bio)geographers with the plant kingdom at the expense of the animal kingdom. Two lacunae are historical (Quaternary) biogeography and the biogeography-society interface, despite both being well represented in contemporary research amongst (bio) geographers. The analysis integrates books published over 35 years, with 10 published before 1983. This may partly explain the dominance of the word 'ecosystem' and the underrepresentation of the human theme, but it does little to explain the lack of historical biogeography.

The German-language textbooks were in some ways more varied in the words they used (we recorded approximately 220 key words, against approximately 70 in English-language books). There are similarities and differences to the English key words: (a) the preoccupation with vegetation is more strongly developed, 'vegetation' occurs in

Table 1.3 Introductory biogeography texts written by geographers or used in geography in the Anglo-American and 'Continental' traditions that were used to extract key words for the context analysis

Title	*Authors and publication dates*	*Country of first publication*
Anglo-American School		
Systematic and Regional Biogeography	Morain (1970)	United States
A Geography of Plants and Animals	De Laubenfels (1970)	United States
Introduction to Biogeography	Seddon (1971)	United Kingdom
Principles of Biogeography	Watts (1971)	United Kingdom
Biogeography	Robinson (1972)	United Kingdom
Basic Biogeography	Pears (1977)	United Kingdom
Biogeography: Natural and Cultural	Simmons (1979)	United Kingdom
Plant Geography	Kellman (1980)	United States
Biogeography: Structure, Process, Pattern and Change Within the Biosphere	Jones (1980)	United Kingdom
Geography of the Biosphere	Furley and Newey (1983)	United Kingdom
Introduction to World Vegetation	Collinson (1988)	United Kingdom
Biogeography: A Study of Plants in the Ecosphere	Tivy (1993) (1st ed., 1971; 2nd ed., 1982)	United Kingdom
Fundamentals of Biogeography	Huggett (1998)	United Kingdom
Biogeography	Bhattacharyya (2003)	India
Biogeography: Space, Time and Life	MacDonald (2003)	United States
Environmental Biogeography	Ganderton and Coker (2005)	United States
Continental School		
Einführung in die Biogeographie von Mitteleuropa	Freitag (1962)	(West) Germany
Allgemeine Vegetationsgeographie	Schmithüsen (1968)	(West) Germany
Vegetationsgeographie auf Ökologisch—Soziologischer Grundlage	Schmidt (1969)	(East) Germany
Biogeographie	Aario and Illies (1970)	(West) Germany
Arealsysteme und Biogeographie	Müller (1981)	(West) Germany
Vegetationsgeographie	Klink and Mayer (1983)	(West) Germany
Biogeographie und Landschaftsökologie	Hoffmann (1985)	(West) Germany
Biogeographie, Artbildung, Evolution.	Sedlag and Weinert (1987)	(East) Germany
Vegetationsgeographie	Reichelt and Wilmanns (1989)	(West) Germany
Ökologie der Lebensräume	Tischler (1990)	Germany
Tiergeographie	Sedlag (1995)	Germany
Allgemeine Pflanzengeographie.	Richter (1997)	Germany
Vegetation und Klimazonen	Walter and Breckle (1999) (1st edn. 1970)	Germany
Handbuch der Ökozonen	Schultz (2000)	Germany
Vegetationszonen der Erde	Richter (2001)	Germany
Biogeographie	Beierkuhnlein (2007)	Germany

Table 1.4a The ten most frequently occurring key words in chapter and section titles in biogeography textbooks published in the Anglo-American biogeography tradition. Equivalent words that also occur in the Continental School list (Table 1.4b) in italics. See Table 1.3 for titles of books analysed.

Key words (in descending order of occurrence)	*Number of occurrences in total*	*Number of books that used key word (n = 16)*
Ecosystem	40	9
Distribution	26	8
Biogeography	23	7
Plant	19	6
Environment	16	8
Soil	14	5
Vegetation	14	5
Realm	11	4
Communities/ Community	10	5
Change	10	4

Table 1.4b The eleven most frequently occurring key words in chapter and section titles in biogeography textbooks published in the 'Continental School' biogeography tradition. Equivalent words that also occur in Anglo-American tradition list (Table 1.4a) in italics. See Table 1.3 for titles of books analysed

Key words (in descending order of occurrence)	*Number of occurrences in total*	*Number of books that used key word (n = 11*
Vegetation	26	8
Zonobiom and *Ökozone/n*	16	5
*Vegetation**	14	8
Verbreitung (distribution)	9	5
Pflanzen	9	5
Biosphäre	9	2
Tropen	8	2
Differenzierung	7	2
Ökologisch	6	4
Erde	6	4
*formen	6	3

*indicates word used as a root or suffix, e.g., Vegetationsgürtel.

both lists and there are also nine occurrences of 'Pflanzen' on the German list. The distribution-spatial pattern theme is also strongly developed again with 'Verbreitung', 'Zonobiom', and 'Ökozone/n'. The strongest theme in English books, ecology, is weakly represented in German books (e.g., only six occurrences of ökologisch). This might be partly explained by the fact that the list consists predominantly of books written by geographers, a choice that was purposeful. The word frequency would undoubtedly change if books written by biologists are included, as it would for the English-language books. Again, the historical biogeography and biogeography-society themes are poorly represented. But themes we might have expected to see well represented in German list such as 'Landschaftsökologie' and 'Pflanzensoziologie' were not.

In Table 1.4a, four of the top ten key words—ecosystem, biogeography, distribution, and communities/community—also appear in the seventh edition of Cox and Moore's *Biogeography: An Ecological and Evolutionary Approach* (2005). We have already noted that this was the most frequently used English-language textbook in the survey of biogeography teaching. But we also include it here because it is interesting to speculate if any other sub-discipline of geography has given up its 'own' influence in training its undergraduates in the way that biogeography appears to have done. Peter Moore—a frequent contributor to *Progress in Physical Geography*—is a biologist, as was Barry Cox.

We have used other evidence to try and unravel what biogeography is to contemporary geography. These include Cowell and Parker's (2004) analysis of biogeography publishing in the *Annals of the Association of American Geographers*; Veblen's (1989) and Young et al.'s (2004) review of biogeography in North America; review articles in *Progress in Physical Geography*; and inputs from a range of colleagues. Four biogeographies clearly survive alongside each other in geography departments globally and we suggest a fifth might be emerging:

1 A biogeography that is in essence ecological, which focuses mainly on the distribution of contemporary and recent vegetation (and in the latter context hybridizes with the palaeoecological theme in historical biogeography). Major contemporary research themes include the role of climate (and to a lesser extent other environmental factors) in determining spatial distribution patterns; vegetation dynamics, plant disturbance ecology and succession; and land-use and land-cover change. It is often called 'ecological biogeography', but is not ecology.[5] At one time it would also have been recognized in almost

all biology departments, but developments in molecular biology and the status afforded biomedical research have reduced the importance of organismic and population biologists, who mainly contribute to this area. In a number of biology departments in the United Kingdom, for example, departing ecologists have not been replaced. Those remaining have developed close alliances with (bio)geographers; sometimes they have even moved to geography departments. Yet, in many areas of applied biology (e.g., wildlife and fisheries, range management and forestry departments in North America) 'ecological biogeography' remains credible. Fellow biogeographers in biology and applied biology departments remain a major opportunity for peer-to-peer research collaboration. Indeed the similarities in questions asked and methods used by 'biological' and 'geographical' ecological biogeographers are so similar that there is a convincing argument that such collaborations are not even cross-disciplinary.

2 The second theme is 'historical biogeography', which, in geography, focuses mainly on the changing distribution of vegetation during the Quaternary. Also practised in biology and geology, it derives from the geological tradition of paleobiology (see the following chapter, Blumler et al.), which can be divided into paleontology (concerned with deep time and, primarily, evolutionary questions) and Quaternary studies (concerned more with environmental reconstruction). In geology departments, the focus has mainly been on plant evolution over a longer geological time scale than the Quaternary, which most (bio)geographers focus on. In biology, the main focus until the advent of cladistic biogeography and phylogeny was, like geography, mainly on the Quaternary. But developments in cladistics and phylogeny (see Riddle, this volume) have led many biologists to extend their time scales of interest, and geographers have been encouraged to engage with these debates (e.g., Young, 2003). It can be argued that whereas (bio) geographers are mainly interested in the past distributions of individual plant species or plant communities, geologists have been interested in a more holistic view of changing distribution patterns *and* evolutionary trends in individual taxa, and biologists mainly in the evolutionary trends. Historical biogeography is part of an environmental reconstruction tradition, and it is intellectually broader than changing vegetation distributions. For example, it has made major contributions to archaeological investigations and climate change science.

3 A third biogeography has a very strong spatial component and relies heavily on a group of geospatial technologies: remote sensing, geographic information sciences, and spatial modeling (see Section IV, this volume). We call this 'spatial biogeography'. Though it is clear that these techniques are, in a biogeographical context, used to help answer important questions within an ecological and, to a lesser extent, historical biogeography we do not accept the argument that these technologies simply provide part of the toolkit for biogeography. Developments in remote sensing technologies, algorithms for information extraction (from remote sensing data), spatial modeling, and geographic information science as well as increased computing power—have enabled biogeographers to (a) acquire information they could not have done using other methods, (b) store, retrieve, and analyse data in ways that could not be done previously, and (c) analyze these data by harnessing developments in geostatistics and spatial modeling alongside immense computing power. These developments have enabled new types of biogeographical study: for example, global biome mapping and monitoring, and biocomplexity modeling. In our opinion, this is now a clearly recognizable type of biogeography.

4 The fourth type of biogeography is that which links biogeography with societal issues. This has always overlapped with the aspects of historical biogeography that contribute to the archaeological agenda, but nowadays most scholarship derives from a series of contemporary 'jumping off' points (as well as some in recent history, say the last half millennium). These mainly include major global environmental issues, such as global climate change, biodiversity, deforestation, and desertification, which have led biogeographers to become active in topics like conservation and ethnobiology and to engage closely with environmental historians, ecological economists, and political ecologists in social science. There are important sub-areas within this field. For example, animal and crop domestication literature, when written by geographers, is inherently biogeographical. Conservation biogeography is the latest, high-profile sub-field within the biogeography-society area. Not only are (bio)geographers playing an important role in this sub-field (see, for example, the compilations edited by Zimmerer and Young (1998), and Adams (2008)), but they are engaging with human geographers and a plethora of natural and social scientists, and placing biogeography firmly in the psyche of the wide range of people reading conservation literature. This field is potentially very broad and we concluded the book with a section linking biogeography and society.

5 We speculate about the emergence of a fifth type of 'biogeography', one that has strong currency

within geography and is being led by social scientists. That is research into relationships between 'the human'—at scales ranging from the individual to society—and 'nature'—from individual biological entities to a wider nature. In general, nature-society research is not being led by (bio) geographers but by human geographers (e.g., Philo and Wilbert, 2003; Whatmore, 2002, 2007; Wolch 2007; Wolch and Emel, 1998). Unlike much of the scholarship in the themes identified above, some conservation ecology excepted, there is greater focus on animals than plants: "Flora … remains an even more ghost-like presence in contemporary theoretical approaches" (Jones and Cloke 2002: 4). Perhaps our speculation only arises because this biogeography is, in general, not being led by (bio)geographers, though there are exceptions (e.g., Head and Aitchison, 2009).

The contemporary global synthesis of biogeography can be compared to the situation that Watts (1978) saw emerging in the 'new' biogeography in Britain of the 1970s. He identified five trends:

(a) investigations of soil-vegetation-environment complexes;
(b) relationships between major vegetation types and particular animal species;
(c) analyses of distributions of individual species and of the influencing processes;
(d) Quaternary community or ecosystem change; and
(e) mankind-ecosystem-community relationships.

The most striking differences in our list and Watts's trends are the dearth of work on vegetation-animal relationships that he predicted (some types of landscape ecology excepted) and the spectacular growth in the use of remote sensing, GIS, and spatial modeling in biogeography.

Spellerberg and Sawyer's (1999) five major 'schools' of biogeography or areas of specialist study (Table 1.5) provide the opportunity for a more recent comparison. They also provide a comprehensive view of biogeography, which, when compared to the five biogeographies identified above, clearly indicates the niches that (bio) geographers occupy within the whole of biogeography, that is, ecological, historical, analytical, and applied. The majority of (bio)geographers could hardly be considered active in Spellerberg and Sawyer's dispersalist (some U.S. West Coast scientists excepted), vicariance, regional, and taxonomic biogeographies.

