bioGENESIS

Providing an evolutionary framework for biodiversity science

bioGENESIS Science Plan and Implementation Strategy

bioGENESIS
a core project of DIVERSITAS

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Report N°6, bioGENESIS Science Plan and Implementation Strategy

© DIVERSITAS 2009 – ISSN: 1813-7105 ISBN: 2-9522982-7-0
Suggested citation: Michael J. Donoghue, Tetsukazu Yahara, Elena Conti, Joel Cracraft, Keith A. Crandall, Daniel P. Faith, Christoph Häuser, Andrew P. Hendry, Carlos Joly, Kazuhiro Kogure, Lúcia G. Lohmann, Susana A. Magallón, Craig Moritz, Simon Tillier, Rafael Zardoya, Anne-Hélène Prieur-Richard, Anne Larigauderie, and Bruno A. Walther. 2009.
bioGENESIS: Providing an Evolutionary Framework for Biodiversity Science. DIVERSITAS Report N°6. 52 pp.

Cover images credits: J Cracraft, C Körner, B A Walther, D M Hillis, D Zwickl, and R Gutell

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Approved by the Scientific Committee of DIVERSITAS

DIVERSITAS
an international programme
of biodiversity science

bioGENESIS
a core project of DIVERSITAS

Preface


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The stunning diversity of life is being diminished at an unprecedented rate owing to human impacts on the environment around the globe. Although much progress has been made in understanding biological diversity since Carl Linaeus in the 18th century and Charles Darwin in the 19th, it is clear that we still know little of the true diversity of life on Earth. Our lack of knowledge now severely compromises our ability to recognize and to respond appropriately to the rapid environmental changes that are occurring. Never before has it been so urgent – for the maintenance of nature and for our own well-being – to discover, to monitor, and to maintain biological diversity.

Although the study of evolution fundamentally underlies our understanding of biological diversity, evolutionary biologists – including systematists, paleontologists, biogeographers, and population geneticists – have played a rather limited role in responding to the biodiversity crisis. Yet, it is increasingly clear that the insights and tools of evolutionary biology are not just useful, but necessary in identifying and combating changes in biodiversity. The successful application of evolutionary biology in this arena requires increased integration, not only among the evolutionary disciplines, but between evolutionary biologists, ecologists and social scientists, all focusing on problems of immediate relevance to society.

In recognition of the need to integrate evolutionary knowledge and perspectives, DIVERSITAS, the international programme of biodiversity science, has initiated a new Core Project, bioGENESIS. The aim of bioGENESIS is to catalyse the international communication and integrated research that are necessary to bring evolutionary approaches to bear on pressing biodiversity issues in a timely fashion and on a global scale. bioGENESIS will inspire a new generation of research that will fuel a truly integrative, socially relevant biodiversity science.

It is already clear that several areas of evolutionary investigation are of direct significance to understanding and managing biodiversity. We urgently need new strategies and tools to discover and properly document biodiversity, including genetic and phylogenetic diversity. We need to coordinate interdisciplinary analyses of the dynamics of evolutionary diversification in the past, to make better predictions about responses to global change. We also need to understand and incorporate rapid evolutionary change in modelling responses to anthropogenic drivers. Overall, we must learn to harness evolutionary knowledge more effectively in our efforts to conserve biodiversity and promote human well-being. Corresponding to these broad needs, three primary foci have been identified within bioGENESIS:

FOCUS 1 New strategies and tools for documenting biodiversity

FOCUS 2 The causes and consequences of diversification

FOCUS 3 Evolution, biodiversity, and human well-being

This document, the Science Plan and Implementation Strategy of bioGENESIS, is the result of international meetings and consultations held over the past three years involving scientists from a variety of relevant disciplines. The Science Plan is by no means an end in itself, but is intended to be a flexible road map that will evolve as new data and ideas are generated. We hope that it will engage more and more scientists working at the interface of evolutionary biology and biodiversity science and will generate exciting new avenues of research. Similarly, we hope that the activities proposed here will enable scientists, resource managers, and policy makers to implement programmes and policies that reflect the relevance of evolution in addressing the biodiversity crisis.

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DIVERSITAS

DIVERSITAS is an international, non-governmental programme under the auspices of ICSU, IUBS, SCOPE and UNESCO (see side bar), that addresses the complex scientific questions posed by the loss of and change in global biodiversity. By connecting individuals across natural and social science disciplines, and across national or regional boundaries it addresses issues of global concern, thereby adding value to research projects being undertaken around the world at the national and disciplinary levels.

In accordance with the mandate developed by its sponsoring bodies, the mission of DIVERSITAS is two-fold:

- To promote an integrative biodiversity science, linking biological, ecological and social disciplines in an effort to produce socially relevant new knowledge.
- To provide the scientific basis for the conservation and sustainable use of biodiversity.

DIVERSITAS Sponsors

- International Council for Science (ICSU)
- International Union of Biological Sciences (IUBS)
- Scientific Committee on Problems of the Environment (SCOPE)
- United Nations Educational, Scientific and Cultural Organisation (UNESCO)

Scientific Core Projects

The primary means by which DIVERSITAS carries out its mission is through catalysing research aligned with its four Scientific Core Projects. Collectively, DIVERSITAS Core Projects comprise a cycle of discovery, analysis and information sharing that supports the application of socially relevant knowledge:

- bioGENESIS provides an evolutionary framework for biodiversity science, focusing on new strategies for documenting biodiversity, the causes and consequences of diversification, and evolution in relation to biodiversity conservation and human well-being.
- bioDISCOVERY focuses on developing a scientific framework to investigate the current extent of biodiversity, monitor its changes, and predict its future changes.
- ecoSERVICES explores the links between biodiversity and the ecosystem functions and services that support human well-being, and seeks to determine human responses to changes in ecosystem services.
- bioSUSTAINABILITY concerns itself with the science-policy interface, looking for ways to support the conservation and sustainable use of biological resources.

Cross-cutting Networks

DIVERSITAS also establishes Cross-cutting Networks, on specific topics or ecosystems, which embrace issues addressed in all four Core Projects:

Global Mountain Biodiversity Assessment (GMBA)

Steep terrain, extreme climates, and severe land-use pressure make mountain ecosystems among the most endangered in the world. Established in 2002, GMBA synthesises knowledge on ethical, ecological, economic and aesthetic values to tackle issues of societal relevance, including land-use management practices such as fire, grazing and erosion.

Global Invasive Species Programme (GISP)

Non-native organisms that cause, or have the potential to cause harm to the environment, economies, or human health, invasive alien species (IAS), are one of the most significant drivers of environmental change worldwide. GISP aims to conserve biodiversity and sustain human livelihoods by minimising the spread and impact of such species.

freshwaterBIODIVERSITY

Despite their critical role for basic life support, freshwater ecosystems remain poorly understood. In addition to identifying and monitoring freshwater biodiversity and its role in ecosystem functioning, this network seeks to understand how biological and social processes interact.

agroBIODIVERSITY

Examining both agricultural and plantation systems, this network promotes research on how contrasting land-use patterns affect biodiversity, ecological economics, and standard economic gains.

ecoHEALTH

This network studies the relationships between plant and animal biodiversity and (re)emergence of infectious diseases and the consequences for wild biodiversity and human societies.

Earth System Science Partnership (ESSP)

Recognising the links between biodiversity and other areas of global concern, DIVERSITAS is a founding member of the **Earth System Science Partnership** (ESSP; www.essp.org). In addition to DIVERSITAS, this partnership includes three other programmes that focus on global issues such as climate change and human impacts on the planet:

- International Geosphere-Biosphere Programme (IGBP)
- International Human Dimensions Programme on global environmental change (IHDP)
- World Climate Research Programme (WCRP)

Established in 2001, ESSP supports the integrated study of the Earth system: its structure and functioning, change occurring within the System, and the implications of change for global sustainability. ESSP currently oversees four Joint Projects.

Global Environmental Change and Food Systems (GECAFS) develops strategies to address food provision concerns while also analysing the environmental and socioeconomic consequences of adaptation and mitigation.

Global Carbon Project (GCP) investigates carbon cycles and energy systems to develop policy relevant knowledge that encompasses natural and human dimensions, as well as their interactions.

Global Water System Project (GWSP) examines how humans are altering the global water cycle, the associated biogeochemical cycles, and the biological components of the global water system, as well as human response to these changes. This project is closely aligned to freshwaterBIODIVERSITY.

Global Environmental Change and Human Health project (GECHH) investigates how environmental change worldwide affects human health and well-being, with the aim of developing policies for adaptation and mitigation. This project is developed in conjunction with ecoHEALTH.

National Committees and Regional Networks

One of DIVERSITAS' primary objectives is to create a worldwide network in support of biodiversity science that fosters integration across disciplines and establishes links at regional and international levels. Two types of bodies play important roles in the achievement of this objective: National Committees and Regional Networks.

National Committees enlarge DIVERSITAS' scientific and policy networks, thereby helping to establish crucial links between national biodiversity programmes and international framework activities. They also make it possible to implement and, where necessary, to adapt the DIVERSITAS Science Plan to local and regional concerns. Because many issues related to biodiversity transcend national boundaries, it is often essential for several countries to collaborate in scientific research and policy development.

The knowledge and experience gained through such integrative approaches is invaluable across the DIVERSITAS network.