Some aspects of biogeography are poorly represented in contemporary geography. The most obvious relate to the 'all living organisms' part of

Table 1.5 Spellerberg and Sawyer's (1999) Schools of Biogeography and the overlap with the 'biogeographies' of contemporary geography (in bold in first column)

Spellerberg and Sawyer's Schools of Biogeography	*Level of development in contemporary geography (parentheses refer to chapters in this book related to this school)*
Ecological Biogeography	Strongly developed (all Chapters in Sections II and III)
Historical Biogeography	Very weakly developed (if at all) over evolutionary and many geological timescales; strongly developed over Quaternary timescales (Willis et al., Marchant and Taylor)
Dispersal Biogeography	Inherent in historical studies of vegetation and in vegetation reconstruction; received prominence in the Berkeley School (Blumler)
Vicariance Biogeography Panbiogeography Cladistic Biogeography	Weakly developed in contemporary geography
Analytical Biogeography	Well developed in geography: e.g., remote sensing, landscape ecological, and spatial modeling (all chapters in Section IV)
Regional Biogeography	Weakly developed generally; best developed in the 'Continental School'
Taxonomic Biogeography	Very weakly developed, if at all
Applied Biogeography	Very strongly developed in geography: e.g., conservation, ethnobotany, invasive species, fire ecology (all chapters in Section V)

the definitions of biogeography. For many decades, most (bio)geographers have lacked significant engagement with animals—zoogeography. In what was, arguably, the first biogeography textbook in English written by somebody closely connected with geography, Marion Newbigin (1936) gave plants and animals almost equal weighting in '*Plant and Animal Geography*', considering their distributions and the links between their distributions. The main area where we engage with animals is in some types of landscape ecology, though even this aspect of landscape ecology is not well developed in geography. We do not espouse necessarily revisiting animal distributions in the ways that Newbigin outlined, albeit that this is possible. Beyond the burgeoning nature-society area that (bio)geographers could contribute too, we consider very fruitful areas in zoogeography for (bio)geographers to make an impact lie in the consideration of pathogens and their vectors—an area that is generally under researched in biogeography—and the biogeography of marine organisms. The world's oceans and seas have been a major lacuna for geography, and marine biodiversity is a vastly under-researched area.

1.4 DIVERGENCE

A century ago, biogeographers were generally familiar with each other's literatures, whatever their disciplinary home. But as disciplines emerged in the early twentieth century biologists, geographers, and geologists developed particular emphases within a broad biogeography. Consequently the broad communion of biogeographers became less connected. Divergence has increased in the last half century, not least in part because of the seemingly exponential proliferation of scientific publications.

In Anglo-American geography, there was a significant expansion in biogeography from the mid-1960s through the 1970s. In the United Kingdom, this period was the peak time in biogeography textbook publishing (Table 1.3); the Biogeography Research Group of the IBG (now RGS-IBG) was established with Len Curtis, John Taylor, and Bob Pullan as its first officers; and, importantly, David Watts and John Flenley (at that time both at Hull University) become the first editors of the *Journal of Biogeography* in 1974. There were parallel expansions in North America, Australia, and New Zealand. For example, the Biogeography Speciality Group of the AAG was established in 1981 with Jerry MacDonald, Lee Henry Slorp, Tom Veblen, Hartmut Walter, and Dean Wilder as its first officers.

Despite the growth in biogeography in the English-speaking academy in the 1960s and 1970s, by the early 1980s Rogers (1983) noted that the growth of biogeography teaching, graduate training, and the number of biogeographical faculty in North American departments had fallen behind that in the United Kingdom. Nonetheless, he identified three very influential departments—the California system campuses at Berkeley and Los Angeles (UCLA), and Wisconsin. McGill University provided the greatest concentration of biogeography within Canadian geography. As we argue, biogeography in North America has overtaken that in the United Kingdom in volumetric terms, mainly due to a late 1980s and early 1990s slump in the United Kingdom. Ten years prior to our writing this, Agnew and Spencer (1999) identified biogeography as a core sub-discipline in British physical geography. Yet others writing at the same time disagreed, arguing that other disciplines had taken it over (Gregory et al., 2002). Joyce (2009) and Whittaker and Sax (2003) suggest that this was due to ecology (in particular) being better organized than biogeography, but this is possibly only part of the reason for the decline in British biogeography during the 1990s.

What stimulated the expansion of biogeography in Anglo-American consciousness in the late 1960s and 1970s? A combination of interviews with biogeographers active in the 1970s conducted for this book and other data suggest that there may have been four main factors. First, there was the demand for increased access to higher education starting in the 1970s (and which continues to the present day). Second, the number of higher education establishments began to expand in the 1960s in both the United Kingdom and United States, and higher education participation rates increased. The same happened in Germany, with biogeography positions being created during the expansion of existing, and the foundation of new, universities during the 1970s. Third, was rising student demand for courses related to the 'environment', the profile of which had been heightened by the environmentalism of the 1960s. This was a strong trend in both North America and Europe: for example, in Germany during the aftermath of the Limits to Growth report, there were heated public debates about the fate of tropical rainforests and nuclear power. The fourth and final factor is the role of agency—both individual and institutional.

In the United Kingdom, the expansion of higher education establishments, student numbers, and the strong position of geography in secondary school curricula created a demand for geography, with biogeography being seen as integral to physical geography. For many North American departments in the United States,

expanding into biogeography was relatively straightforward for many departments that were dominated by climatologists and geomorphologists. In essence, it was a demand-led phenomenon. It had parallels in Britain, where the publication of 10 biogeography textbooks by U.K.-based authors in the 1970s and the early 1980s is testament to the demand for course materials in geography departments in universities and polytechnics at that time. In the United States, the environmental movement of the 1960s and 1970s increased academic and popular interest in environmental issues. Biogeography clearly falls under that umbrella, and it may have led some geography departments to offer courses that were relevant to these national debates, but the biggest beneficiaries of the environmental wave were biology departments.

The role of individual and institutional agency is also important in the development of biogeography in the late twentieth century. In North America, many biogeographers, including many who work at the biogeography-society nexus (some of whom may not consider themselves biogeographers), have influences that can be traced back to the Berkeley School of American Geography (see Blumler et al., this volume). Developments in biogeography were part of the wider Berkeley School, which originated in Carl Sauer's (1899–1975) interests in human-environment interaction (e.g., Sauer, 1941; 1952; 1956). Key biogeographical themes researched by the Berkeley School included fire, invasive species, ethnobotany, conservation, historical ecology, agricultural origins, and crop genetics. Many themes were influenced by developments outside the Berkeley School—most notably, historical ecology, which was well advanced in Europe—and some, such as agricultural origins and crop genetics, have waned in importance within geography. The broader cultural geography that the Berkeley School espoused, and which influenced Berkeley School 'biogeography', has been usurped by a newer cultural geography that had its origins in sociology and which first gained prominence in British geography in the 1980s (e.g., Valentine, 2001). New cultural geography has studied the natural world in different ways to most (bio)geographers, let alone biogeographers in biology and geography, and has only recently engaged with the natural world in a way that (bio)geographers can confidently and comfortably contribute to (e.g., Phillips et al., 2008): this is the speculative fifth type of biogeography we alluded to above.

Members of the Berkeley School advised a generation of biogeographers who later dispersed throughout U.S. geography. Key among these were Jonathan Sauer (see Blumler et al., this volume) and Thomas Vale (Wisconsin), Thomas Veblen (Colorado), and Robert Frenkel (Oregon). Biogeographers such as these went on to train many of the current mid-career and older biogeographers in North American geography departments. As a consequence, the Berkeley School has promoted an enduring heritage amongst the teaching and research of some biogeographers to the present day, even though its currency within human geography has waned.

A parallel line of agency in North American biogeography dates back to the time when, as biogeography in geography departments expanded further, many turned their attention to graduate students trained in biology in their search for a second biogeographer. This influence has a shorter history than the Berkeley School but nonetheless has had important influences on the composition of biogeographers within contemporary North American biogeography. This trend was initiated by the geography department at UCLA when they appointed Walt Westman—a student of Robert Whitaker's at Cornell—who went on to train a number of biogeographers in a hybrid biology-geography tradition. Like those influenced by Berkeley School professors, many of Westman's students have gone on to train significant numbers of practising biogeographers in geography departments in North America.

At the start of the expansion of biogeography in the 1960s and 1970s historical biogeography was a well-developed area in the United Kingdom, . The key influence here was the Sub-Department of Quaternary Research (SDQR) at Cambridge, and its two directors up to that time—Sir Harry Godwin (1901–85) and Richard West. This interdisciplinary center was established after the Second World War, though a group of Cambridge-based scientists were working on archaeological themes in the English fenlands before then. These included Godwin, a plant ecologist who introduced palynology, which had developed in Scandinavia in the early twentieth century, to Britain and was influenced by the work of the Danish palynologist Johannes Iversen (1904–72) (West, 1988). His counterpart in North America was the botanist Paul Sears (1891–1990). Godwin went on to become the SDQR's first director in 1948. He was influenced by phytosociology, having close contact with both A.G. Tansley (also at Cambridge) and European plant ecologists through international phytogeography excursions. Godwin trained a generation of interdisciplinary Quaternary scientists who worked in the United Kingdom, Australia, and New Zealand, one of whom—Richard West—succeeded him as the SDQR director and in turn trained a cohort of PhD students, including influential historical biogeographers in geography, biology, and geology. SDQR also created an environment of hybridization with,

for example, geographers using facilities in SDQR that were not available to most geographers elsewhere in the 1970s. Many of them were seeking jobs when universities began their expansion in the 1970s (Turner and Gibbard, 1996). As U.K. geography departments expanded in the 1970s, they also hired from people with biological training, especially in the area of historical biogeography (e.g., John Flenley, who co-wrote the following chapter). This trend was parallel with that in the United States but hiring from the biological sciences was not as strong in the United Kingdom as it was on the other side of the Atlantic.

Other agents influencing British biogeography in the second half of the twentieth century were either less dominant or less clear. The Berkeley School had little influence—though Ian Simmons (1979) acknowledges the influence of a sabbatical at Berkeley; David Harris (Institute for Archaeology, University of London) was trained by Carl Sauer; and David Watts at McGill researched in the 'Sauerian mould'—and very few geographers adopted European plant sociology. Two 'domestic' influences do seem to have had some traction. First, there was the local and landscape studies school promoted by W.G. Hoskins, see for example Hoskins (1955), which influenced biogeographers such as Robert Eyre (Eyre, 1963) at Leeds into an ecological biogeography that acknowledged human occupation of the landscape. Second, there was the cadre of scientists, including biogeographers, who had worked on natural resource issues (e.g., Stobbs, 1963) and in overseas universities (for example, Monica Cole; Royal Geographical Society, n.d.)

Divergence in biogeography occurred in two forms during the twentieth century. First, biogeography took on increasingly different stances in biology, geography, and geology. Second, differences emerged among the major groupings of (bio)geographers in geography—in continental Europe, Britain, and North America.

1.5 THE IVORY ARCHIPELAGO

Joyce (2009: 1) states that divergence may have led to isolation and lack of recognition of a "shared, cognate science built upon a considerable lineage of conceptual achievements." That may be too strong a statement, nonetheless: the proliferation of topic areas, concerns, and theoretical structures in the broad arena of biogeography means that nobody today is truly 'on top of the field'. This is, of course, an issue across the entire spectrum of academia. As the evolutionary biologist David Wilson puts it:

> It is easy for scientists and intellectuals to smile at the ignorance of . . . the general public, but the fact is that they're not much better. The Ivory Tower would be more aptly named the Ivory Archipelago. It consists of hundreds of isolated subjects, each divided into smaller subjects in an almost infinite progression. . . . Each perspective has its own history and special assumptions. One person's heresy is another's commonplace. (2007: 2)

We appreciate the biogeographical analogy—courses in biogeography often include discussion of how archipelagos differ from both single islands and continents in terms of evolutionary pathways and in terms of biodiversity. We also agree with the implication that academic disciplines are not quite islands unto themselves: typically there are a few, transdisciplinary connections but these may be quite limited and only between cognate fields. Alternatively, it might be appropriate to speak of an 'Ivory Tower of Babel' (pun intended), because of the pronounced differences in language, terminology, and jargon that have evolved in different fields, sometimes making them mutually incomprehensible.

Contributing factors are the rise of electronic publishing, the 'gold standard' of research, and the ratings of departments (and individuals) according to bibliometrics. This has had the effect of constraining the literature cited to a narrower range concentrated in 'select' journals (Agnew, 2009; Evans, 2008). In biogeography that has elevated journals, such as the *Journal of Biogeography* and its spin-off journals, major ecology journals published by national societies (e.g., the Ecological Society of America and the British Ecological Society), and top-line journals like *Nature*, *Science*, *Proceedings of the National Academy of Sciences*, and *Philosophical Transactions of the Royal Society B* at the expense of smaller, highly specialized journals in biogeography, such as those published by natural history museums and regional societies (e.g., *Castanea*, Southern Appalachian Botanical Society; *The Great Basin Naturalist*, Brigham Young University; *American Midland Naturalist*, Notre Dame University). Agnew (2009: 3) commented, "Who reads journals any more, looking to experience the joy of serendipity, particularly when those journals have low impact factors?" We add to this our broad inability to process materials in other languages as evinced by the bibliographies of many papers. English-speaking biogeographers are simultaneously at an advantage and disadvantage because all high-impact factor journals are in English (which attract non-native English speakers to submit their best material to them) and affords those who read and speak the language

fluently the dubious luxury of ignoring biogeographical literature not written in English. The strength of biogeography in German-speaking geography allows a vibrant peer-reviewed literature to be published; unfortunately, much of it fails to stimulate the minds of English-speaking biogeographers. Given the nature of the human brain, which is great at mimicry but not terribly good at "thinking outside of the box" (cf. Pinker, 2003), the long-range impact is likely to be the decreased ability to achieve paradigmatic breakthroughs. Thinking outside of the box requires reading outside of the (disciplinary) box, paying attention to specialist journals with low citation indices, and reading outside of the English language.

Land degradation is a cogent example of the type of problem that can arise because the ivory archipelago exists. It is widely perceived as a serious global environmental problem, especially as manifested in topics like deforestation and desertification and their impacts on ecosystem services and people's livelihoods. Biogeographical evidence of vegetation change (e.g., forest loss, decline in forest quality, and forest recovery—the so-called forest transition) is highly relevant to 'deforestation' discourses. Vegetation dynamics (and therefore biogeographical contributions) have not played such an important role in desertification as they have in deforestation, probably due to lower amounts of vegetation in ecosystems thought susceptible to 'desertification' and much weaker links to another major global problem—biodiversity—which is lower in arid and semi-arid ecosystems, and was not on the global environmental issues menu when desertification rose to prominence in the 1970s. In fact, at the 1992 Rio Earth Summit, political trade-offs were made between 'desertification' and 'biodiversity' to enable the Convention to Combat Desertification and the Convention on Biological Diversity to proceed simultaneously.

While some scientists agree with Jared Diamond (2006) that land degradation has become so serious that it threatens our civilization with collapse, many nonequilibrium ecologists and biogeographers, geomorphologists, and human geographers argue that the degradation thesis has, for the most part, been disproven (e.g., Blaikie and Muldavin, 2004; Blumler, 2002, 2006). Many scientists—Diamond among them—appear to be unaware of the existence of this critique; others, we assume, presume that it must not be empirically based. Several geographers who would not categorize themselves as biogeographers have carried out excellent, empirical 'biogeographical' research that has chipped away at the degradation edifice (e.g., Bassett and Bi Zueli, 2000; Brower and Dennis, 1998; Davis, 2007; Fairhead and Leach, 1996; Turner, 1998). Interestingly, most of these studies focus on arid and semi-arid ecosystems: ecosystems in which the geomorphologist David Thomas (1993; Thomas and Middleton, 1994) demonstrates convincingly that there is little empirical evidence to support the existence of widespread desertification.

While quite a few mainstream environmental scientists—some biogeographers among them—appear to accept the viewpoint that land degradation has little empirical support, other critics, who at times are vitriolic in their antiscience stance, nonetheless have gathered some solid scientific data that counter the orthodox views on land degradation. The irony here is that some of the 'successful biogeographical research' in this area has been carried out by human geographers—typically political ecologists or cultural ecologists—whose influences stem from critical social theory. Most academics would presume that critical social theory and science cannot merge, but as F. Scott Fitzgerald (1945) pointed out, "the test of a first-rate intelligence is the ability to hold two opposed ideas in the mind at the same time, and still retain the ability to function." A final irony is that, although this situation cries out for hypothesis testing and debate, there is very little debate, let alone hypothesis testing. Have we reached an impasse where each camp is convinced that its understanding is correct, so much so that they rarely engage in face-to-face debate but rather proclaim their positions in 'their' journals? This is an outcome of the current failure to read outside of one's sub-discipline, so that one person's heresy can indeed become another's commonplace, to paraphrase Wilson (2007: quoted above).

1.6 AIM AND STRUCTURE OF THE HANDBOOK

Given the divergent trends in biogeography, it appears we have embarked on a Sisyphean task in editing this book. That would be true if we were cataloging all aspects of biogeography, but the aim of the handbook is to reflect (as comprehensively as possible) the current state of biogeography as a sub-discipline of geography. The differences in biogeography within geography meant that obtaining agreement on the 'main' areas, and then identifying 'acknowledged' leaders was extremely difficult (see the foreword). Furthermore, as we wanted to take a global approach to biogeography, some topics do not appear as full chapters and some 'acknowledged' leaders (in say one country) do not appear as

chapter authors. We have attempted to celebrate our differences in both topic and author choice. A further aim was to link to other disciplines, in particular biology, where we felt there were important developments that biogeographers in geography should be more actively engaged with. Chapters on classification (Angelika Schwabe and Anselm Kratochwil), phylogeny (Brett Riddle), biodiversity gradients (macroecology) (Jens Mutke), and bioindication (Yordan Uzonov) are chapters written by biologists in the hope of stimulating geographers.

The book has five sections, each with an introduction. Section I reviews key *theories* and *concepts* in biogeography. Biogeography has been criticized as being light on theory, or having only one theory—the Equilibrium Theory of Island Biogeography (ETIB). We take issue with such criticisms and focus on theory and concept at the start of the handbook. If broadly defined, biogeography is rich in theories, many of which are still (rightly or wrongly) still debated: for example, evolution, vegetation succession, and ETIB. We trace the evolution of biogeographical theories in the first chapter in this section (Mark Blumler, Anthony Cole, John Flenley and Udo Schickhoff), and examine theories of biodiversity (Duane Griffin) and theory in landscape ecology (John Kupfer). Related to these theories are a series of key concepts: classification (Angelicka Schwabe and Anselm Kratochwil); phylogeny (Brett Riddle); and refugia (Kathy Willis, Shonil Bhagwat and Mary Edwards).

Section II considers current knowledge about *gradients* and the importance of *disturbances*. Most biogeographers the world over see spatial and temporal patterns as the essence of biogeography. Individual chapters explain spatial patterns (gradients) (Jens Mutke); abiotic and biotic controls on spatial patterns (Udo Schickhoff); the influence of disturbances in general (Anke Jentsch and Carl Beierkuhnlein); and the impacts of fire (Neal Enright) and climate change (Tim Sparks, Annette Menzel, Josep Peñuelas and Piotr Tryjanowski) on spatial and temporal changes in distributions.

Section III was the hardest to reach agreement on. It reconsiders what we know about selected *biomes* and *environments*. Consensus was hard to reach because all biomes are important to biogeographers. However, there are simply too many to include in this handbook, and also we did not want to ignore important environments that do not easily fit biome models. We selected four broad zonal regions that, more or less, map onto biomes and three environments. There is a bigger point here. We consider biomes to be a form of regional geography, which in itself gets poor treatment in contemporary geography. In the United States, regional geography is taught far more extensively than it is the United Kingdom, for instance, but regional geography or area studies is not a mainstream research theme on either side of the Atlantic. Authors have written personal essays on these, rather than following a model. The polar and subpolar regions (Ingo Möller and Dietbert Thannheiser) were chosen because of debates over the use of these environments and the evidence that climate change is impacting these biomes more so than many others. Boreal forests (Daniel Kneeshaw, Yves Bergeron and Timo Kuuluvainen) were selected because of their significance in terms of the global carbon budget. Savannas (Jayalaxshmi Mistry) remain something of an ecological conundrum because of the coexistence of grasses and trees; and tropical forests (Ken Young) have witnessed significant landcover change since the 1950s. We balanced the biome essays with three 'environments'. The choice of mountains (Udo Schickhoff) reflects the significant amounts of research conducted globally on mountain biogeography and ecology and was driven by concerns about biodiversity conservation and climate change. The chapter on agricultural environments (Chris Stoate) also reflects biodiversity concerns. The choice of urban environments (Claire Freeman) was stimulated by concerns about increasing urbanization and also reflects research on urban ecology.

Section IV examines how *mapping* and *modeling* is used in biogeography. This area has seen tremendous growth since the 1980s with the increased availability of different types of remotely sensed data (as a primary data source), developments in GIS, spatial modeling, and increased computing power. Two chapters consider remote sensing for mapping biogeographical distributions (Giles Foody and Andrew Millington) and as inputs for modeling (Joanne Nightingale, Stuart Phinn and Michael Hill). Three chapters consider different approaches to modeling that are used extensively in biogeography: predictive modeling (Niall Burnside and Stephen Waite), simulation modeling (George Malanson), and biocomplexity (Steve Walsh, George Malanson, Joe Messinia, Dan Brown and Carlos Mena). The importance of landscape ecology in this area is represented by a consideration of spatial patterns by Tom Albright, Monica Turner and Jeffrey Cardille.

Section V explores the links between *biogeography and society.* We have been highly selective. The major area of contemporary concern—biodiversity conservation—is explored in detail by Rob Marchant and David Taylor, Geoff Griffiths and Ioannis Vogiatzakis, and Patrick Osborne and Pedro Leitão. We explore vegetation as resource in Robert Voeks's chapter on ethnobotany, and vegetation as a hazard in Mark Blumler's chapter

on invasives. Importantly, we provide one illustration of how ecological biogeography can be utilized, through the vehicle of bioindication (Yordan Uzonov).

1.7 BIOGEOGRAPHICAL FUTURES

The role of this handbook should be not only to celebrate the diversity of biogeography and biogeographers, and applaud the very real contributions made within each tradition and subject area; but also to point out divergences, identify debates, and encourage engagement with critical, unresolved issues. The sub-discipline is in rude health in some countries but is doing little more than 'hanging in there' elsewhere. Since the 1960s biogeography has expanded and contracted in response to trends in both higher education and geography. It seems to us that biogeography could often be accused as being guilty of not promoting itself and not organizing itself within geography. Compared to geomorphology, for example, it has been a 'bit player'.

Gregory et al. (2002) point out the paradox that, while biogeographers work in geography, evolutionary biology, and the environmental sciences, most biogeographical research is conducted in biology departments and ecological research centers. The implication is clear—the frontiers of biogeographical research currently lie outside geography. Joyce (2009), in an upbeat commentary in *Area*, suggests that British biogeographers are increasing their engagements with economics, geomorphology, social sciences, archaeology, and marine biology. The first comment is unnecessarily pessimistic, but if we continue to reproduce the narrow definition of biogeography referred to earlier in this chapter, it is clear how Gregory's paradox comes about and that the death knell is being rung for biogeography in the discipline of geography. Joyce's assessment suggests that we should expand our interdisciplinary linkages, and while interdisciplinary research is an important element of any discipline nowadays, and essential in tackling important global issues, overemphasis on interdisciplinarity can devalue individual disciplines. Without a core biogeography, and (bio) geographers who self identify with it, there will be no interdisciplinary future for biogeography in geography departments.

NOTES

1 Cox and Moore's textbook, in at least one of its editions, was the most widely used undergraduate textbook in the English-speaking universities surveyed, and it has been translated into Chinese and German.

2 In fact, biogeography is so well developed in Argentina that it is represented in a series of 12 university-level textbooks, each representing a subdiscipline (Petanga de del Río, 1992).

3 The survey response rate from Brazilian geography departments was poor, and the status of biogeography in Brazil at that time comes from various individual sources.

4 At this point we introduce the term (bio)geographer to indicate those biogeographers who have trained in and/or practice their biogeography within geography departments to distinguish them from biogeographers in other disciplines.

5 Even though it is not ecology, some geographers are confused by what we do or how we label ourselves. Demeritt (2009), in an editorial on environmental geography, notes one of the contributions of physical geography/ers to environmental geography is ecology, but not biogeography.

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SECTION I

Revisiting Theories and Concepts

We start with a series of chapters organized around the themes of biogeographical theory, concepts, and thought. Theory is, of course, an important and necessary part of science. Ideally, it is tested and modified in the face of contrary evidence. This is easier said than done in biogeography, given the complexity of interactions and the possible role of historical contingency. As a consequence, there are widely diverging opinions concerning several major theories in this field: a theme that resonates throughout this section.

By its very nature, theory is prone to overgeneralization. This is a necessary part of the scientific process, which involves repeated attempts to generalize from limited data, hopefully coming closer to the truth with each iteration. Scientific theory, then, is always a work in progress. But this also has the unfortunate consequence that uncritical application of scientific theory to policy and planning in the real world can be problematic (for examples, see Chapter 1).

We could not include all biogeographical theory, choosing instead to provide first an overview (Blumler et al., Chapter 2). In addition to outlining the history of biogeographical thought, and describing how the various traditions within biogeography came about, this chapter concentrates on several key theories. Next Duane Griffin (Chapter 3) reviews theories purporting to explain patterns of species diversity—a puzzle of longstanding interest to biogeographers and one that takes on much greater meaning today when so much conservation concern is focused on species declining toward extinction. Biodiversity theory is itself extremely diverse, with little clear consensus though the proponents of differing viewpoints for the most part tolerate each other—but there are exceptions (Kaiser, 2000).

We follow with chapters treating subfields of biogeography. John Kupfer's Chapter 4 describes landscape ecology—a major but relatively new area, dating from Forman and Godron (1981), and Naveh and Lieberman (1984), though with considerable development since then, most notably the level of quantification that has paralleled developments in remote sensing and GIScience. Chapter 5 treats classification, a field that also features a highly developed terminology, much of it elaborated in Europe. Appropriately, then, our authors (Angelika Schwabe and Anselm Kratochwil) are German. This chapter demonstrates the expanding influence of phytosociology, not just within Europe but globally—though it sometimes is modified when adopted overseas. Phylogeography, treated in Brett Riddle's Chapter 6, is an even more recently derived branch of study, dating from Avise et al. (1987). Finally, we end this section with Kathy Willis et al.'s chapter by reviewing recent evidence bearing on traditional beliefs regarding refugia. Though less theoretical, it is included here both because of the importance of the refugial concept, and because much of the evidence is paleobotanical, an area otherwise underrepresented in this volume.

Chapter 2, on the history of biogeographical thought, proved difficult to write: different traditions have reached contrasting conclusions regarding key developments, concepts, or even about what matters in biogeography. Problematic areas

include, but are not limited to, the nature of communities; succession and vegetation dynamics; the role of disturbance; classification; vicariance versus dispersal; island biogeography theory; contingency versus rules; and the proper use of theory and modeling in scientific study. Within this context, Mark Blumler et al. concentrated on three key theories. The first—evolution—is undeniably biogeography's greatest contribution to science. Consideration of its development raises questions about contemporary biogeographical research. Evolution came out of the natural history tradition, and Darwin made heavy use of the Comparative Method; neither is much utilized today. Theories of vegetation dynamics and succession are currently in a confused state, with highly divergent views and relatively little tolerance of alternatives. In fact, while it probably deserved a separate chapter, we decided that there might not be anyone who could cover the subject in a manner that was fair to all. Vegetation dynamics relate also to equilibrium versus nonequilibrium models in ecology and biogeography, yet another aspect of theory that remains unresolved, with divergent perspectives. Finally, the chapter examines the Equilibrium Theory of Island Biogeography (MacArthur and Wilson, 1967), perhaps the most influential yet also the most problematized biogeographical theory of recent times.