Capacity building

The quest to expand knowledge about biological diversity holds inherent challenges. While most species are located in tropical areas, financial resources and technical capacity are severely lacking outside the developed world. Thus, it is critically important to pursue science while also making technological advances more widely available and building the skills necessary to carry out integrative research. As far as possible, all DIVERSITAS activities will be designed to support direct involvement of scientists from all regions of the world.

II

Evolutionary biologists – including systematists, paleobiologists, biogeographers, and population geneticists – have long endeavoured to document how many species exist on Earth, to understand the processes whereby these species originated and adapted, to chart how they are distributed, and to infer how they are related to one another in the tree of life. These are monumental scientific challenges of direct relevance to understanding and conserving biodiversity. Yet, despite much progress, our knowledge of the earth's diversity remains far from complete. In fact, in some groups of organisms, including most microbial lineages, the task of discovering unknown species has only now become possible, thanks to the development of new molecular and phylogenetic tools. Our limited knowledge seriously compromises efforts to cope with the rapid erosion of biodiversity around the globe. We are under-prepared to recognise changes that are occurring or to formulate appropriate responses.

While much fundamental work remains to be done, we can formulate broad areas of evolutionary investigation that are of direct significance to understanding and managing biodiversity. New strategies and tools are urgently needed to discover and properly document biodiversity. We need to coordinate interdisciplinary analyses of the dynamics of evolutionary diversification in the past, so as to provide better predictions about responses to global change. We also need to understand and incorporate the rapidity of evolutionary change in modelling biodiversity responses to anthropogenic impacts. More generally, we must make better use of evolutionary biology in our efforts to conserve biodiversity and promote human well-being.

Addressing these key issues depends on bringing together, in various new combinations, our ever-expanding baseline data on species identities, distributions, and phylogenetic relationships, as well as knowledge of the relevant underlying evolutionary processes. At present, the ability to connect and employ this information is limited and idiosyncratic. While some highly useful tools have been developed within each domain, these are as yet insufficient, and are poorly integrated and deployed, in part owing to limited coordination of the relevant scientific communities. DIVERSITAS, through the bioGENESIS Core Project, will play a key role in catalysing the international communication that is needed to tackle these problems in a timely fashion and on a global scale. In turn, this will promote a truly integrative biodiversity science that serves the needs of society.

The key issues that require concerted research efforts by evolutionary biologists are identified here as focal areas within the bioGENESIS Core Project of DIVERSITAS. These are highlighted because they are

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fundamental to our understanding of the origins and maintenance of biodiversity, but also because they will enhance ongoing efforts within the other DIVERSITAS Core Projects and Cross-cutting Networks. This list of focal areas and tasks, however, is not intended to be comprehensive or exclusive. Rather, these are viewed as several among many evolutionary issues of direct relevance to the core mission of DIVERSITAS to understand, conserve, and sustainably use biodiversity. We expect that the scope of bioGENESIS will be refined and expanded as its plan of work is carried out.

Within each focal area we illustrate a series of tasks with boxed examples, which highlight concrete studies and findings. In addition to the 22 boxes included in this document, in the text below we reference a set of supplemental boxed examples (labelled Box S1, Box S2, etc.), which can be accessed through the DIVERSITAS bioGENESIS web pages (http://www.diversitas-international.org). These supplemental boxes provide additional case-studies, and boxes will be added to the web site as the activities of bioGENESIS develop. Along with each task, we also provide a list of Research Objectives and Activities. These are not meant to be exhaustive, but simply to provide examples of activities of current interest. In all cases, our mission is to promote international networks, scientific participation, and access by a wide variety of user communities.

FOCUS 1.
New strategies and tools for documenting biodiversity

Tremendous progress has been made in discovering and documenting biodiversity since the time of Linnaeus. Over the past three centuries approximately 1.7 million species have been described, yet it is clear that many more species exist – easily more than ten times the number discovered so far (Heywood 1995). Likewise, we have discovered and named only a tiny fraction of the more inclusive branches of the tree of life, which provide us with the foundation for organizing and navigating all biological information (Cracraft and Donoghue 2004). At the same time, biodiversity is being lost at an unprecedented rate owing to human activities (Pimm *et al.* 1995, 2006; Hughes *et al.* 1997). In well-studied groups of organisms, such as birds and mammals, extinction rates now far exceed the background rates characteristic of most of geological time. If systematic biology proceeds along its current trajectory, we have no hope of discovering the vast majority of species before many (perhaps most) of them are driven to extinction.


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Dramatic changes are needed to greatly accelerate the rate of discovery. Although we recognise the rapidly expanding need for taxonomic expertise, and fully support the increased training of specialists on particular groups of organisms, we also appreciate that on the critical time scale – over the next 30 to 50 years – we are not likely to experience a major increase in the number of taxonomists upon whom this work ultimately depends. Therefore, we must increase dramatically our efficiency – from the collection of specimens in the field, to the discovery and description of new species and clades, to rendering these data readily accessible and interoperable with other biodiversity information. The aim of Focus 1 is to identify and facilitate the implementation of new strategies and tools to greatly speed the pace of this fundamental research, thereby providing a more effective pipeline from field exploration, through laboratory and museum studies, to databases accessible to relevant user communities. Here we see especially direct connections to the assessment efforts that form one of the primary foci of the bioDISCOVERY Core Project.

TASK 1.1 Discovering the unknown

DIVERSITAS, through bioGENESIS, will play a key role in establishing and maintaining international expertise, protocols, infrastructure, and data sharing mechanisms relevant to the discovery and description of biodiversity. Through bioGENESIS working groups and the formation of strategic partnerships with other relevant organizations (GBIF, TDWG, IBOL, GTI, GEO, CoML, EDIT, etc.), we envision the development of international standards for biodiversity repositories and "species discovery" centres, including best-practices for field work, for the collection and curation of voucher specimens, for imaging and DNA sequencing technologies, for the digitization of legacy data, for tissue – and DNA – banking and microbial culture facilities, and for the development, maintenance, and connectivity of relevant databases.

We will especially promote efforts to document the biodiversity of bacteria (Box 1), fungi (Box 2), and other microbes. These groups are expected to contain the majority of unknown taxa (Box S1), some of which will prove to be of enormous value to humans (e.g., in the development of new drugs and bio fuels; e.g., Smith *et al.* 2008; Box 2). As biological communities are generally composed of few dominant species, and many more that are rare, special attention must be given to improving the efficiency of discovering and describing low-abundance organisms. For microbes, the sequencing of environmental samples (metagenomics) has created the possibility of advancing our understanding of microbial diversity by orders of magnitude. Likewise, for small plants and animals, new "industrial-strength" sampling protocols have greatly accelerated the discovery of unknowns (e.g., Bouchet *et al.* 2002; Box S1).

bioGENESIS working groups will also address issues surrounding **(1)** access to materials and collection, which currently present impediments to progress in the discovery and description of biodiversity; **(2)** the development of local taxonomic capacity (including the work-force of in-country para-taxonomists; Box S2), focusing on providing training in low- and high-tech field, museum, and laboratory methods; and **(3)** access to, and utilisation of, spatial environmental information and new tools for spatial analysis, including GIS-based niche-modelling and prediction techniques, to increase the efficiency of field-sampling and discovery.


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Research Objectives and Activities

- Develop improved strategies and best-practices for global inventory and the discovery and description of biodiversity, increasing the efficiency of field sampling and the quality and accessibility of collections. This objective integrates with activities being carried out under the GTI and in GBIF, and links directly with the bioDISCOVERY Core Project and its ongoing involvements in the GEOSS effort (GEO BON).
- Promote the application of next generation DNA sequencing technologies to reveal the biodiversity and functions of microbes. This initiative relates directly to the assessment of global genetic diversity described below under Task 3.4.
- Facilitate the formulation of new policies regarding the collection of biological specimens for scientific research. This relates directly to Access and Benefit Sharing (ABS) under the CBD. bioGENESIS activities have already stimulated discussions that are informing the development of an international ABS regime.

BOX 1. Molecular approaches to discovering microbial diversity in the oceans

From the very beginning of life on Earth, microorganisms have been responsible for the cycling of materials through the biosphere. Although knowledge of the diversity and functioning of microbes is indispensable for understanding biological processes in the ocean, relatively little is known to date. Most microbes are not yet cultured and the function of most of their genes is still unknown. It is highly likely that undiscovered microbial diversity will reveal entirely new biological functions and chemical compounds, some of which will provide the raw material for human innovation into the future.

The application of molecular techniques, especially metagenomic approaches, has revealed an enormous diversity of undescribed, mostly uncultivable microbes (National Research Council 2007). Recent studies conducted in the Sargasso Sea using whole genome shotgun sequencing revealed the presence of 148 previously unknown bacterial phylotypes (Venter *et al.* 2004; Fig. 1.1). In addition, more than 1.2 million previously unknown genes were identified. Progress in sequencing technology has made it possible to analyse huge numbers of genes very rapidly. Sogin *et al.* (2006), for example, developed the parallel tag sequence method and used this in combination with pyrosequencing technology. Their analyses revealed the presence of an immense number of low-abundance populations, which accounted for most of the observed phylogenetic diversity in deep-sea samples from the Atlantic (Fig. 1.2).