One source of tension in writing this chapter concerned the nature of science. The lead author has published on the history of thought and consequently has interacted with the history of science community. Scientists tend to see their disciplines in progressionist terms, much as Newton famously did, as a series of great minds "standing upon the shoulders" of their predecessors. In contrast, science historians view science as being constrained and channeled by social context and sometimes doubt about whether any real progress is achieved. Both perspectives are present in the chapter, which reflects the relative positions of the four authors. For what it is worth, our own opinion is that both perspectives have merit.

Biodiversity is arguably the central concern of contemporary biogeography and is a major concern of the environmental movement. Maybe then a consequence is that Griffin's Chapter 3 deserves greater comment than the others in this introduction (but see also Mutke, Chapter 9). Truly, today we have a 'tangled bank' of theories about what makes some places species-rich and others not. Griffin sees hopeful signs of increased understanding, while the review that he most frequently cites (Palmer, 1994) suggests that progress has been limited, though this article is now 15 years old. The information explosion and recycling of old theories in new guise has created a morass that no one person can hope to survey completely, though Duane Griffin has made a yeomanly effort—only to be asked to remove many of the references to save space! We note that the terms of debate have changed dramatically over the years, as have the prominent theories. Thirty years ago, for instance, much of the discussion revolved around equilibrium versus nonequilibrium theories of diversity (Connell, 1978). Both types of theory still have currency, yet Griffin's treatment does not make this distinction, suggesting that it no longer is considered terribly relevant. But there also does not seem to be any particular reason for this change, other than that scholarly interest happened to turn in new directions.

In attempting to resolve the very confusing mass of data about species diversity, one issue may be whether all species truly are equivalent, even within phyletic groups. One may recall J.B.S. Haldane's famous (possibly apocryphal) quip, when asked if he believed in God, that "the Creator has an inordinate fondness for beetles." Beetle diversity must exert an inordinate influence on insect diversity. Another concern is proximate versus ultimate causation. Environmental heterogeneity—which is later referred to as geodiversity (Mutke, Chapter 9)—is generally accepted as a promoter of high diversity, but in the classical examples of tropical rain forests and coral reefs it is life itself that creates the heterogeneity. (Admittedly, limestone on land also typically weathers to create heterogeneous microenvironments. Plant species diversity is typically greater on limestone, than on other substrates, at least in part for this reason.)

Another issue is the possible role of historical contingency. One can arrange evolutionary biologists along a continuum, from the late Stephen Jay Gould, who believed that there are few if any rules in nature, to E.O. Wilson, who tends to discount historical contingency. Gould (1989) famously claimed that if there were a million Earth-like planets, then only on one would life evolve beyond the unicellular level. Diversity would be much lower, surely, on such planets than on ours. Since Gould's death, the biogeographical community has moved further toward a Wilsonian view than it already had done (Gould never represented the consensus), but few would argue that historical contingency plays no role at all. Griffin does represent the consensus view when he states, "All systems (above the quantum level, at least) are governed by deterministic processes and thus exactly predictable in principle," while also accepting that in practice this may never be fully achievable. But if, as some physicists are arguing, the universe is in the nature of a hologram (Bekenstein, 2003), then determinism (cause and

effect) may not be as characteristic as most scientists believe.

Historical contingency seems particularly apropos given that biodiversity has increased throughout time (Sepkoski and Miller, 1998). If biodiversity is as much an evolutionary as an ecological feature, diversity itself may be sufficiently an accidental by-product in that it is not explicable on theoretical grounds. During the Cambrian Explosion, life was far more diverse in the sea than on land; in all likelihood if scientists had been alive then they surely would have argued for the importance of water to life and suggested that the landmasses are too dry to support high levels of biodiversity. Similar arguments are made today about deserts, but overall the land has become far more diverse (in species, not phyla) than the sea even though the latter covers approximately two-thirds of the Earth's surface and is deeper than the continents are high. Can we be certain sure that deserts, tundra, and other relatively recent (geologically speaking) extreme environments will not eventually become as diverse as tropical rain forest? Given also that massive colonization of land occurred only after nearly four billion years of evolution, how can we state with any degree of certainty that the process must now have reached equilibrium, after only a few hundred million additional years? Furthermore, since the sun's decreasing warmth is according to one estimate likely to eliminate multicellular life within about 500 million years (Brownlee and Ward, 2007), life's evolutionary trajectory on this planet may have mostly run its course. Life may go extinct as the planet becomes uninhabitable before it has had the time to reach maximum equilibrium diversity levels.

Kupfer's (Chapter 4) thorough treatment of concepts, methods, and metrics of landscape ecology illustrates that, like phylogeography (Chapter 6), the field is both recent and rapidly expanding. Consequently, in both cases, it is difficult as yet to evaluate the claims of their practitioners. Landscape ecology seems particularly relevant to the conservation questions that arise out of habitat patchiness, especially where anthropogenic, such as forest fragmentation. Given the proliferation of metrics, it is pertinent to ask which are the most useful for different biogeographical questions? This leads to a much broader question: how do we measure the utility of our methods? This question applies to many areas of biogeography covered in this book, and it is not meant to be a sideswipe at landscape ecology.

Chapter 5 illustrates in great detail a point made in Chapter 2: the Continental School has emphasized classification. Although classification generally was abandoned in the Anglo-American world through much of the twentieth century under the influence of Gleasonian ideas, it is making a strong recovery. For the most part, Anglo-Americans rely on approaches already developed in Europe. Schwabe and Kratochwil's thorough treatment of terminology is likely to be very useful for those who have not been exposed to this literature. As they point out, the phytosociological approach with its emphasis on relevés for vegetation sampling and characterization is spreading and seems ready to become the predominant method globally. We believe its recent spread in the United States, albeit in modified form, reflects a desire among conservation organizations to identify communities for purposes of preservation. There also is a connection to the rise of biome and global change modeling, which biogeographers (and others) are actively engaged in across the world. Certainly the return to classification generally reflects both motivations, as Schwabe and Kratochwil clearly explain.

Riddle's Chapter 6 on phylogeography details the rapid rise in the use of genetic data, combined with the assumption of a constant molecular clock, to work out phylogenies that are superior to those derived solely from morphological data, and to provide new estimates of divergence times. The fossil record must tend to underestimate time since origination of taxa, because the record is so incomplete that fossils are unlikely to be found that correspond to the first generation of the taxon in question. On the other hand, it is not out of the question that the molecular record may sometimes give an overestimate, since mutation rates are not constant but tend to increase during times of environmental stress, for example, during mass extinctions. Regardless, it is undeniably true that the molecular data provide a fresh and illuminating perspective on evolutionary history.

Willis et al.'s Chapter 7 demonstrates that traditional beliefs on refugia in the Amazon and Europe need modification and that the reality is more complex than traditionally thought. Many European species found refuge during the most recent glacial periods in local microenvironments north of the Mediterranean, the traditionally favored refuge area. We note that this new information leaves us still wondering as to the cause of the extinctions of trees such as the hemlock (*Tsuga*) and tulip tree (*Liriodendron*), which left Europe with a depauperate arboreal flora compared to the eastern United States and east Asia. Because these extinctions occurred in the Pliocene or early Pleistocene, they may not be readily accessible through palynology, which is generally more informative about the recent past.

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2

History of Biogeographical Thought

Mark A. Blumler, Anthony Cole, John Flenley, and Udo Schickhoff

2.1 INTRODUCTION

Some 250 years of research and scholarly writing on what modern biogeography is principally about—the causes of the spatial distribution of living things—preceded the 1974 watermark of the first publication of the initial volume of the *Journal of Biogeography*. Early theoretical contributions came out of the natural history tradition, as it developed within disciplines such as biology, geography, and geology; they were not always published under the name of biogeography. While there are excellent overviews of the history of ecological, environmental, and evolutionary thought that discuss aspects of biogeography (e.g., Botkin, 1990; Glacken, 1967; McIntosh, 1985; Worster, 1977), no comprehensive treatment exists. The major textbooks (e.g., Cox and Moore, 2005; Lomolino et al., 2006) are excellent but do not cover all biogeography traditions, and different traditions perceive its history somewhat differently. So, in reviewing this history, our challenge is to correctly interpret the past. There is a danger of overstating some contributions, omitting others, and failing to see the importance of events that were far removed from the issues of our time.

2.2 BIOGEOGRAPHY IN THE ANCIENT WORLD

The origin of modern science is usually traced back to the Greeks, but it would do well to remember that it developed within a Christian context. Biology, in particular, incorporated and held on to Christian concepts for a long time (Blumler, 1996). The traditional definition of species, with its emphasis on sharp reproductive barriers, is Creationist: if God created each species separately, there would be little possibility of interbreeding. Actually, hybridization leading to speciation, or the fusion of formerly separate species through allopolyploidy, is pervasive among plants and other organisms (Anderson, 1949; Arnold, 1992). Yet even Ernst Mayr, arguably the most influential evolutionary biologist of the twentieth century, continued to defend a (modified) biological species concept until his death (Mayr, 1996). The nature of species remains a matter of discussion. The ecological niche also is in part a Christian concept, related to the 'balance of nature'. If God created each species separately, he must also have devised each for its appropriate place and function in a harmonious Nature—that is, its niche. Linnaeus (1751), for instance, employed this concept, though he termed it 'station' (Worster, 1977). In the twentieth century, the niche concept was re-invigorated by the proliferation of equilibrium models in ecology. Yet across the sciences, the past century has seen a shift from viewing nature as static, and in equilibrium, to seeing it as dynamic, and even chaotic. In biogeography, the theory of evolution and the application of plate tectonics to biotic distributions both represent this shift, as does the shift from equilibrium to nonequilibrium ecology, among many Anglo-American practitioners.

From the Greeks came varied perspectives, including conceptions of nature as mutable

or dynamic. Theoprastus' approach to biogeography was inductive (Raup, 1942), while Aristotle's was deductive. One Greek influence was the division of the Earth into torrid, temperate, and frigid zones (still reflected in the *tierra caliente*, *templada*, and *fria* zones along the Andes). This tripartite division was carried over in the early classification of the Earth into what we now term biomes, for example, tropical rain-, temperate deciduous-, and boreal forest biomes (de Laubenfels, 1975). Via de Candolle (1855), it became the basis of Köppen's (1918; Köppen and Geiger, 1930) widely taught climatic classification system, intended to match climate with vegetation. But since we now know that at times in the past 'tropical' rain forest has extended as far as the Arctic Circle (Cox and Moore, 2005), it may be time to consider other groupings.

2.3 DISCOVERIES THAT CHALLENGED LONG-HELD VIEWS

As Europeans sent out explorers and colonizers during the centuries after 1492, discoveries in the New World, especially, raised doubts about the literal interpretation of the Bible. Were the American Indians descendants of Noah, and if not, were they even human? If two of every animal survived the Flood on Noah's Ark, how did armadillos migrate from Mt. Ararat to North America, and why didn't any stay in Asia? If God created each species for its own special niche, how could alien species invade and replace natives? Such considerations, along with the fossil record and other geological evidence for change and a long duration of the Earth's history, increasingly caused educated Europeans to regard the Bible as metaphorical rather than literal.

Modern biogeography is usually said to have originated with Humboldt, who focused on the aggregates of vegetation in nature, in relation to environment. Previously, individuals such as Carolus Linnaeus (1707–78) had organized nature taxonomically and had begun the process of determining species distributions. Linnaeus promoted a binomial nomenclature we still use today. In his work at the University of Uppsala from 1741 onward he was sent plant and animal specimens from around the globe. The tenth edition of Linnaeus's (1758) *Systema Naturae* classified some 4,400 species of animals and 7,700 species of plants. Linnaeus's intellectual descendants, such as Wildenow, Engler (1879-82), Sclater (1858), and Wallace (1876), were able to use the accumulating information on the distribution of named species to begin to delineate the world's floral and faunal provinces or realms, though only gradually was it realized that these distributions must have changed over time.

Contemporary to Linnaeus was Georges-Louis Leclerc, Comte de Buffon (1707-1788), whose thinking about plant and animal distributions had a profound influence on the next two generations of naturalists, including Charles Darwin. Buffon's thinking and therefore his contribution to biogeography differed in a number of important ways from that of Linnaeus. First, he concluded that the age of the Earth was much greater than 6,000 years as commonly believed at the time. Using the cooling rate of iron as a proxy for time, he calculated its age had to be closer to 75,000 years. In his multivolume *Histoire naturelle, générale et particuliére* (1761), Buffon drew on mounting field evidence to suggest that despite similarities in local environment and climate, different regions of the Earth had distinctive mammals and birds—a relationship later known as Buffon's Law. This seemed to imply some innate ability in living things to adjust to local environments through a process he called 'improvement' or 'degeneration'. However, reasoned Buffon, if species were immutable as generally thought, then their inability to 'improve' would have surely prevented them from migrating across inhospitable places following the Flood. This conclusion seemed to be further confirmed by the fact that some animals retained redundant or vestigial parts—suggestive of gradual development rather than spontaneous Creation. Based on this reasoning, Buffon's theory of dispersal involved climate-mediated migration from a possible center of origin in the previously warmer climes of northwestern Europe. Somehow, he theorized, populations of the New and Old World became separated on continental-scale islands during this migration phase and then changed.

> Hence, it is not impossible, that, without inverting the order of Nature, all the animals of the New World were originally the same with those of the Old, from whom they derived their existence; but that, being afterwards separated by immense seas, or impassable lands, they would in the progress of time, suffered all the effects of a climate that had become new to them, and must have had its qualities changed by the very causes which produced the separation. (Buffon, 1761)

Johann Reinhold Forster (1729–98), a scientist on Cook's second voyage, confirmed Buffon's law and extended it to include plants as well as mammals and birds across all regions of the world. He also drew attention to the fact that the diversity of plant species decreased from what he called the

'luxuriance of vegetation' in the tropical isles toward the 'rigorous frost of the Antarctic regions'. Forster (1778) developed one of the first frameworks for classifying plant assemblages around the world into regions of biotic similarity.

Alexander von Humboldt (1769–1859) is generally credited with being the first to approach the study of vegetation quantitatively and to stress the importance of environment in determining the distribution of communities. After Humboldt, there was increasing emphasis not only on defining floral and faunal provinces, but also on defining and explaining what we now call biomes, though admittedly the two were conflated for some time (de Laubenfels, 1975). Humboldt made contributions in areas we now recognize as climatology, geomorphology, and geology (Humboldt and Bonpland, 1805), and his role in the development of geography is well recognized (e.g., Martin, 2005).

Humboldt also recognized that the latitudinal gradient in biodiversity (see Mutke, this volume) described earlier by Forster could be identified in local elevational zones as a result of what we today call temperature lapse rates. This was especially evident in his surveys of the vegetation on Mount Chimborazo in modern-day Ecuador. These discoveries led him to further studies of climate-mediated change in plant communities, for which he employed mapping techniques based on isothermal lines. Humboldt's investigations inspired a series of European phytogeographers (including de Candolle, 1820; Drude, 1890; Grisebach, 1872; Schimper, 1898; Schouw, 1822; Warming, 1895), who developed a more sophisticated understanding of the world's biomes and their relationships to the environment. De Candolle (1820) already was discussing endemism and disjunctions in the early nineteenth century. By the late nineteenth century, Wagner and van Sydow's (1889) map showed all the modern biomes, except Mediterranean scrub. Schimper added the latter and argued that it represented a striking illustration of evolutionary convergence—a notion still widely promulgated today, though the reality is more complex than generally recognized (Blumler, 1991, 2005).

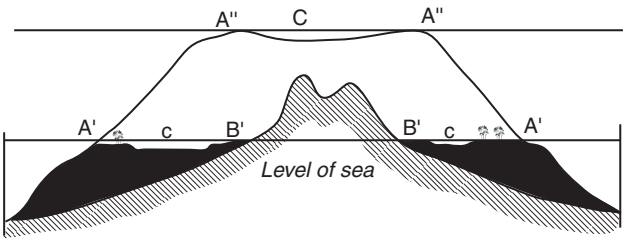
2.4 UNIFORMITARIANISM AND DEEP-TIME

Uniformitarianism and the notion of geological or 'deep-time' were proposed by a Scottish geologist, James Hutton (1726–97)—dubbed by some as the 'father of geology'. Field discoveries led him to challenge the prevailing 'Neptunist' theories of the time, which proposed that rocks had precipitated out of a single flood. It seemed to Hutton that the rocks formed in the sedimentary deposits he had witnessed, originated from a series of successive floods (Dean, 1992). Given that modern depositional, erosional, and uplift processes were gradual and occurred over long periods of time, it seemed only reasonable to conclude that the Earth was far more than a few thousand years old (Briggs, 2004). Widespread acceptance of uniformitarianism and deep-time, decades later, was largely due to the advocacy of the Scottish geologist Charles Lyell (1797–1875) and his colleague John Playfair (1798–1819). Ironically, while uniformitarianism was of major importance in understanding the Earth's history and in the development of the theory of evolution, it would much later serve as a barrier to acceptance of catastrophist theories of the K/T boundary and other mass extinctions.

While Lyell championed uniformitarianism, it was a contemporary French geologist, Adolphe-Théodore Brongniart (1801–76), who recognized the opportunity to use the geological record as a basis for recording the history, classification, and distribution of fossil plants. In the first volume of *Histoire des végétaux fossiles* in 1837, Brongniart demonstrated the value of studying botanical changes (especially extinctions) with respect to time. He showed that successive geological time periods could be characterized by the dominance of different plant life forms. Brongniart had reasoned that the close interrelationship between the Earth and the living things it supported implied that if the Earth's biophysical processes were mutable, then it should be possible to find evidence of the transmutation of species.

This idea of species transmutation (evolution) was not new at the time. Darwin (1809–82) began work on his theory of natural selection. Hutton (1794) had also advocated 'uniformitarianism for living creatures,' and the idea of evolution by acquired characteristics had been advocated by the French naturalist Jean-Baptiste Lamarck (1744–1829). William Paley had put forward the idea of divine design in nature. Geoffroy Saint-Hilaire had attempted to expand the evolutionary thinking of Lamarck, while Robert Chambers's writings inspired Wallace.

Darwin's initial inspiration was Humboldt, whose name he mentions more often in his journal of the *Beagle* than any other scientist (Darwin, 1845). Darwin might not have gone on the *Beagle* expedition had he not read Humboldt. As the ship's scientist, he modeled himself after Humboldt, particularly in the breadth of his observations (Worster, 1977). For instance, his explanation of the origin of coral atolls from volcanic islands remains an important contribution to



A'A', Outer edges of the barrier-reef at the level of the sea, with islets on it.
B'B', The shores of the included island.
cc, The lagoon-channel.
A''A'', Outer edges of the reef, now converted into an atoll.
C', The lagoon of the new atoll.
N.B.–According to the true scale, the depths of the lagoon-channel are much exaggerated.

Section of coral-reef

Figure 2.1 Darwin's model of coral atoll formation (after Darwin, 1845)

geomorphology (Figure 2.1). His other major inspiration was Lyell.

As is well known, exploration and biogeographical observations were crucial to the development of Darwin's theory. The spectacular success of the alien plant cardoon (*Cynara cardunculus*) in the Argentinian pampas seemed counter to the perfect Creation. Patterns on the Galapagos seemed particularly contradictory to what one might have expected the Creator to have designed, in three key respects (Sauer, 1969). First, Darwin noted the occupation of diverse Galapagos niches by species closely related to South American mainland taxa occurring in very different environments; second, he noticed the lack of similarity of the Galapagos fauna to that of the climatically and geologically similar but geographically distant Cape Verde Islands; and finally, as he was about to sail he was told that the tortoises varied from one island to another. While he could not confirm this about the tortoises, he was able to use his specimens to verify that a similar differentiation occurred in other taxa, such as finches. He came to understand that all three patterns were best explained as due to chance overseas dispersal from the nearest mainland, followed by speciation and what today we call 'adaptive radiation'.

Also well known, and therefore not repeated here, is the story of how Darwin delayed publication of his ideas about natural selection, until Wallace's independent development of the theory forced him to do so. As he had anticipated, Darwin's (1859) opus faced criticism from many quarters, including the Church. However, in the long period taken to prepare his manuscript he had been meticulous in paying attention to the internal consistency of his arguments, the faithful documenting of observations and inferences, and consideration of likely objections. He drew upon numerous subjects to advance his argument, including biogeography (Firenze, 1997). For instance, he pointed out that the southern continents have highly differentiated faunas, while the northern continents do not. Thus, he drew on the taxonomic evidence accumulated by earlier biogeographers. The pattern was best explained as due to the isolated positions of the southern continents, in contrast to the connectedness of those in the north. As Darwin put it,

> Barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions. . . . We see the same fact in the great difference between the inhabitants of Australia, Africa, and South America under the same latitude; for these countries are almost as much isolated from each other as is possible. (1859: 345)

He also pointed out that the barrier of Panama explained the great difference in the marine faunas of the Pacific and Atlantic Oceans. In contrast, when a continent extends over a long latitudinal range, one encounters what we would now term ecotypic or clinal variation, because of common origin somewhere along the latitudinal gradient:

> The naturalist in travelling . . . from north to south never fails to be struck by the manner in which

> successive groups of beings, specifically distinct, yet clearly related, replace each other. He hears from closely allied, yet distinct kinds of birds, notes nearly similar, and sees their nests similarly constructed, but not quite alike, with eggs coloured in nearly the same manner. (1859: 346)

Darwin noted, too, that while large mammalian herbivores are present on every continent, they are absent from most islands, such as the Galapagos, where they are replaced by giant tortoises and iguanas (Worster, 1977). Again, this seemed to be the result of dispersal rather than of Creation. Even clearer was the greater dispersal capacity of some plants, explaining their greater ability to colonize isolated islands, compared with mammals—and he pointed out that bats were an unsurprising exception. He discussed what we now call the Great American Interchange between North and South America, giving a modern explanation for the greater success of northern animals in the south as opposed to vice versa:

> I suspect that this preponderant migration from north to south is due to the greater extent of land in the north, and to the northern forms having existed in their own homes in greater numbers, and having consequently been advanced through natural selection and competition to a higher stage of perfection or dominating power, than the southern forms. (1859: 370)

In discussing island biogeography, Darwin noted both the tendency of islands to have fewer species than equivalent continental areas, and also what we now term 'disharmonic' floras and faunas. His explanation again was that isolation prevents dispersal. In this context, he even wrote about insular woodiness, more recently discussed by Carlquist (1965) with respect to the Asteraceae.

> Islands often possess trees or bushes belonging to orders which elsewhere include only herbaceous species . . . trees would be little likely to reach distant oceanic islands; and an herbaceous plant, though it would have no chance of successfully competing in stature with a fully developed tree, when established on an island and having to compete with herbaceous plants alone might readily gain an advantage by growing taller and taller and overtopping the other plants. (Darwin, 1859: 381)

Finally, Darwin noted the impact of alien species on isolated islands such as St. Helena:

> He who admits the doctrine of the creation of each separate species, will have to admit, that a sufficient number of the best adapted plants and animals have not been created on oceanic islands; for man has unintentionally stocked them from various sources far more fully and perfectly than has nature. (1859: 379)

He was unable to complement these dispersalist arguments with vicariant explanations for distribution (see below), because during his day no one believed that the continents moved. In arguing in support of his theory, Darwin marshaled additional evidence from several other fields besides biogeography. But as Firenze (1997) has pointed out, the biogeographical evidence is the easiest for the layperson to grasp, and it is the most effective in countering Creationist arguments, yet, unfortunately, it is seldom if ever employed today in debates over evolution.

Alfred Russell Wallace (1823–1913) also began his career with an expedition to South America, during which he studied the Rio Negro's zoology, botany, physical geography, and the languages and customs of its indigenous peoples. In short, he, too, was a geographer, as well as a naturalist. He then traveled to Indonesia, where he developed his version of the theory of evolution. (As was also true for Darwin, the theory fell into place when he connected Malthus's [1798] ideas about population growth to his biogeographical observations. It was the tendency of populations to produce more offspring than would ultimately be able to survive that gave natural selection a chance to operate.) As illustrated by the famous 'Wallace's Line,' he also contributed to the determination and mapping of faunal provinces. Subsequently, he discussed the existence of latitudinal diversity gradients.

For Wallace and Darwin it was the influence of extensive travel and time spent on 'strange' continents and oceanic islands, and seeing things that didn't fit conventional thinking, that led them to question conventional wisdom. For Darwin, it was in the year following his five-week stay on the Galapagos Islands that he began to reflect on the immutability of species.

While Wallace's work in the Malay Archipelago had largely convinced him of the verity of natural selection, it was at the urging of others, including Darwin, that he undertook a general review of the geographic distribution of animals. Initially, this work was hindered due to the immaturity of systems of classification. However, with developments in this field, by 1874 he was able to resume. He succeeded in greatly extending the regionalized system of geographic distribution developed earlier by Sclater (1858), a contribution that still forms the basis of eco-zones in use today. Wallace's (1876) two-volume epic was both a scholarly and synthetic achievement. Wallace based his global distributional scheme on a discussion of all of the

current and historic factors then known to influence animal distribution patterns within each region. For example, he theorized about the extentionalist ideas of land bridges, the effects of periods of glaciation, elevational gradients on mountain ranges, and the influence of regional vegetation on potential ranges of animal dispersal. In addition to this, he provided tables of all of the families and genera of higher animals with details of their distributional locations. When completed, it served as the definitive textbook on biogeography for decades to come.

In *Island Life* (1881), Wallace greatly assisted the process of reviewing, classifying, and consolidating the thinking of the time about islands. Until it was published, thinking about the significance of oceanic islands in elucidating likely causes of biological distributions and patterns of species richness had not generally been connected with thinking about continents. Wallace drew this distinction and noted the central role that islands played in the study of biological patterns. *Island Life* achieved more than a refocusing of what was then well known about continental, environmental factors of distribution. It extended the range of natural selection and thus showed how new species emerge in small isolated populations.

Evolutionary biologists and natural historians have continued to note differences between oceanic islands and continents, and to speculate on the causes of the differences (e.g., Carlquist, 1965). Adaptive radiation, so frequently encountered on oceanic archipelagos, continues to be of great interest. The vagaries of dispersal to isolated islands continue to be investigated and discussed (e.g., Ridley, 1930; van der Pijl, 1982). This type of research receded into the background during the heyday of the Equilibrium Theory of Island Biogeography (see below), but it never died out completely.