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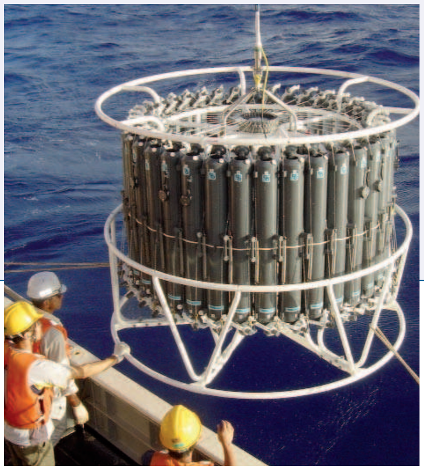

FIG. 1.1. Collection of seawater for metagenomic analyses, ©K Kogure.

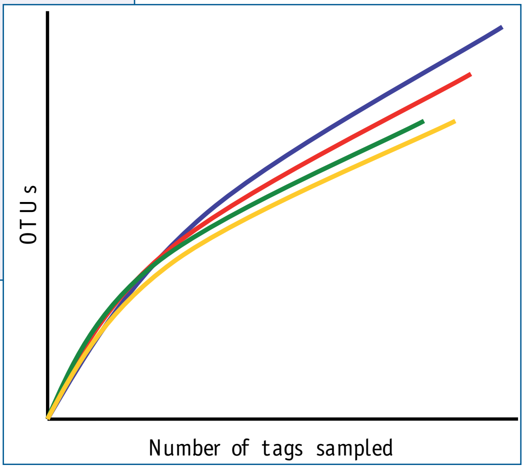

FIG. 1.2. Rarefaction of microbes (after Sogin *et al.* 2006), ©K Kogure. OUT, Operational Taxonomic Units.

BOX 2. "Myco-diesel" from an endophytic fungus

One argument for conserving biodiversity is that undiscovered species might yield products of importance to humans. However, the link between undiscovered biodiversity and potential usefulness has largely been conjectural. Recent studies of endophytic fungi living inside of tropical plants have provided direct evidence of the potential usefulness of undescribed species (Strobel and Daisy 2003). Combining field collecting and culture studies with bioinformatic analyses and assays for bioactive compounds, Smith *et al.* (2008) showed that many previously unknown microbes produce bioactive compounds. Several of the most genetically dissimilar and phylogenetically isolated endophytes were among those that showed high levels of bioactivity.

Studies of one such endophytic fungus, *Gliocladium roseum*, have documented the production of a series of volatile hydrocarbons – including octane and other compounds normally associated with diesel fuel – when grown on a cellulose-based medium and extracts of the host flowering plant, *Eucryphia cordifolia* (Strobel *et al.* 2008). This discovery of "myco-diesel" has clear implications for the production of biofuels, which migh potentially decrease reliance on fossil fuels.

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FIG. 2.1. *Eucryphia cordifolia* (Cunoniaceae), the host plant from which *Gliocladium roseum* was isolated, ©M Donoghue.

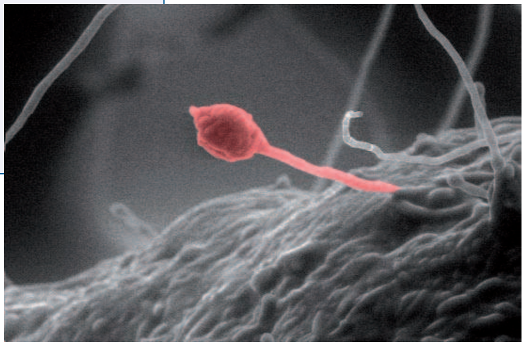

FIG. 2.2. *Gliocladium* sp., showing hyphae and spores, ©M Donoghue.

TASK 1.2 Capturing biodiversity information

The goal of this task is to improve methods of capturing biodiversity information. The bioDISCOVERY Core Project focuses upon advancing biodiversity assessment, tracking biodiversity changes, and developing scenarios of future biodiversity. The bioGENESIS and bioDISCOVERY Core Projects therefore share a common goal to improve the methods of biodiversity assessment, across both spatial and temporal scales, at the level of genes, species, and ecosystems, and in terms of the various functions and processes manifested by biodiversity. bioGENESIS will focus specifically on advancing biodiversity assessment based on evolutionary biology, including systematic biology, phylogenetics, and evolutionary genetics. Both bioGENESIS and bioDISCOVERY will contribute to GEO BON, a global network of biodiversity observation (Box 3). Here too, the aim of bioGENESIS is specifically to enable the deployment of evolutionary methods.

The accurate identification of species is fundamental to biodiversity assessment. It would revolutionise our ability to inventory and monitor biodiversity to develop rapid-capture technologies for identifying known species and discovering new ones. Of special interest is the development of a cost-effective, hand-held, automated species-identifier. The idea is to analyse a tiny sample of an organism; quickly extract, amplify, and sequence a set of target DNA markers; and then to compare these to known sequences to situate the unknown within the tree of life. The design of such a tool is already being pursued for medical diagnostic purposes, but a bioGENESIS working group could help to guide its development to insure maximum benefit to the biodiversity community. Perhaps most importantly, we must help to design the interface between international “bar-coding” efforts (IBOL) and the rapidly expanding “tree of life” databases being generated through individual and coordinated efforts (e.g., the US NSF's ATOL programme).

A key bioGENESIS initiative will be to continue to help in connecting the bar-code and tree of life efforts. The first such meeting, convened at NESCent (Durham, North Carolina, USA) in 2007, focused attention on what new insights might be gained by linking these activities. A crucial role will be to help to scale-up bar-coding standards to multi-locus assays, and in this way increase the connectivity to tree of life databases. Additionally, such workshops will serve to promote the sharing of biological materials and the development of community-wide standards for DNA isolation, vouchering, and storage. They will also address emerging issues surrounding the environmental sequencing of microbes (metagenomics), including the use of these sequences in isolating currently uncultivable organisms and identifying their phenotypes.

New technologies also are needed to make optimal use of digital images. This includes the utilisation of satellite technology for real-time analysis of field images, the use of remote-controlled internet cameras and microscopes, and the development of image recognition identification tools made available as web-services. It is also crucial to develop digital tools to extract data that are currently locked in the world's natural history museums. There may be as many as three billion specimens in these collections, each one accompanied by at least some information on where and when it was collected. We need automated methods to capture these data, requiring little human intervention (Donoghue and Smith 2005). An example is the HERBIS project (www.herbis.org; Box S3), which is attempting to produce a system of web-services to automatically capture and upload the label data associated with a herbarium specimen with a single click of a digital camera.

Another focus will be on streamlining the description of newly discovered species and clades, and developing better ways to translate new discoveries into the knowledge-bases used by decision-makers, including the emerging “Encyclopedia of Life” (EOL). Our bioGENESIS effort, which will be closely aligned with those of EDIT (Box 4) and related developments within natural history museums, will consider the digitisation of existing taxonomic literature and specimens and the development of new electronic publishing mechanisms. We also need to explore how nomenclatural codes and associated databases might best be designed to facilitate rapid publication and the dissemination of new taxonomic discoveries.

Finally, bioGENESIS will coordinate with bioDISCOVERY on the development of better mechanisms to utilise specimen data and related information to facilitate the work of environmental policy makers and the stewards of natural resources on local, regional, and national levels (Box S4). In particular, bioGENESIS can help to coordinate regional efforts (e.g., ERIN in Australia, CONABIO in Mexico, and BIOTA/FAPESP in Brazil), and promote the widespread use of successful strategies.

BOX 3. bioGENESIS and GEO BON

In recognition of the rapid erosion of biodiversity at the level of ecosystems, species, and genes, the international community established targets to significantly reduce the rate of biodiversity loss by 2010. To achieve this and future such targets, GEO, DIVERSITAS, and NASA announced the formation of a new global partnership, GEO BON (http://www.earthobservations.org/cop_bi_geobon.shtml). The newly established Biodiversity Observation Network seeks to develop open resource databases of various observations at the ecosystem, species and gene levels, coordinate and develop the monitoring of biodiversity changes in structure, composition, and function, and provide scientifically rigorous and up-to-date knowledge about on-going biodiversity changes.

In parallel with goals for species and ecosystems, GEO BON will facilitate the global monitoring of genetic diversity, including species phylogenetic diversity, using a combination of remote sensing and *in situ* approaches (Scholes *et al.* 2008). Three broad strategies for observation and analysis of genetic diversity will be employed by GEO BON:

(1) Repeated observation of specific genetic components in selected target species.

(2) Repeated observation of other components (e.g., geographic range) integrated with models that create links to genetic diversity.

(3) Repeated observation of changes in land/water condition (e.g., using remote sensing) integrated with models that act as a "lens" for inferences about corresponding genetic changes.

GEO BON will promote these strategies as a way to enable a range of monitoring approaches, extending from detailed observations for key species to model-based inferences of regional and global genetic diversity loss. In collaboration with GEO BON, and with bioDISCOVERY, bioGENESIS will play a leading role in designing and promoting global genetic diversity assessments to monitor how rapidly genetic diversity is being lost.

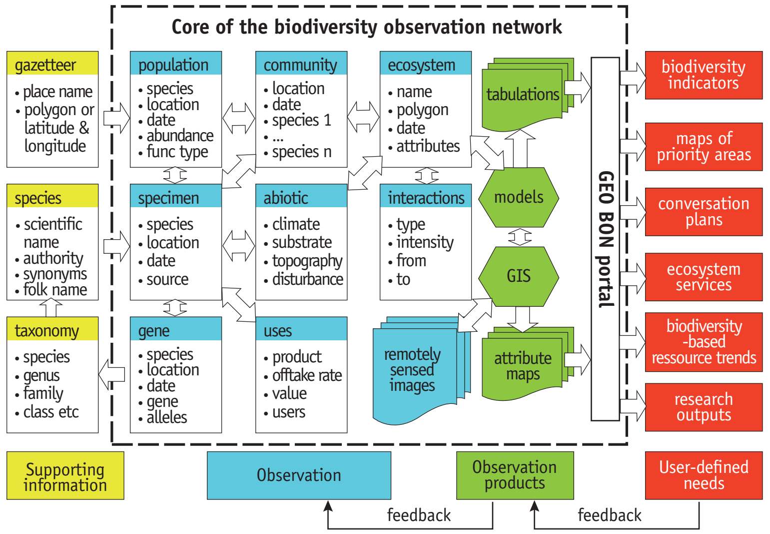

FIG. 3.1. A schematic representation of the core data types, observation products and end uses of an integrated biodiversity observation system. Most of the elements already exist, but are incomplete or dispersed among a wide range of partners. The proposed implementation strategy involves linking them using data-sharing protocols, followed by incremental, needs-led and opportunistic growth (from Scholes *et al*. 2008).

References

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BOX 4. EDIT Scratchpads: Unifying revisionary taxonomy on the Web

Using traditional methods and technologies our knowledge about species is accumulating too slowly to provide even basic information about most living species in less than several centuries. This limits the contribution taxonomy can make to biodiversity analysis. Modern IT technologies can increase both the rate of creation and the accessibility of knowledge on species, simply by individual researchers sharing a common on-line storage facility.

The idea behind the EDIT Scratchpads is simple: make web sites easy to get, easy to use, and easy to read by computers and humans alike. It starts from a vision: being a taxonomist, what would you like to see up on the web for your taxonomic group? Scratchpads are simply template web sites equipped with a number of tools and services that make it easy to add taxonomically relevant material. Initially, this may be no more than a personal statement about research on a group of organisms, but it may grow quickly as it is shared with others having similar interests.

Scratchpads are equipped with a number of tools and services that make it easy to add taxonomically relevant material. As an illustration, one of the first EDIT Scratchpads was devoted to the family Sciaroidea (fungus gnats). While the pages were being built in the UK, taxonomists from Norway found the site through a search engine, and with the permission of the site manager, started adding data of their own. This epitomises the vision that the Scratchpads will nucleate new communities of taxonomic experts.

EDIT Scratchpads illustrate how taxonomy can be transformed through the development and use of new tools that go beyond a change in method and imply a deep cultural change in how scientific knowledge is produced and disseminated. In the DIVERSITAS framework, they contribute to streamlining research to improve our understanding and sustainable management of biodiversity.

FIG. 4.1. Examples of Scratchpads serving different community functions, ©D Robert.

References

http://www.editwebrevisions.info

Research Objectives and Activities

- Develop mechanisms to promote electronic access to specimen-based information, such as best-practices for digitization and georeferencing projects.
- Promote research on innovative identification tools and the development of electronic field guides. This connects directly to elements within bioDISCOVERY.
- Collaborate with the Global Mountain Biodiversity Assessment (GMBA) on the integration of elevational data in georeferencing, distribution mapping, and niche-modelling.

TASK 1.3 Developing phyloinformatics

One of the most profound contributions of the systematics community to our understanding of biodiversity is knowledge of how species are related to one another in the tree of life (Cracraft and Donoghue 2004). This phylogenetic knowledge provides the basis for organising (in predictive classification systems) and navigating biological information of all kinds. Yet, at the present time, our ability to harness this rapidly expanding base of phylogenetic information is greatly hindered by the lack of an appropriate cyber-infrastructure allowing phylogenetic navigation – through clade-based queries – of other biodiversity information. For example, we currently have no way to quickly and accurately chart the geographic distribution of any particular clade of interest, such as the clade that includes the several major lineages of C4 grasses (Edwards *et al.* 2007). This is problematic as phylogenetic knowledge is accumulating rapidly, and older classifications are quickly becoming misleading.

We envision a bioGENESIS working group forming strategic alliances with a variety of relevant partners to shape the development of a comprehensive phyloinformatics infrastructure. Of special relevance is the ongoing effort under CIPRES to re-develop and greatly extend the capabilities of TreeBASE (www.treebase.org; Box 5). A number of efforts are also underway to code phylogenetic trees in KML (the language for drawing objects on Google Earth; http://earth.google.com/), which, in turn, will allow us to visualise patterns of biological diversification across the face of the planet. This technique is useful not only in analysing the geographical evolution of plants and animals (Box 5), but also in determining the site of origin and spread of infectious diseases (Box 6).


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Likewise, the databasing efforts underlying the Tree of Life web project (www.tolweb.org) are crucial to this development, as are the activities of the Encyclopedia of Life (EOL) and the NSF's iPlant phylogeny project that are focused on visualising large phylogenetic trees. There are many other such projects and connections to be made, such as with the major domain-specific data repositories, including GenBank and GBIF. Here we see special opportunities to develop international standards and protocols for the rapid, efficient connection of diverse data types. Among other things, this will entail the establishment of "ontologies" (or controlled vocabularies) for morphological and behavioural traits, and for connecting phenotypes to physiological and ecological functions.

Underlying all such efforts is the continued development of confident phylogenetic knowledge. bioGENESIS will play an important role in helping to stimulate this activity internationally, and in coordinating individual and national efforts along the lines of the US NSF's ATOL project. For example, bioGENESIS has already been successful in promoting tree of life research funding and collaborations within China (Hong et al. 2008). Likewise, bioGENESIS can help guide the development of standards for the naming of clades and the databasing of clade names.

Research Objectives and Activities

- Promote and coordinate international efforts to assemble the tree of life, including extension of the US National Science Foundation's "Assembling the Tree of Life" (ATOL) programme (see http://atol.sdsc.edu/) to Europe, Asia, and other regions.
- Develop mechanisms to integrate phylogenetic knowledge with geographic, morphological, paleontological, and ecological data to promote interdisciplinary studies of biodiversity dynamics.
- Coordinate with ongoing efforts within CIPRES, EOL, and iPlant on the assembly and visualisation of large phylogenetic trees, especially to insure broad international participation and access.

BOX 5. Visualising Evolution on a Global Scale

Evolution, as represented by phylogeny, is a central, unifying, expression of the history of life on Earth, and as such it can serve as a nexus for all sorts of biodiversity patterns: the interconnected causes of gene evolution and adaptation; of ecological diversification and morphological change; and of vicariance and speciation. Phylogenetic data are being published in the scientific literature in ever-increasing abundance (Fig. 5.1; Piel *et al.* 2002), and we can estimate that at least 60,000 phylogenies have been published since inexpensive computers and efficient DNA sequencing methods became available. It is only natural to find ways to trace and visualise spatial patterns of diversification. Google Earth,™ a freely available computer programme for 3D rendering of the earth and georeferenced data, is a perfect choice for visualising the interplay between phylogeny and geography (e.g. Fig. 5.1).

A number of efforts are underway to code phylogenetic trees in KML – the format for rendering objects and features in Google Earth. These include the TreeBASE Google Earth tree browser (http://www.treebase.org/getrees/); SupraMap (Janies *et al.* 2007); Mesquite Cartographer (http://mesquiteproject.org/packages/cartographer/); and GeoPhyloBuilder (https://www.nescent.org/wg_EvoViz/GeoPhyloBuilder). Additionally, GeoPhyloBuilder is built on the ArcGIS information system (ESRI), which potentially takes the user beyond visualization, allowing computational analyses at the interface of phylogeny and geography.

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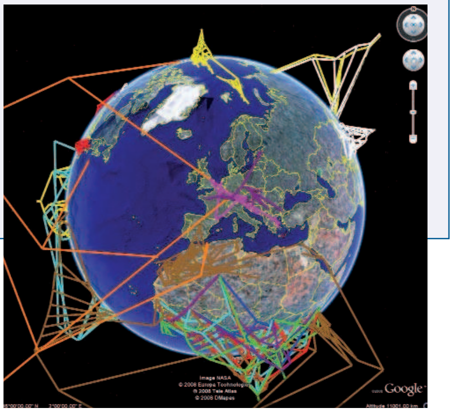

FIG. 5.1. Evolution of the Túngara Frog across the Isthmus of Panama. Phylogenetic relationships show a strong congruence with geography, in which the earliest branching events in the tree reflect an ancient loss of a land bridge between the continents. The TreeBASE Google Earth tree browser (http://www.treebase.org/getrees/) generated the coding of the tree for display in Google Earth, ©W Piel.

BOX 6. Geographic evolution and the spread of infectious diseases

One of the great services of evolutionary biology arises through the examination of evolutionary patterns in a geographic context to gain insights into the historical biogeography of groups of species. The same techniques developed to analyse natural history data can be applied directly to the question of the origin, spread, and transmission of infectious diseases. One such study investigated the spread of the "severe acute respiratory syndrome" (SARS) virus, which became a novel human infectious disease in 2002. Using genomic data to estimate phylogenetic relationships, the resulting tree shows the rapid and global spread of the SARS virus (Fig. 6.1). The tree also shows host shifts into carnivore lineages, contradicting the original hypothesis of transmission from carnivores to humans. Similar approaches have shed light on the origin and spread of West Nile virus, Hanta virus, and other such emerging diseases.