The end of the nineteenth century brought to a close a number of remarkable and defining theoretical achievements in the history of biogeography. Geologists and paleontologists had embraced uniformitarianism, calibrated estimates of the age of the Earth against proxy geological and fossil data, and advanced theories that posited a mutable Earth. Darwin and Wallace had built upon geological discoveries by amassing observational and distributional biological data to confirm the central role of natural selection in the mutability of species. Not only were global biological distributions better documented and classified, but the historical causal factors responsible for these distributions were better understood. This in turn had thrown clearer light on what Darwin (1859) had referred to as the *Origin of Species*. Meanwhile, European phytogeographers, such as Schimper and Warming, were refining the classification of biomes in relation to climate, in terms of the ecophysiology of plant growth; and Warming (1895) had outlined a model of succession to climax that would become the dominant theory (albeit in several versions) in plant ecology for much of the twentieth century.

By the start of the twentieth century, all biogeographers were more or less in communication and were aware of developments within the various branches of the field, even if not always in full agreement. For example, the French regarded Lamarck, not Darwin, as the true father of evolutionary theory (Glick, 1974). Subsequently, several separate schools developed and in some respects their underlying paradigms diverged. Today, biogeographers frequently are poorly informed about developments within schools other than their own.

2.5 HISTORICAL BIOGEOGRAPHY (PALEOBIOLOGY)

De Candolle (1820) was perhaps the first person to distinguish historical and ecological traditions, suggesting that ecological biogeography involved physical causes acting at the present time, whereas historical biogeography depended upon past causes. For example, millions of years may be involved in the action of evolution and tectonics. One problem with a discrete classification framework of this kind lies in the difficulty of the categorization of causes like the Pleistocene glaciations of a more intermediate time horizon. Thus, it is useful to divide the paleobiology (historical biogeography) tradition into paleontology, concerned primarily with deep-time, and evolutionary questions; and Quaternary studies, concerned primarily with environmental reconstruction over the past few million years. Relatively few paleobiologists concern themselves with both, so they can be thought of as two separate traditions (see Millington et al., this volume).

As analytical methods have begun to emerge in historical biogeography over the last century it has become evident that distributional patterns are not the result of a single historical or ecological cause (Crisci et al., 2003). Yet despite the conceptual and theoretical problems associated with tightly defining historical and ecological biogeography, this distinction has persisted throughout the twentieth century.

Palynology, which developed early in the twentieth century, was particularly appropriate for studies of Pleistocene and Recent environments. A single pollen diagram contains information about many taxa through time (see Figure 29.2 in Marchant and Taylor, this volume, for an

excellent example). It may be possible to derive conclusions about presence, relative or absolute abundance, biodiversity, macro- and microclimate, seasonality, migration, extinction, and human presence and impact from such diagrams. This has made it possible to test empirically many of the hypotheses put forward to explain peculiar biogeographical patterns. Most important, palynology had been applied to the former distribution of plants and was shown to be useful in the reconstruction of past environments. Recent decades have seen a proliferation of additional techniques; some (e.g., radiocarbon dating and charcoal analysis) have improved the utility of pollen cores, while other techniques, such as isotopic ratios, have provided independent lines of evidence.

Palynology and these related techniques have led to the publication of regional reviews of the reconstructed Quaternary history of vegetation in almost all the world's regions, after the pioneering works in Northern Europe established the technique's efficacy (e.g., Godwin, 1940 and references therein), including 'difficult' areas like the Arctic (Huntley and Webb, 1988) and the Tropics (Flenley, 1979). There have also been illuminating studies, based on palynology and related techniques, of many specialized aspects of biogeography (e.g., community instability—Davis, 1981; historical taxon mapping—Huntley and Birks, 1983; human-induced deforestation—Williams, 2006; agricultural origins—Yasuda, 2002; environmental history—Oldfield, 2005; and responses to climatic change—Bush and Flenley, 2007). Palynology has also made very important contributions to the data needed for the testing of mathematical models used in the predictions of global warming (e.g., Goudie and Cuff, 2002). Pre-Quaternary palynology is increasingly important in studies of the evolution of plants and in historical biogeography (e.g., Morley, 2000; Flenley, 2007).

As the Earth became more thoroughly explored by biologists, its floristic and faunal realms became better defined (Darlington, 1957; Good, 1974). However, these are viewed in the context of plate tectonics rather than seen as existing immutably since the dawn of Creation. It is becoming more accepted to approach the subject of geographic distribution from an ecological perspective (Cox and Moore, 2005; Lomolino et al., 2006, although some efforts have been made to return the field to a geographic orientation (Craw et al., 1999).

2.5.1 Plate tectonic theory

The theory of continental drift (plate tectonics) had an enormous impact on historical explanations of species distribution patterns. Although there were individuals before him who had proposed that continents moved, Alfred Wegener (1880–1930) published in 1915 a hypothesis supported with considerable evidence. His theory was largely rejected by geologists, supposedly because he did not provide a believable mechanism, but it is more likely it was rejected because his evidence was almost entirely geographical (i.e., his fossil evidence was biogeographical), and because he was an outsider—a meteorologist. This is in contrast to Darwin, who also was attacked for lacking a mechanism for natural selection before the rediscovery of Mendelian genetics, and yet gets full credit today. Wegener still is shunted to the background. In his repeated attempts to persuade the geological hegemony, Wegener suggested several possible mechanisms, including convection currents in the mantle, which would seem similar enough to what we now label plate tectonics.

Plate tectonics superseded the many alternative theories purporting to explain patterns of tectonic activity, such as the contracting and expanding Earth theories (Carey, 1976), and several others that seemed absurd to intelligent laymen (see the marvelous satire by Barks, 1956). These developments had a profound influence on thinking about historical biogeographical causes. They implied the existence of a co-evolutionary interplay between life and a changing Earth landmass, and a differing conception of land bridges than the former understanding (Croizat, 1964).

Leon Croizat (1894–1982) is the most prominent name in the study of the biogeography of the distant past. He not only linked geographic barriers and living things through co-evolution, but he also attempted to relate biological diversity to three principal factors (form, space, and time). This framework is still used for the disciplinary coordination of historical biogeography to this day. Form may be thought of as including both molecular (DNA) and morphological (phenotype) characteristics that are the principal concern of plant and animal systematics. The temporal dimension has been provided by paleontology (fossil evidence of animals and plants) and palynology (fossil pollen evidence of plant pollen), while biogeography has stressed the central role of spatial analysis. Collectively, the various disciplinary strands that make up historical biogeography currently employ at least 31 different techniques (Crisci et al., 2003), an achievement that has, in recent times, led to lively debate as to the actual epicenter of the discipline (Avise, 2000; Craw et al., 1999; Humphries and Parenti, 1986). Yet while a rather diverse methodological orientation has emerged, the scope of historical investigation has remained relatively the

same—geographical arrangement and space-time processes.

While plate tectonics is generally accepted as an important factor in distribution, nonetheless there is far less consensus about the relative contributions made by dispersal and vicariance. In vicariant distributions an ancestral population is divided into subpopulations through the emergence of a barrier they cannot cross (a disjuncture). In dispersal, a preexisting barrier limits the range of an ancestral population. Ever since the early theorizing of Linnaeus, biogeographers had supported distribution by dispersal, an idea that was initially linked with the assumption of Earth immutability (see Riddle, this volume).

However, between 1940 and 1960 dispersal theories were challenged by two botanists, Stanley Cain (1944) and Croizat (1958), who promoted vicariance as an alternative explanation. The subsequent acceptance of plate tectonics made vicariance more plausible. Later, Croizat (1964) tried to resolve indecision about the relative importance of dispersal and vicariance by proposing the existence of alternating cycles of each. This theoretical model was later supported by Craw et al. (1999). Croizat's (1964) focus of attention on species diversity implied that the ecological community-scale was just as important to this type of theoretical analysis, even though geographical distribution research had been strongly dominated by an ecosystem orientation.

While it is useful to distinguish the paleobiology tradition from other branches of biogeography, its practitioners seem on the whole to be apprised of each other's work, and they are aware of developments within other traditions. In contrast, the separation of the 'Continental' and 'American' biology traditions stem from the early twentieth century, when beliefs about succession began to diverge.

2.6 ECOLOGICAL BIOGEOGRAPHY

2.6.1 Succession theory and nonequilibrium ecology

The concept of succession is usually traced to Henry Cowles's (1899) pioneering study of Lake Michigan sand dunes, but Cowles and Frederick E. Clements (1874–1945) borrowed the basic model from Warming, with the bio-utopian aspect of Clements's thought deriving more from Drude (McIntosh, 1985; Worster, 1977) and Herbert Spencer (Raup, 1942; Blumler, 1996). Clements's (1916) theory of plant succession became known as the mono-climax theory, indicating a single equilibrium state. He believed the order and endpoint for succession in a region were determined by climate, a proposition that was challenged on theoretical (Gleason, 1926; Simberloff, 1980) and empirical (Connell and Slatyer, 1977; Walker, 1970) grounds, and it was never accepted in Europe. European thinking about succession was similar except that multiple climaxes were accepted within climate regions, corresponding especially to soil variability. Consequently, Clements and his followers displayed little interest in vegetation mapping below the biome level, while in contrast, on the continent, the Zurich-Montpellier school of phytosociology (Braun-Blanquet, 1928, 1951, 1964) and its competitors developed extremely detailed systems of classification and mapping, which continue to this day.

In contrast, within American biology in the latter half of the century even biomes increasingly were deemed unworthy of discussion, because they were descriptive rather than theoretical. Only with the rise in concerns over global change has the study of biomes undergone a resuscitation. Note that while Braun-Blanquet and other European ecologists sharply distinguished their views on succession from those of Clements, their version was equally equilibrium-based and as such, would subsequently be classified by American nonequilibrium ecologists as 'Clementsian'.

Clements's model combined the Enlightenment ideal of progress with the Romantic idealization of the 'forest primeval', thus giving it a powerful and persuasive emotive content (Blumler, 1996). Gleason's (1926) critique of the reality of communities was in part a Darwinian response to Clements's 'Lamarckian' (really, Spencerian) notion of the community as a superorganism. Gleason's argument, and the ideas of others such as Raup (1964), played an important role in overturning traditional notions of succession in the United States. The following is perhaps the earliest clear statement of the nonequilibrium perspective:

> Ecological and conservation thought at the turn of the century was nearly all in what might be called closed systems of one kind or another. In all of them some kind of balance or near balance was to be achieved. The geologists had their peneplain; the ecologists visualized a self-perpetuating climax; the soil scientists proposed a thoroughly mature soil profile, which eventually would lose all trace of its geological origin and become a sort of balanced organism in itself. It seems to me that social Darwinism, and the entirely competitive models that were constructed for society by the economists of the nineteenth century, were all based on a slow development towards some kind

> of equilibrium. I believe that there is evidence in all of these fields that the systems are open, not closed, and that probably there is no consistent trend towards balance. Rather, we should think in terms of massive uncertainty, flexibility and adjustability. (Raup, 1964: 19)

But the existence of this perspective was not the only reason for the different trajectories that succession theory took in the United States and Europe. Important also was the difference in landscapes: human-dominated in Europe, and 'wilderness' in the United States. In Europe, succession theory was not really amenable to hypothesis testing, since any deviation from the expected climax could be explained in terms of prior human impact. In North America, too, there was little intentional testing of succession theory, but the management of wilderness areas for climax created natural experiments. It turned out that the predictions of the Clementsian model of succession were not always right (Walker, 1970). Repeated failures of management predicated upon Clementsian theory led ultimately to a re-evaluation of the theory (Botkin, 1990), increasing appreciation of the importance of natural disturbance and of the highly contingent nature of vegetation response to disturbance (Sprugel, 1991), and the recognition of additional successional pathways besides Clementsian 'facilitation' (Connell and Slatyer, 1977).

Connell and Slatyer (1977) reviewed the succession literature and concluded that 'inhibition'—where early successional species exclude those that are later in the sequence, unless and until disturbance creates openings in the early successional cover—probably is as frequent (if not more so) as facilitation or tolerance. Inhibition arguably is not really succession, since it requires additional disturbance after the disturbance that initiates succession (Blumler, 1993). 'Chronic patchiness' (Botkin and Keller, 1994), where the first species to occupy a site after disturbance is able to outcompete and exclude all subsequent arrivals, also is not succession in the normal sense. There are even cases of reverse succession, for example, when annuals outcompete and replace herbaceous perennials and woody plants (Blumler, 1993) and when herbs replace woody plants after nitrogen fertilization (e.g., Wood et al., 2006). Consequently, nonequilibrium ecologists now prefer 'vegetation dynamics' to 'succession' (Glenn-Lewin et al., 1992), and they generally accept the Gleasonian view that communities are of limited validity (Gleason, 1926; Whittaker, 1975; Davis, 1981). In the English-speaking world, 'climax' is now usually placed in quotes, because it is considered imaginary (Botkin and Keller, 1994).

2.6.2 Ecosystem ecology

In contrast, ecosystem ecology (Odum, 1969) incorporated Clementsian assumptions. It became increasingly popular over approximately the same time period as did nonequilibrium ecology. Ecosystem ecology caught on especially within the environmental movement and among those scientists concerned with biogeochemical cycling and simulation modeling. Succession theory was not really relevant to those studying biogeochemical cycling, but it did pertain to simulation modeling. Robert MacArthur's contributions (see below), such as the Equilibrium Theory of Island Biogeography (MacArthur and Wilson, 1967), also were equilibrium based. Equilibrium and nonequilibrium theories continue to co-exist—somewhat uncomfortably—for instance, in theorizing about species diversity (Connell, 1978). The equilibrium models of the 1900s (see the quote by Raup, above), which dominated the sciences and social sciences then, are now generally abandoned; but this is less true within ecology and biogeography. The co-existence of equilibrium and nonequilibrium perspectives does not resemble the Kuhnian model of an outmoded paradigm being overturned. It bears somewhat more similarity to Gould's (1981) example of repeated influence on scientists from the larger society. The environmental movement, and society as a whole, tends still to believe in a balance of nature, and so researchers are attracted to equilibrium models. However, this does not seem to be a complete explanation for their continuing popularity among ecologists and biogeographers.