References

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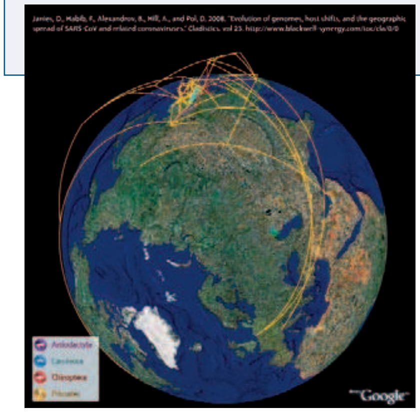

FIG. 6.1. Phylogeny of SARS-CoV (yellow lineages) and related coronoviruses from potential source populations (other coloured lineage). Superimposing phylogeny on geography (using Google Earth) allows us to visualise the origin of the virus in Asia and its rapid evolution (represented by long branch lengths) and spread through human populations, ©D Janies.

FOCUS 2.
The causes and consequences of diversification

Our understanding and management of extant biodiversity can benefit greatly from knowledge of changes in diversity through time. This provides both a historical perspective within which to interpret modern patterns and a framework for generating predictions about future changes. The idea behind Focus 2 is to understand how various drivers (climate change, episodes of invasion, etc.) have influenced biodiversity in the past, so as to enable better predictions of future change.

Great progress has been made in understanding the causes and consequences of diversification through time using a combination of paleontological and phylogenetic approaches. However, there are still wide gaps both in knowledge and in communication among the practitioners of these disciplines, as well as with those studying the genetics of speciation and adaptive radiation. Furthermore, and perhaps most importantly from the standpoint of DIVERSITAS, connections between evolutionary research, including the possibility of rapid evolutionary change, and ecology, including the study of present-day ecosystem function and the design of predictive models of biodiversity change, have been very limited. Through the bioGENESIS Core Project, DIVERSITAS will improve integration among these disparate communities.

TASK 2.1 Evolutionary change in diversity

It is clear that past environmental changes have impacted diversity on a variety of spatial and temporal scales. Such problems have been approached from various directions, with results of varying accuracy and precision. For example, Egan and Crandall (2008) successfully documented how diversification rates changed with past global climate changes resulting from Pleistocene glacial cycles (Box S5). However, it remains difficult in many cases – using paleontological data directly, or using phylogenies – to distinguish among a variety of possible causal factors (e.g., climate change vs. entry of a clade into a new geographic region vs. the origin of innovations in a clade) and downstream consequences (e.g., on rate of speciation vs. rate of extinction; Moore and Donoghue 2007). One common concern relates to the precision with which we can infer the timing of lineage-splitting events. Another is the reliability of the models used to locate shifts in diversification in the fossil record or in phylogenetic trees.

A bioGENESIS working group will focus directly on these issues. The aim of this group will be to enhance international communication across the relevant disciplines, and also to refine the key tools and models needed to make comparisons from which relevant biodiversity predictions can be drawn. For example, it may be possible to refine measures of the lineage-specific or functional selectivity of mass extinctions in the past, or the resilience or rebound dynamics following mass extinction events, again measured in both phylogenetic and functional terms. More generally, this activity would encourage the integration of tree-based and paleobiological approaches, and would expand modelling efforts to encompass the wide variety of outcomes now apparent in phylogenetic comparisons (e.g., the existence of ancient clades now containing just one or a few long-surviving species).

Critical to our understanding of the genesis of biodiversity is the relationship between speciation, the evolution of adaptive traits, and patterns of geographical distribution. Aspects of the problem have been studied in relative isolation by phylogenetic biologists, students of speciation, evolutionary developmental biologists,

Research Objectives and Activities

- Promote the integrated analysis (involving phylogeneticists, paleobiologists, population geneticists, and ecologists) of rates of speciation and extinction in relation to environmental changes, morphological and physiological innovations, and the movement of lineages into new geographic regions.
- Develop better methods to extrapolate/predict overall biodiversity patterns from studies of selected lineages, e.g., based on responses to common environmental gradients and historical processes.
- Apply these new approaches in the context of a chosen system; e.g., working with the Global Mountain Biodiversity Assessment (GMBA) on diversification at high elevations.

paleobiologists, and biogeographers. Integration across these disciplines would provide a much clearer understanding of the relationship between the origin of novelties within populations and the evolution of species differences, and between modes of speciation (sympatric, allopatric, etc.) and patterns of character evolution and/or the resulting distribution of geographic ranges. In-depth studies on groups showing exceptionally high diversity, such as cichlid fishes (Box 7), and those involving hybrid speciation, such as arctic primroses (Box 8), are accelerating our understanding of these relationships. A bioGENESIS working group focused on these issues will draw together these disciplines to develop a coherent general model of diversification, which could then be applied, for instance, to understanding the dynamics underlying the existence of biodiversity hotspots.

BOX 7. Rapid radiation of cichlid fishes in East African lakes

One of the most intriguing questions in evolutionary biology is how biological diversity has been generated, especially when this appears to have taken place very rapidly. The Great East African Lakes (Victoria, Malawi, and Tanganyika) have witnessed the evolution of nearly 2,000 species of cichlids in the last 1-10 million years. In Lake Victoria, most of the species appear to have arisen in only 15,000 years, before which the lake bed was almost entirely dry. This spectacular burst of recently diverged but phenotypically diverse species offers a special opportunity to studying the underlying generative mechanisms.

Diversification in this system is thought to be the result of both natural and sexual selection. Natural selection has acted through adaptation to habitat (e.g., rocks, sand) and diet (e.g., snails, fish, zooplankton). Sexual selection has acted through divergence in male colouration and behaviour, coupled with female preferences for those colours and behaviours. These drivers of speciation may be acting in a particular sequence, starting with divergence in habitat use, then feeding morphology, and then colour (Kocher 2004).

Diversification in African cichlids is now being impacted by human activities. In addition to extinction caused by introduced predatory fishes, such as the Nile perch, eutrophication has reduced water quality and thereby degraded the sexual signals that influence species recognition (Seehausen *et al.* 1997). Jointly these processes have greatly reduced the diversity of cichlid species in Lake Victoria. These findings call for more attention to the nature of species differences and how these will respond to human influences.

References

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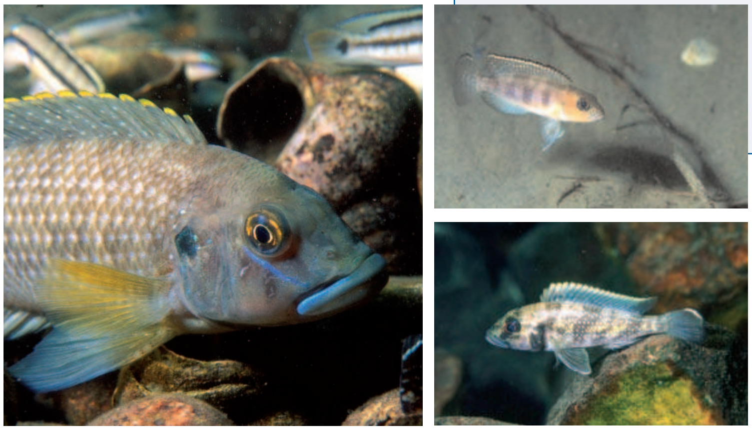

FIG. 7.1. Diversity of cichlids: radiation of trophic morphologies and male colour patterns (Kocher, 2004), ©L Ruber.

BOX 8. Climate change, habitat fragmentation, and hybrid speciation in primroses

A relatively large proportion of plant species, especially in the arctic, are polyploids, i.e., their chromosome numbers are multiples of the number in related diploid species. One proposed explanation for this observed distribution of ploidy levels is the so-called secondary contact model (Stebbins 1985). According to this model, climatic and geological changes that cause the fragmentation and subsequent secondary contact between differentiated populations favour the origin of new species through hybridization, followed by chromosome doubling. Successive cycles of climate change, habitat fragmentation, and secondary contact can drive the evolution of species to progressively higher ploidy levels (Fig. 8.1).

In a group of arctic primroses *(Primula sect. Aleuritia)*, polyploid, self-fertilising species tend to occur at higher latitudes than their diploid, outcrossing relatives. Evidence from phylogenetic trees generated from maternally – and biparentally – inherited genes clarified the relationships between diploid progenitors and polyploid derivatives (Figure 8.1), suggesting that speciation via secondary contact provides a plausible scenario for correlated changes in ploidy level and reproductive strategies. During the Pleistocene, glacial advances fragmented the ranges of the diploid species, while glacial retreats allowed ranges to come into contact again, promoting the origin of polyploid taxa through hybridization. The scarcity of suitable pollinators at higher latitudes might explain the higher re-colonisation success of the polyploid, selfing species in comparison with their diploid, outcrossing relatives.

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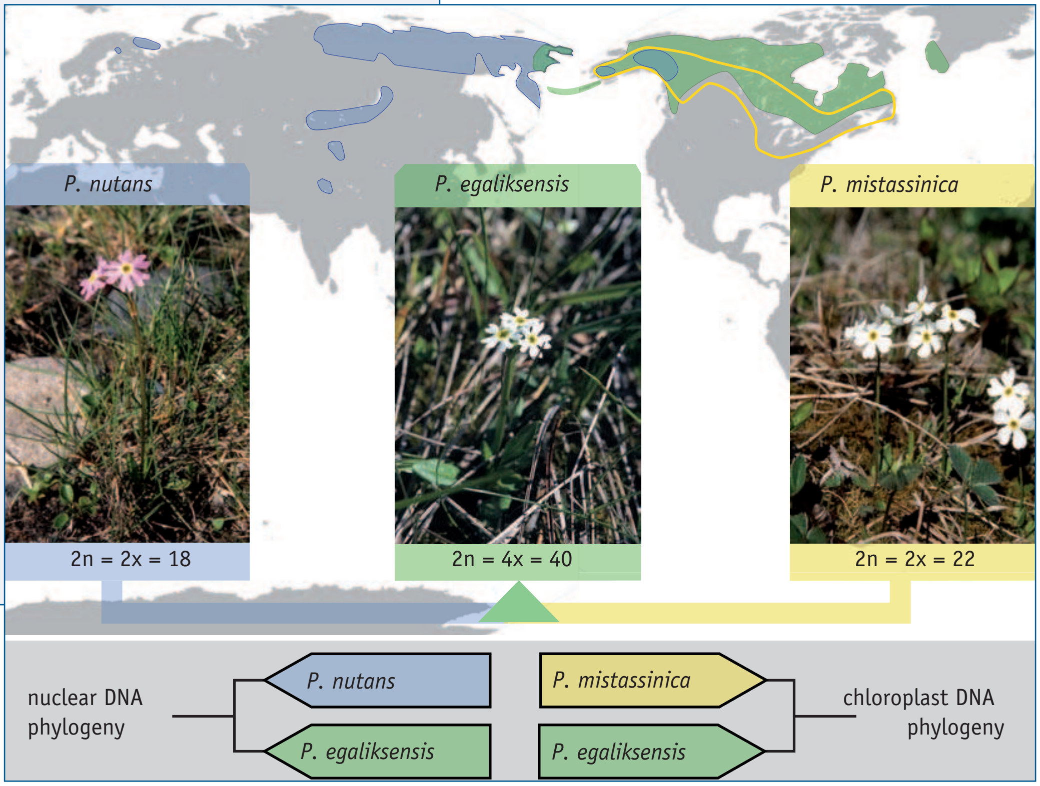

FIG. 8.1. Phylogenetic trees show that the diploid, outcrossing *Primula mistassinica* and *P. nutans* gave rise to the tetraploid, selfing *P. egaliksensis*. The geographic distribution of *P. egaliksensis* overlaps with the ranges of the two diploid parents, ©E Conti.

TASK 2.2 The evolutionary history of biotic assembly

Generations of biologists have focused on describing and understanding the composition and function of biotic communities. Ecological assemblages, at whatever spatial scale, have histories – they were pieced together through time, by the movement of species into and out of the system, or by *in situ* speciation and extinction events. Interactions among species and ecological functions have changed throughout this assembly process. The species in a local assemblage may be clustered phylogenetically (i.e., closely related) if habitat filtering was the dominant process shaping community memberships, or phylogenetically widely distributed or overdispersed (i.e., less closely related) if competitive exclusion of ecologically similar close relatives was the predominant factor (Webb *et al.* 2002; Box S6). Likewise, spatial patterns of biodiversity have changed over time (Box 9), and our understanding of these patterns would benefit from historical analysis. At present we possess adequate spatial data for relatively few areas and groups of organisms. Much more detailed information is necessary to identify hot spots of diversity and to explain how species came together to form the ecosystems we now know. The aim of Task 2.2 is to integrate the historical and spatial analysis of biotic assemblages across a variety of scales, from local assemblages to ecosystems and regional species pools.

The species now present in any assemblage came to occupy the same area – and to interact with one another – through a particular sequence of historical events. Some of the species in the system have been interacting (and potentially coevolving) for longer, and some for much shorter, periods of time. At times in the history of life there have been episodes during which species have come newly, and quite rapidly, into contact (e.g., Vermeij 1991). Examples include the great biotic interchange between North and South America (Marshall *et al.* 1982), and the wholesale effects on species ranges of glacial cycles during the Pleistocene (Roy *et al.* 1996; see also Box 8). Human activities have recently brought species together at an unprecedented rate through the introduction of exotic species, some of which having become aggressive invasives.

Some progress has been made in inferring sequences of community assembly and patterns of species movements through the integration of paleontological, phylogenetic, and biogeographic methods (Box 9). These same approaches can reveal how environmental changes have shaped current genetic diversity. However, much remains to be done to comprehend the assembly of particular biotas and to extract any general assembly rules. This requires the development of a conceptual and methodological framework for bringing together knowledge of the fossil record, phylogeny, biogeography, and lineage divergence times, along with geographic and climatological information related to organismal function (e.g., physiology and dispersal ability).

Evolutionary analyses may also help to explain spatial patterns of diversity, for example, the widely cited latitudinal diversity gradient (Box 10). Critical elements in elucidating the establishment of such gradients include the inference of ancestral and descendant areas of distribution, the timing of lineage diversification and changes in rates of speciation and extinction, the extent to which lineages track their ancestral ecological niches through time and space ("niche conservatism"), and the effects of Quaternary climate change on local extinction and colonization. Bringing these elements together will result in a far richer understanding of the origin of biodiversity gradients.

A bioGENESIS working group will be organised to foster collaboration among different scientific communities, including paleobiologists, phylogeneticists, ecologists, climatologists, and geologists. These connections will enable investigations of such questions as: In any given ecosystem, how many of the species originated *in situ*, versus having originated elsewhere and then filtered into the system at a later date? For those that moved into the system, are there any patterns involving source regions and times of immigration? Are there particular functional traits that originated within the system, or preferentially filtered into the system through species movement? Can we identify character shifts that were brought about by the entry of species into the system and subsequent interactions in a new setting? How does the phylogenetic relatedness of species within an ecosystem relate to the functioning of the system? Focus 2.2 will serve to explore and promote the integration of historical and ecological knowledge relevant to such questions about biotic assembly.

Greater knowledge of the effects of past climatic cycles on species origins can also inform the prediction of future evolutionary dynamics. How will climate change affect habitat fragmentation and therefore, hybridisation between species in the future (cf. Box 8)? Can we predict how temperature increases will change biotic distributions and opportunities for secondary contact among differentiated populations? By fostering the integration of phylogenetic tools with ecological niche modelling, bioGENESIS activities will improve our ability to make informed choices for the conservation of areas where different species and biotic communities come in contact, under current and future climate projections (see also Focus 3).

Research Objectives and Activities

- Promote the integration of analyses of biome and community-level assembly processes, bringing together phylogenetic, biogeographic, and ecological approaches.
- Apply new analytical approaches in the context of selected study systems; e.g., tropical forests of Southeast Asia in conjunction with CTFS and DIWPA; tropical montane diversity in conjunction with NESCent working groups; and Mediterranean ecosystems.

BOX 9. The assembly of regional biotas

Understanding how diversity evolves within local, regional, and continental biotas, and thus contributes to diversity within assemblages at these different scales, requires analyses of speciation among closely related groups, insights into how Earth history may have driven large-scale shifts in species distributions, and information on the effects of climate change on the expansion, contraction, and shuffling of species distributions over time. Examples of highly diverse biotas that might be studied from these perspectives include the rainforests of the Amazon Basin or northeastern Australia, the deserts of Australia, the savannah/grasslands biotas of eastern and southern Africa, and the biotas of high montane areas (e.g., Pennington *et al.* 2006).

It has been proposed, for example, that lowland forest populations of South American birds and other organisms were passively transported to high altitudes by the rapid uplift of the Andes, thus contributing to the montane ecosystems we see there today. Many of these montane species assemblages were later subjected to repeated bouts of allopatric and sympatric speciation as altitudinal vegetation zones were raised and lowered as a function of cyclical climate change during Plio-Pleistocene times (Ribas *et al.* 2007).

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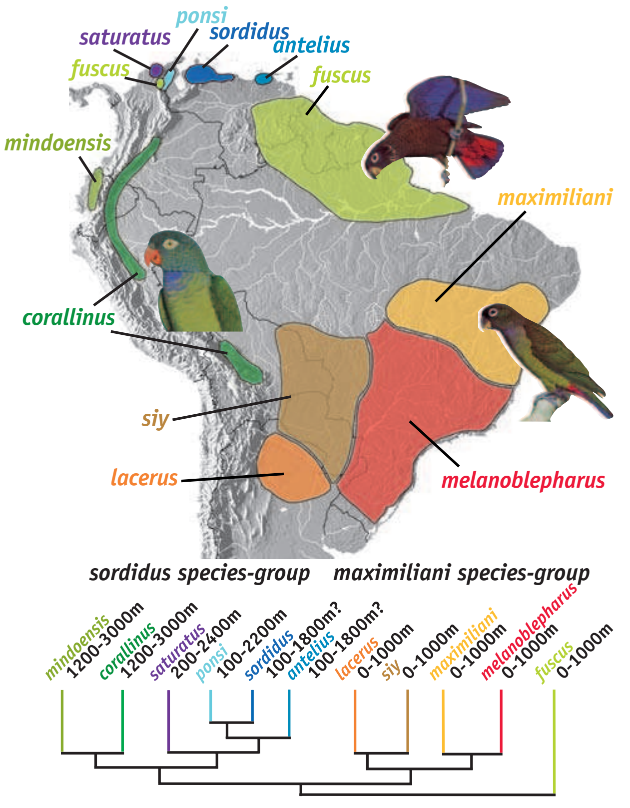

FIG. 9.1. Distributional and altitudinal ranges of one lineage of South American parrots in the genus *Pionus* (from Ribas *et al.* 2007). One lineage, the *maximiliani* species-group, is lowland, whereas its sister-lineage, the *sordidus* species-group, is high montane. Species in the Andes breed at high elevations but extend down to lower elevations during the winter in search of food. The sister-lineage of all of these species (not shown) also has lowland-high montane sister-clades. More distant relatives are lowland forest taxa, thus showing that montane lineages have been independently derived from lowland ancestors.