2.6.3 The continental school

On the European Continent (but not the British Isles, which was influenced more by American developments), the twentieth century saw a continued emphasis on describing and analyzing vegetation-environment relationships, complemented by the development of systems of vegetation classification. In their influential textbooks, Warming (1895), Schimper (1898), Schröter (1904), and others advocated a causal approach in vegetation studies and contributed to establishing vegetation science as an important branch of ecology around the turn of the century. The advancement of physiological plant ecology (e.g., Larcher, 1994) facilitated consolidating findings on environmental relationships of vegetation types. Heinrich Walter was the most influential exponent of ecophysiologically based vegetation studies that led to his global vegetation surveys (e.g., Walter, 1973; Walter and Breckle,

1982–91, 1985). Contemporary efforts were directed into the development of standardized vegetation-analysis methods, which allowed the systematic classification of plant communities and quantitative evaluations of community data. The evolution of continental-European phytosociology —the Zurich-Montpellier School—is intrinsically tied to the name of Josias Braun-Blanquet (1884–1980). His textbooks (1928, 1951, 1964) have influenced vegetation science for decades, and his approach found acceptance in many regions of the globe (but not in the United States and Great Britain). Wrongly identified for some time as the mere description of plant communities by Anglo-American vegetation ecologists, the Braun-Blanquet approach was designed as an ecological approach and goes far beyond pure community typology (Mueller-Dombois and Ellenberg, 1974; Dierschke, 1994; see also van der Maarel, 2005). For instance, the ecological tradition of continental-European vegetation science that included experimental approaches as well, has allowed for the accumulation of particularly rich knowledge on the environment of plant communities and the ecological behavior of participating species, reflected, for example, in the system of indicator values for central European vascular plant species regarding moisture, soil nitrogen status, soil reaction, soil chloride concentration, light regime, temperature, and continentality (Ellenberg et al., 1992; see Uzunov, this volume). Ellenberg also developed a widely noted global classification system of plant formations (Ellenberg and Mueller-Dombois, 1974) and summarized the available knowledge of the ecology of central European vegetation in classical textbooks (Ellenberg, 1988, 1996).

Ecological biogeography on the European continent during the twentieth century was on the one hand heavily influenced by vegetation ecology, further developed mainly by (geo)botanists focusing on plant species and communities and their distribution and environmental relations. On the other, biogeography received special impetus from physical geography (especially plant or vegetation geography), whose exponents focused on regions and landscapes and their biocoenological setting (e.g., Schmithüsen, 1968). Based on their spatial perspective on relationships among landscape elements, physical geographers shaped the emerging discipline of landscape ecology. Carl Troll (1899–1975) introduced the term 'Landschaftsökologie' (landscape ecology), motivated by the novel perspective on landscapes offered by aerial photographs (Troll, 1939). He defined landscape ecology as the study of the complex spatial and temporal interactions between biocoenoses and their environmental conditions in a given landscape section (Troll, 1966). Troll's concept was broadened by Schmithüsen (1976) and Neef (1967), who explicitly integrated humans and their activities into the continental-European concept of landscape ecology. Based on the theoretical fundament of a holistic landscape science, elaborated by the above 'founding fathers', efforts toward integrated, interdisciplinary research concepts pertaining to environmental issues and land-management problems (e.g., the UNESCO Man and Biosphere program) have been reinforced since the 1970s. At the same time, the central European concept of landscape ecology was adapted and modified by emerging schools of landscape ecology in other parts of Europe and elsewhere (e.g., Naveh and Lieberman, 1984; Forman and Godron, 1986; see Kupfer, this volume). Compared to vegetation ecology, plant geography, and landscape ecology, the impact of animal ecology and zoogeography on European biogeography was meager. The insufficient integration of animal ecology and vegetation ecology is still considered a methodological deficit, even though efforts toward unifying theories and concepts are being strengthened (e.g., Kratochwil and Schwabe, 2001).

Influences from continental Europe on North American and British biogeography have been idiosyncratic. Raunkiaer (1934) elaborated Warming's concept of 'life forms', an approach that received a mixed reaction both in Europe and in the United States (Raup, 1942). Subsequently, Raunkiaer's life-form classification influenced those interested in describing 'functional types' as a means of enabling predictive biome modeling (e.g., Shugart, 1997). Küchler (1947, 1967) brought the German vegetation mapping tradition to the United States and found a vacant niche because of the near absence of mapping there. His influence persists in maps of 'potential natural vegetation' and in the equilibrium succession-to-climax assumptions of some biome models. As Prentice et al. (1992: 132) put it, "the climatic control of plant distribution has not been regarded as a central research field in ecology or biogeography for fifty years or more." Their statement was true for the United States, though not for Europe. When American interest was rekindled, German approaches were available to serve as a template.

While we have emphasized German research, other European nations were on parallel tracks and were generally aware of each other's work, including the Russians. The latter influenced the Chinese (e.g., Grubov, 1969), while the imperialist powers influenced their former colonies. Consequently, the Continental school exerts great influence throughout the non-English-speaking world. For instance, UN vegetation maps reflect

the Continental tradition. Only in one or two countries, notably Britain and Israel, was there any merging of the Continental and American approaches.

2.6.4 The Berkeley School

Meanwhile, a branch of biogeography had arisen within the Berkeley School of American Geography, originating in Carl Sauer's (1889–1975) interest in human-environment interaction and, especially, agricultural origins and dispersals (Sauer, 1941, 1952, 1956). Sauer was influenced by his advisors at the University of Chicago and their strong interests in the historical geography of settlement; his primary intellectual allegiance was to nineteenth-century German geographers such as Ratzel, whose own major influences were Darwin and Haeckel (who coined the term 'ecology'). Abiding biogeographical themes have included, besides agricultural origins and dispersals (Blumler, 1992; Blumler and Byrne, 1991; Sauer, 1993), crop genetics and evolution (Blumler, 2003; Zimmerer, 1996), fire (Minnich, 1983; Vale, 2002), vegetation dynamics (Veblen, 1992), historical ecology (Minnich, 2008), invading species (Mensing and Byrne, 1997), ethnobotany (Voeks, 1997), landscapes (Gade, 1999), conservation (Zimmerer and Young, 1998), environmental thought (Blumler, 2002; Lewis, 1992; Zimmerer, 1994), and. in general, human-environment interaction. The broad interest of Berkeley School members in manifold human-environment interactions is associated with a generally broader concern for conservation than the intense focus on biodiversity characteristic of the American biology school.

Nonequilibrium theory was rapidly accepted within the Berkeley School, perhaps more so than in American biology, reflecting geography's emphasis on contingency and complexity. Both Gleason (1922) and Raup (1942) had published in the *Annals*, and Raup specifically aligned himself with Sauer and with Hartshorne's idiographic orientation. Sauer's son, Jonathan, trained in biology with his father's close friend Edgar Anderson, whose interest in weeds, dumps, gardens, and so on was congruent with the Berkeley School human-environment orientation. But J. Sauer's understanding of vegetation dynamics differed sharply from Anderson's Clementsian views. Tim Brothers, one of J. Sauer's students, described his perspective this way:

> He distrusted grand theories, particularly those arrived at by reasoning from general principles, and he took delight in pointing out examples to contradict them. He did not believe in deterministic models of plant succession, island diversity, plant migration or crop domestication. . . . Above all, Sauer was interested in the myriad interactions between people and plants. His discussions of crops and weeds were not just about the plants concerned but about the cultural contexts that produced them. . . . This emphasis continues to distinguish biogeography as done by geographers from the versions practiced by many other kinds of scientists. (Brothers et al., 2009: 170)

Widespread acceptance of nonequilibrium ecology is illustrated by the many publications of Tom Veblen (e.g., 1992) and his students, on vegetation dynamics and natural disturbance; equally numerous palynological papers (American palynologists especially in geography tend to align with Margaret Davis's [1981] Gleasonian views on communities, whereas in Europe, for instance, she is less influential); as well as occasional contributions from others (e.g., Brown, 1993).

2.7 THE AMERICAN BIOLOGY SCHOOL

2.7.1 Robert MacArthur and the theory of Island biogeography

At about the same time that plate tectonics was gaining acceptance, and just as American plant ecology was beginning to shift toward a nonequilibrium perspective, Robert MacArthur brought equilibrium models from economics into ecology and initiated a trend, which continues, of emphasizing the theoretical over the descriptive. Although the bulk of his work was ecological, not biogeographical, he did contribute some work toward the latter (e.g., MacArthur, 1972).

Much of the concern was with niche assembly of communities, using the equilibrium assumption of one niche, one species—an assumption, it is now known, that does not always hold (Shmida and Ellner, 1984). MacArthur and E.O. Wilson (1963, 1967) established an enormous influence on biogeography when they drew attention back to the role of island area in explaining species distribution. Islands had come to the attention of biogeographers in early theorizing around centers of origin, the mapping of species distributions, and in Wallace's *Island Life*. MacArthur and Wilson were puzzled by the same observations that had drawn the attention of early biogeographers as to why islands have fewer species than do sample areas of the same size on continents. This led them to propose their Equilibrium Theory of Island Biogeography (ETIB).

Islands are useful as biological laboratories because they are of limited size and have clear boundaries. Insularity is found not only in a sea. For example, there are islands of woodland in a sea of pasture, islands of pasture in a sea of arable land, ponds in a sea of land, caves in a sea of rock, cool mountains in a warm lowland, and high-UVB mountains in a low-UVB lowland (Flenley, 2007). Initially, the same principles were thought to apply, and therefore the ETIB was broadly applied in conservation and the design of nature reserves. Some pointed out, however, that oceanic islands are embedded in a much more hostile matrix than are habitat islands on land, with significant consequences, for example, for invading species.

A plot of the number of species on an island against the area of the island on a log-log scale is described by the equation:

$$S = CA^z \quad (1)$$

where S = number of species, A = island area, C = a constant depending on taxa, region, etc., and Z is a constant (about 0.3 in this case).

The conclusion is that large islands have more species (or genera in the case quoted above). MacArthur and Wilson explained this as an equilibrium reached through time, between the immigration of new species and the extinction of species already there. When few species are present, the immigration rate is high, as all arrivals are new species. When many species are present, most new arrivals represent species already there; therefore, the immigration rate drops. This balance between immigration and extinction is illustrated in Figure 2.2. When few species are present, only a few are available to become extinct; therefore, extinction is low. When many species are present, many are available to become extinct, and their average population size is low; therefore, extinction is high.

This is modified in two ways. A far (isolated) island receives less immigration than a near one. A large island has fewer extinctions than a small one (because larger populations are less likely to hit zero) (Figure 2.3). Therefore, large near islands usually have a high diversity, while small far islands usually have low diversity (see Figure 2.4). All of this assumes equilibrium conditions. A similar though not identical result could be produced by a nonequilibrium model in which far islands just take longer to fill up, through immigration and evolution (adaptive radiation). In fact, MacArthur and Wilson suggested that in evolutionary time the number of species on isolated islands would creep upward, a point that most have overlooked, and that Sauer (1969) suggested violated the fundamental reasoning behind the model.

The best way to detect an equilibrium is the presence of turnover (i.e., change of the species list through time, without change in the total number of species). The island is then said to be saturated. MacArthur and Wilson expected rapid turnover, which empirical studies for the most part have not verified.