BOX 10. Evolutionary factors shaping species diversity gradients

The differential distribution of species richness across geographical regions and biomes has been documented for many different types of organisms, both on land and in the marine realm. Recent studies have integrated evolutionary and ecological processes to explain the high concentration of species in tropical regions and the corresponding latitudinal diversity gradient.

The "tropical niche conservatism" hypothesis (reviewed in Wiens and Donoghue 2004) explains higher tropical diversity as a function of the longer occupation of tropical areas by many lineages, with expansion into temperate areas limited mostly by freezing temperatures. In support of this hypothesis, a study of hylid frogs in the Americas documented a significant correlation between species richness and time of colonisation of an area, and identified temperature seasonality as the most important factor limiting the spread of four hylid lineages (Wiens *et al.* 2006).

Similarly, the "out of the tropics" model of Jablonski *et al.* (2006) postulates higher rates of taxonomic origination in tropical waters, and subsequent expansion into extratropical regions. The spatial patterns of first occurrences and changes in latitudinal distribution of marine bivalves, documented from the Neogene fossil record, support this model by finding higher speciation and lower extinction rates in the tropics, and greater immigration into extratropical regions.

It is likely that many different factors play a role in establishing such diversity gradients, including the relative ease or difficulty of adapting to new climatic regimes and the availability of corridors for movement (Donoghue 2008).

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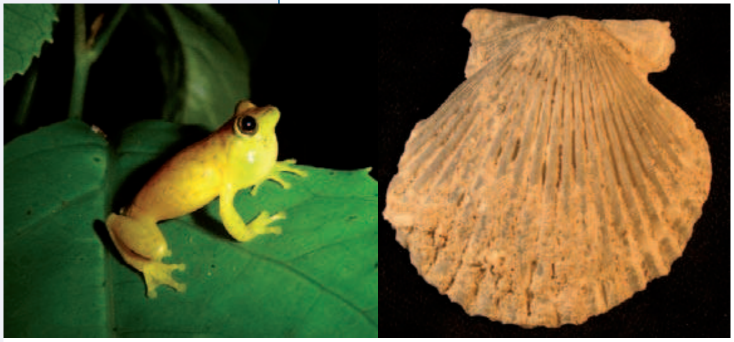

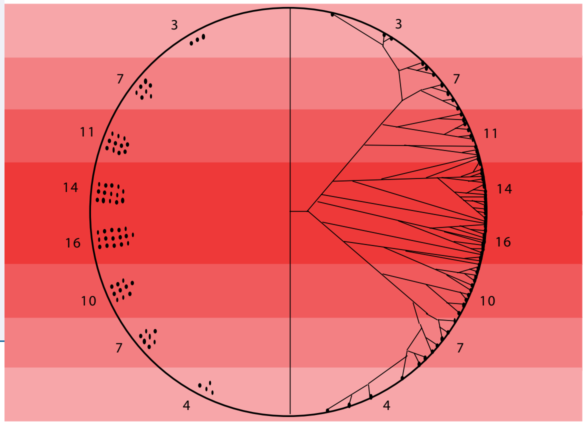

FIG. 10.1. Left: *Exerodonta melanomma* (Hylidae), a treefrog from Oaxaca, Mexico, ©U García; right: *Agropecten circularis* (Pectinidae), a marine bivalve from the Pliocene Infierno Formation, Baja California, Mexico, ©F Sour; bottom: origination and initial diversification in the tropics (shown on the right) as an explanation for the latitudinal species diversity gradient (represented on the left) (from Wiens and Donoghue 2004).

TASK 2.3 The evolution of functional traits

Phylogenetic analyses frequently reveal the recurrence of form in evolution, including parallelisms, convergence, and the independent loss of traits. These cases can be examined for historical correlations with other parameters. This may, for example, help us to understand whether a particular trait evolved as an adaptation following exposure to certain environmental circumstances, or, rather, the evolution of the trait under different circumstances allowed the subsequent occupation of a new environment (Box 11, S7). Such studies provide powerful insights into the ecological functions of traits as well as into the forces that shape community assembly (see Task 2.2).

It is clear that many important ecological functions have evolved independently in separate lineages, sometimes apparently tightly clustered in phylogeny, and sometimes arising very distantly in the tree of life. This raises an important, though still largely unaddressed question, namely, the extent to which independently evolved traits really do function similarly enough that they can be treated as single categories in modelling ecosystem-level processes (Box 12). That is, to what extent are independently evolved traits really functionally redundant? Alternatively, to what extent should independently evolved traits be modelled as possibly responding quite differently to relevant environmental changes?

There are already some important indications that independently evolved functions might perform differently enough to be misleading in some circumstances. For example, species from several grass lineages that appear to have evolved C4 photosynthesis independently have shown significantly different growth responses to elevated CO_2 levels. Likewise, levels of the enzyme carbonic anhydrase have been shown to differ significantly among C4 grasses representing independently evolved lineages. Levels of carbonic anhydrase are critical in interpreting oxygen isotope fractionation and, in turn, in calculating global primary productivity and identifying potential carbon sinks (Box 12).

A bioGENESIS working group focused on these issues will draw phylogeneticists and functional biologists together to provide a critical assessment of the validity of using

BOX 11. Drivers of morphological evolution in Bignoniaceae

Analyses of the relative timing of evolutionary changes in organismal traits can test specific hypotheses on the drivers of morphological evolution and shed light on the ecological function of traits. For example, ecological changes that occur after the occupation of a new habitat suggest adaptation to the novel conditions (Larson and Losos 1996). Alternatively, morphological changes that occur before the occupation of a particular habitat suggest that the new morphology may have served as a "key innovation" allowing occupation of the novel conditions.

In the plant clade Bignonieae (Bignoniaceae) the evolution of several distinctive morphological characters is directly linked to certain habitat transitions. Specifically, repeated transitions from the liana growth form to the shrub habit are strongly correlated with the colonization of dry open habitats, together with the loss of tendrils, and the evolution of rounded seed wings. In general, these features appear to have evolved after the inferred habitat transitions, suggesting that the derived morphological traits are indeed adaptations to the new habitat (Lohmann *et al.* in prep.).

FIG. 11.1. Sample of the morphological diversity in Bignonieae, ©L G Lohmann.

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independently evolved functional groups in modelling responses to environmental change or in comparing similar ecosystems assembled independently in different regions. Here we see immediate opportunities for collaborations involving the ecoSERVICES and bioSUSTAINABILITY Core Projects within DIVERSITAS. A cross-project working group has already been formed to address these issues through the Centre for Population Biology at Silwood Park (Imperial College, UK). This effort is focused on how ecosystem functions relate to the evolution of underlying organismal traits, and how the phylogenetic distribution of the key functions themselves might bear on the assessment of risks to ecosystem services in the face of environmental changes. The focus here on "feature diversity" also bears directly on the development of appropriate measures of biodiversity within bioSUSTAINABILITY Core Project (see also Focus 3).

Research Objectives and Activities

- Develop analyses to assess the possible impacts of the convergent evolution of traits on their ecological function; e.g., using global plant trait databases.
- Stimulate analyses of the evolution of key enzymes and metabolic pathways related to ecosystem function, especially bridging genomics and ecology in microorganisms.
- Develop new approaches to assessing risks to ecosystem services that directly incorporate the phylogenetic distribution of ecological functions.

BOX 12. Taking trait evolution into account in modelling global climate change

Global ecological models, such as those that enable predictions of climate change, have accommodated variation in the traits of organisms mainly by reference to major functional classes, such as "trees" or "C4 grasses." These models can be refined by taking into account phylogeny and evolutionary changes in the traits of interest.

For example, grasses in which C4 photosynthesis originated independently may respond differently to elevated levels of CO_2 (Kellogg *et al.* 1999). Likewise, plants from separate C4 grass lineages show different levels of the key enzyme carbonic anhydrase, and estimates of primary productivity that assume uniformly low levels in C4 grasses (e.g., Gillon and Yakir 2001) may be biased. Furthermore, some widespread and locally dominant C3 grasses, such as *Phragmites australis*, produce the low levels of carbonic anhydrase found in their C4 relatives (Edwards *et al.* 2007). Knowledge of carbonic anhydrase levels is critical in interpreting oxygen isotope fractionation and, in turn, in inferring global primary productivity. A more accurate estimate of the global uptake of atmospheric CO_2 could be obtained by taking into account the phylogenetic distribution of this key enzyme.