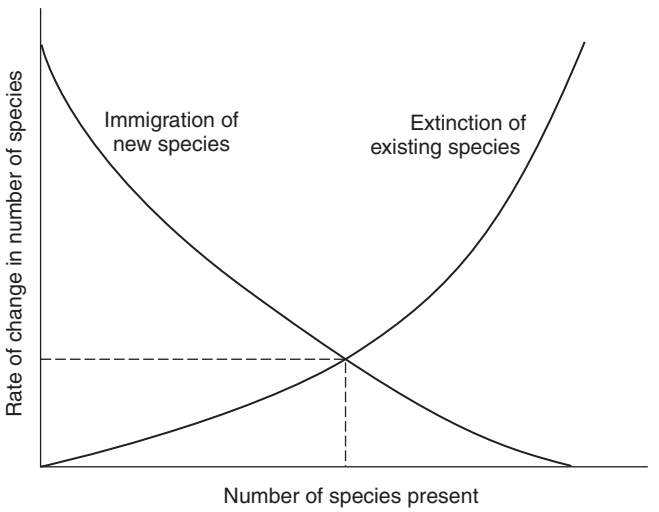


Figure 2.2 The equilibrium model of the biota of an island (after MacArthur and Wilson, 1963)

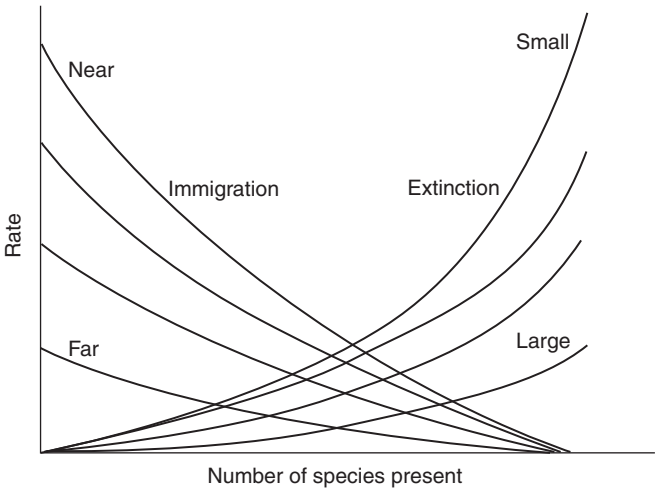


Figure 2.3 The relationships between rates of species immigration and extinction with island size (small and large) and isolation (near and far) (after MacArthur and Wilson, 1963)

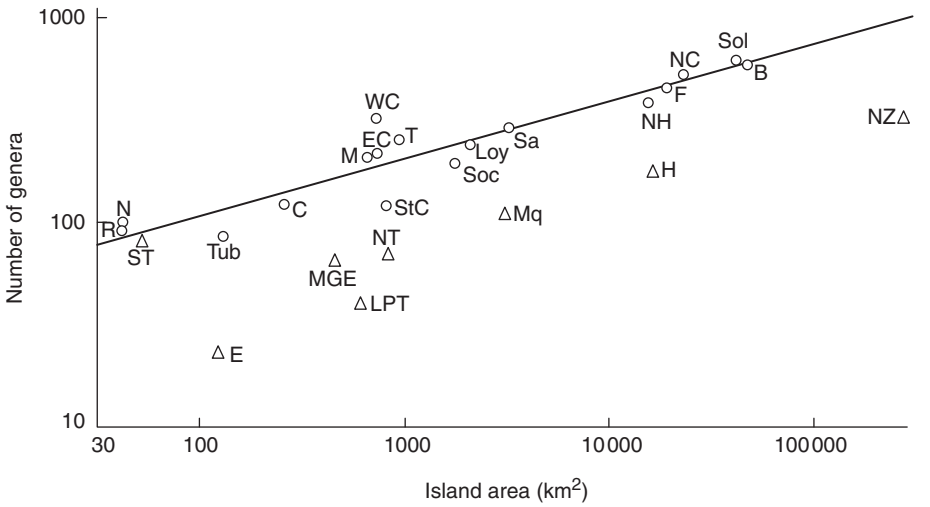


Figure 2.4 The relationships between island area and diversity of conifers and flowering plant genera in the Pacific Islands. The more isolated islands are indicated by triangles. The data from the other islands lie very close to a straight line (the regression coefficient), suggesting that generic diversity in these islands is almost entirely controlled by island area—the correlation coefficient is 0.94, indicating a very high degree of correlation. The islands are B – Bismark Archipelago; C – Cook Islands; E – Easter Island; ED – East Carolines; F – Fiji Islands; H – Hawaiian Islands; Loy – Loyalty Islands; LPT – Line, Phoenix, and Tokelau groups; M – Marianas; MGE – Marshall and Gilbert Islands, Tuvalu; Mq – Marquesas; N – Norfolk Island; NC – New Caledonia; NG – New Guinea; NH – Vanuatu; NT – Northern Tuamotu Islands; NZ – New Zealand; Ph – Philippines; R – Rapa Island; Sa – Samoa group; Soc – Society Islands; Sol – Solomon Islands; ST – Southern Tuamotu Islands; StC – Santa Cruz Islands; T – Tonga group; Tub – Tubai group; WC – West Carolines. Date from Van Balgooy, 1971 (after Cox & Moore, 1993)

There are exceptions to the overall generalization. Most of these are islands isolated in their location. The most extreme case is Easter Island, with a known native higher plant flora of 48 species (Flenley and Bahn, 2002). The depauperate nature of the flora, and especially the presence of only one tree and two shrub species, was originally explained as a result of its exceptional isolation. However, the study of fossil pollen (Flenley et al., 1991) and fossil wood and charcoal (Orliac, 2000) have shown that the island was once well forested, with numerous additional woody species, including an extinct palm. The decline of the forest and the flora occurred almost entirely within the archaeologically known time of human occupancy starting at perhaps AD 800 or earlier (Cole and Flenley, 2008), and many bird species were extirpated or made extinct also during that period. Since the people were constructing giant stone statues with weights up to 80 tons, and were moving them distances of several kilometers, it seems almost certain that a large amount of timber was used in the moving process. The combination of this with agricultural clearance for cropping easily explains the deforestation. The continuing ability of the island to support vegetation is evidenced by the approximately 160 introduced species that now grow on the island. Easter Island illustrates the need to interpret data with caution.

The ETIB assumed an ongoing or dynamic interplay between local extinction and immigration rates in maintaining optimal levels of species diversity for a given island area—a kind of index for ecological potential or carrying capacity—and relative distance from species source. The theory was effective in (a) drawing greater attention to biodiversity in general (MacArthur, 1972); (b) promoting the conservation movement by promoting theory development around (what are today much criticized) principles for reserve design; (c) theoretically underpinning the development of metapopulation biology (Levin, 1970); and (d) attempting to provide a methodological basis (generally not used today) for the estimation of extinction rates.

The theory has not been without its critics (Gilbert, 1980; McIntosh, 1980; Sauer, 1969; Slobodkin, 1996; Whittaker, 1998 Williamson, 1981). McIntosh (1985: 280) reported that the theory "was variously described as a revolution, as nomothetic, or as fairyland." In the earliest and perhaps the most withering attack, Sauer (1969) questioned almost every aspect of the ETIB, though he also praised sections of the book that dealt with ancillary matters, such as speculations about the role of stepping-stone islands. Interestingly, these sections are today almost forgotten in the intense focus over what MacArthur and Wilson themselves acknowledged was a simplified model. Over the years, biogeography textbooks have drastically altered their evaluation of the ETIB, from entirely positive to decidedly mixed. Metapopulation theory (Hanski and Simberloff, 1997) has perhaps been the most important subsequent development. Otherwise, with the exception of Hubbell's (2001) 'unified neutral theory of biodiversity and biogeography', ETIB's theoretical development has somewhat foundered.

MacArthur's models were generally borrowed from economics, so it is unsurprising that MacArthur and Wilson's (1963) original model is identical to the supply and demand curves used by economists to determine partial equilibrium market prices based on the so-called multifactor theory of value. The same model, although applied in a different domain, suffers from similar limitations.

First, there is the problem of appropriate system time horizon and the implications this has for defining equilibrium conditions. It is evident that both economic markets and island ecosystems collapse (Flenley, 1985; Whittaker et al., 1989) and then move toward new equilibrium points or what theoretical ecologists refer to as neighboring basins of attraction (Gunderson and Holling, 2002). The ability to move between one equilibrium point and another challenges the more traditional view that ecological equilibrium points are fixed and stable (i.e., movement away from equilibrium is quickly followed by a return to the same fixed point) (see Sprugel, 1991 for a similar argument regarding 'natural' vegetation).

An additional problem for the ETIB—one that does not apply in economics—is the role of evolution. The history of life shows generally increasing biodiversity, despite occasional mass extinctions. Thus, it may be that equilibrium has not yet been achieved, even in the oldest persisting environments, and that islands, which are inherently rather short-lived, are likely to see a continuing increase in diversity due to adaptive radiation, until they begin to sink beneath the waves. Certainly, adaptive radiation is a major feature of island systems, suggesting that (a) not all niches are immediately filled and (b) evolutionary processes can fill them, though this takes time. Recently, Whittaker et al. (2008) expanded the ETIB to take account of these variables.

As will be evident from this book, the ETIB still exerts major influence on the research agenda about island biogeography and reserve design. Wilson, who unlike MacArthur is still alive, continues to be praised for development of the theory (e.g., Quammen, 1996). The phenomenon of 'relaxation' (Diamond, 1982)—the often prolonged time it takes to lose species down to the

equilibrium level after habitat destruction—was recognized soon after the promulgation of the ETIB, but some conservationists continue to assume instantaneous equilibration with reduced areas after habitat destruction. In retrospect, it seems odd that so much was, and still is, made of an equilibrium model, during a period when nonequilibrium theory supposedly was replacing equilibrium theory, in the United States and other English-speaking countries. Wilson's (1959) earlier proposal of a 'taxon cycle' in ants colonizing islands remains fertile (e.g., Ricklefs, 2005), and this may ultimately prove more useful than the more ambitious ETIB, while relaxation is proving to be a concept with serious implications that reserve managers and others in conservation need to recognize and understand (e.g., Rosenzweig, 2003)—in contrast, perhaps, to the ETIB.

The American Biology School has become highly theoretical since MacArthur. Its proponents tend to assert that the field 'matured' when it became so (McIntosh, 1985). This appears to reflect the preference for deduction over induction in the sciences. But not all have found this approach useful. For instance, McIntosh (1980) reviewed developments in theoretical ecology and concluded that the search for explanation has proven 'frustrating'. Nonetheless, according to McIntosh (1985: 273): "Theoreticians . . . are a resilient lot, and the difficulty of identifying constants, laws, or rules has not inhibited them." Even Hutchinson, who was the inspiration for the rise to prominence of mathematical theory, had the following, cautionary remarks:

> Many ecologists of the present generation have great ability to handle the mathematical basis of the subject. Modern biological education may let us down if it does not insist, and it still shows too few signs of insistence, that a wide and quite deep understanding of organisms, past and present, is as basic a requirement as anything else in ecological education. (1975, quoted in McIntosh, 1985)

In this regard, it is well to remember that the greatest contribution of biogeography to science, the theory of evolution, resulted from natural history studies.

2.8 RECENT DEVELOPMENTS

Resilience theory was a natural extension of the nonequilibrium era in ecology (Holling, 1973, 1978, 1986) and eventually it drew attention to the existence of a feedback between community complexity and loss of resilience that would form the basis of a far-from-equilibrium base theory (Gunderson and Holling, 2002). It is as yet unclear how widely this theory will be accepted. Despite the repeated claims that nonequilibrium theory has won out within American biology, equilibrium concepts repeatedly reassert themselves. In part this is because equilibrium mathematical theory and modeling are more tractable and give less contingent, more confident (if you accept the assumptions) predictions. Also, the environmental movement remains deeply tied to equilibrium notions because of its bio-utopian beliefs, such as in the balance of nature (Blumler, 1996). For instance, Worster (1977) was suspicious of attempts to overthrow Clementsian succession, even impugning the motives (on the basis of precious little evidence) of Gleason and Raup, though later (Worster, 1990) he offered some grudging acceptance of nonequilibrium theory. Most biogeographers are environmentalist, so beliefs that take hold within the movement can exert great influence on scientists. The information explosion also appears to be playing a role, in that the impossibility of thorough literature review carries with it the possibility for theories considered outmoded in some circles to be treated as received wisdom in others.

Prior to 1900, all biogeographers were reading a common literature. But for much of the twentieth century there was little communication between the Continental and American biology schools. The last American to review Continental approaches to vegetation study was Whittaker (1962, 1973), and relatively little attention was paid to those works in the United States. Occasionally, continental biogeographers came to the United States and attempted to promote continental ideas (e.g., Mueller-Dombois and Ellenberg, 1974) but with little impact. In contrast, Continental biogeographers have not been terribly positive about vegetation studies in the English-speaking world. For instance, Westhoff (1970, quoted in McIntosh, 1985) divided vegetation studies as "the practical, the logical, the usual Anglo-American, and the negative" and stressed the implication that "the usual Anglo-American terminology regarding the science of vegetation research is neither practical nor logical." Nonequilibrium ecology has had little influence on the Continental School. A few attempts have been made to consider nonequilibrium theory, but on the whole these do not seem to accept its fundamental premises (e.g., Barbero et al., 1990).

The rise of concern over species extinctions (biodiversity) and global change, in parallel in Europe and in the English-speaking world, has produced a merger in recent years. A recent example of cross-tradition communication is in biome modeling (e.g., Cramer et al., 2001), which began

with Box's (1981) correlational model based on functional types. Box studied in Germany with Lieth and Walter, though it is unclear how much of his work they influenced. In any case, biome modeling in the English-speaking world was given its more influential impetus by Woodward (1987), who translated the eco-physiological approach of the Germans into terms that Anglo-Americans could appreciate. Woodward also drew upon European notions of succession, though currently some modelers are attempting to incorporate nonequilibrium-based vegetation dynamics.

2.9 CONCLUSIONS

The overall decline of knowledge of the scientific literature is unfortunately fostering a decreasing awareness of alternative perspectives. All schools of biogeography have something to offer, which is not to say that their underlying beliefs are necessarily correct in all particulars. They cannot be, since the views of one school sometimes contradict those of another. We agree with Robert May (1981, quoted in McIntosh, 1985), who opposes "naïvely simple formulations of The Way To Do Science" promulgated by 'doctrinaire vigilantes'.

We find the detailed vegetation mapping, classification, and analysis of the Continental school fruitful. We also would argue that Heinrich Walter's work is a 'must-read' for any student of vegetation. While the criticisms of McIntosh (1980, 1985) and others of the theoretical bent of the American biology school undoubtedly have merit, the school evidences an undeniable and exciting creativity, repeatedly coming up with new approaches that may prove groundbreaking (e.g., Brown, 1995). Finally, the Berkeley School might be criticized for being overly concerned with the historical or the practical, but on the other hand, its intersection with the social sciences and with the abiotic physical environment has added perspective that at times has enabled its practitioners to produce illuminating, if unfortunately overlooked, critiques of existing scientific theory. American geography's respect for local peoples and its inherent orientation toward 'adaptive management', even before Holling (1978) coined the term, have had the result that it has repeatedly produced sensible and sensitive prescriptions regarding land use in poor countries (e.g., Zimmerer and Young, 1998).

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