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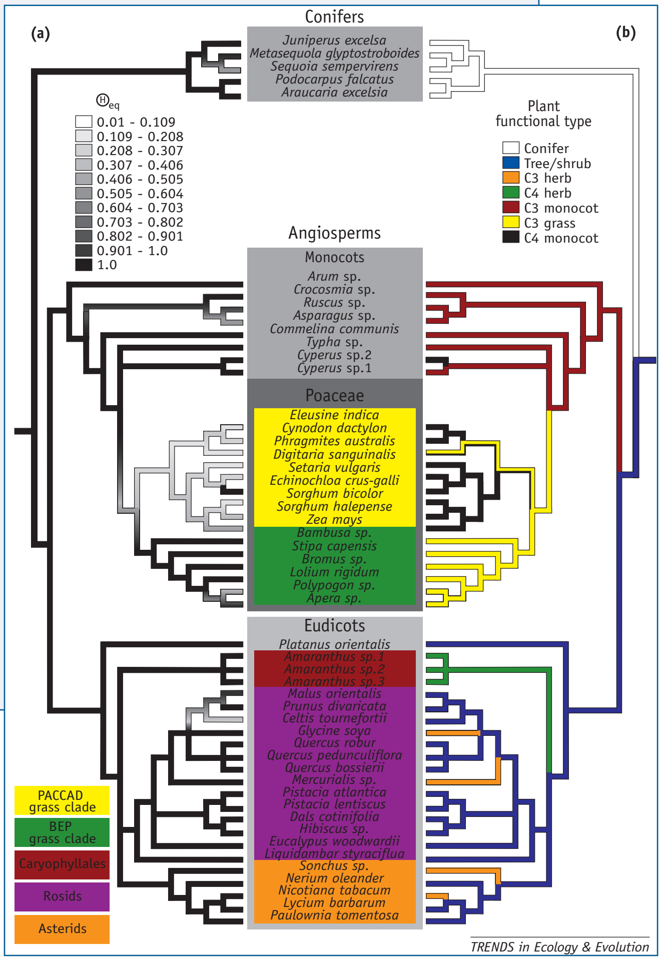

TRENDS in Ecology & Evolution

FIG. 12.1. Evolutionary shifts in grasses between C3 and C4 functional groups (shown on the right) are not significantly correlated with evolutionary shifts (shown on the left) in the level of the enzyme carbonic anhydrase (measured by Ⓗeq) (from Edwards *et al.* 2007). Note that *Echinocloa crus-galli*, which represents a separate origin of C4 photosynthesis, has higher values than other C4 grasses. Also, the C3 grass *Phragmites australis* has low values similar to its C4 relatives.

TASK 2.4 Rapid evolution and eco-evolutionary dynamics

Charles Darwin famously believed that evolution required “the long lapse of ages.” This perspective continued to prevail for more than a century, at which time evidence began to emerge that evolution can actually occur rapidly (Palumbi 2002). Darwin's own Galapagos finches illustrate this point: the beak size of the medium ground finch, *Geospiza fortis*, evolved recently in response to changing seed availability (Grant and Grant 2006; Box S8). This is a good example of the action of the main driver of evolution, natural selection – individuals with genes that improve survival (or fecundity) produce more offspring and thereby increase the frequency of those genes into the future. Rapid evolutionary change can also be driven by sexual selection, which increases the frequency of genes that influence mating success. An example comes from male Trinidadian guppies *(Poecilia reticulata)* that evolve high colour in low-predation environments – females prefer to mate with colourful males and predation no longer selects against high colour (Endler 1980; Magurran 2005). Finally, evolutionary change can be driven by random effects, for example, genetic drift. If population sizes are small enough, these changes can be rapid, such as when relatively few individuals with particular traits colonise a new location.

Speciation – the evolutionary divergence of one species into two – can also be rapid, sometimes driven by the mechanisms described above. For example, African cichlid fishes in Lake Victoria have diversified through natural selection (diet) and sexual selection (mate choice) from a few species into hundreds in less than 15,000 years (Box 7). On even shorter time scales, many species of insects have, over less than 100 years, formed new “host races” adapted to introduced plants and have become reproductively isolated from their ancestors on native plants (see Task 3.1; Box S9). Other genetic mechanisms, such as polyploidyzation, can cause very rapid speciation (see Task 2.1; Box 8).

It has now been firmly established that some species show appreciable evolutionary change on very short time scales. These changes presumably influence the success of those organisms – but this has been little studied except in parasites and pathogens. HIV population size, for example, decreases after anti-viral drugs are given to a patient, but then increases again after the evolution of resistance to those drugs (see Task 3.3; Box 19). Similar dynamics have been observed in rabbits *(Oryctolagus cuniculus)* introduced into Australia and the myxoma virus subsequently introduced to control them (Dwyer *et al.* 1990). These results suggest the need to add evolution into models of population dynamics, so as to better predict pathogen outbreaks, species invasion, and population declines (see Task 3.3).

Rapid evolution of one species also may have consequences for other organisms, for community structure, and perhaps even for ecosystem function. One major research effort in this area falls under the umbrella of “community genetics.” Recent findings indicate, for example, that plant genes account for a significant proportion of variation in water cycles, nutrient cycles, below-ground carbon storage, and the above-ground diversity of herbivores (Whitham *et al.* 2008; Box 13). These results clearly demonstrate that standing genetic variation matters to ecological process. More recent work is concentrating on whether rapid evolutionary changes in this genetic variation have significant ecological consequences. A US NSF-FIBR project is examining whether the rapid evolution of guppy populations in Trinidad, referred to above, is influencing aquatic communities and nutrient cycling (Palkovacs *et al.* in press).

It is critical to note that many rapid evolutionary changes are associated with human impacts. Fish, mammal, and plant populations subjected to human harvesting have rapidly evolved smaller sizes and earlier reproduction (Box 14). Additional examples are presented below under Focus 3 of rapid evolution (and even speciation) in response to climate change and introduced species. Collectively, these cases illustrate the critical role that rapid evolution can play in the response of populations to human-caused environmental change, and the need to take evolution into account in modelling responses to such changes. A bioGENESIS working group focused on these issues will promote the integration of evolutionary approaches in understanding ecological dynamics, and provide clear links to related DIVERSITAS efforts.

Research Objectives and Activities

- Stimulate theoretical predictions and empirical testing of rapid evolution and its ecological consequences.
- Promote applications of evolutionary approaches to elucidate the dynamic relationship between genetic variation and aspects of ecosystem function.

BOX 13. Genetic variation matters to ecological processes

The genetic properties of organisms have long been known to influence their survival and reproductive success. More recently, it has been recognised that these properties can also influence community structure and ecosystem processes.

Recent work in the area of "community genetics" (Whitham *et al.* 2006, 2008) has shown that cottonwood trees (*Populus* spp.) that are less genetically similar to one another house less similar arthropod communities, and that these communities are, to some extent, passed on from parent to offspring trees. Some community-level consequences of genetic variation are therefore heritable. Perhaps even more striking, selection on genetic variation has been shown to influence ecosystem function. Specifically, the amount of foliar condensed tannins in cottonwood trees has a genetic basis. This genetic variation affects nitrogen cycling in forests; increased tannins in the leaf litter increases nitrogen mineralization and, therefore, tree growth. In addition, beavers (*Castor canadensis*) avoid high-tannin trees, which increases the relative frequency of such trees in areas with beavers. In turn, this leads to increased tannins in the surrounding water and soil, which changes the aquatic invertebrate community, influences decomposition rates, and feeds back on tree growth.

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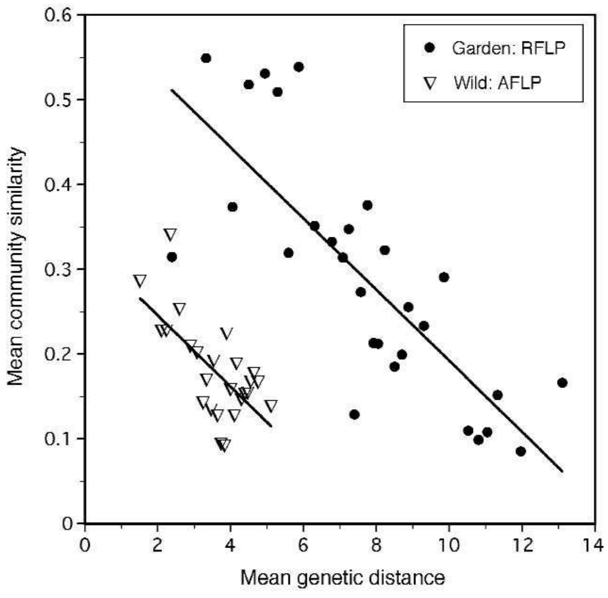

FIG. 13.1. Cottonwood trees, which are more genetically dissimilar to one another house more dissimilar communities of arthropods (from Bangert *et al.* 2006). This pattern was observed in trees planted in a "common garden" and in wild populations. Beavers favor trees with particular genotypes, which may influence community and ecosystem properties.

BOX 14. Harvesting can cause undesirable rapid evolutionary change

Humans often harvest animal and plant populations for commercial or recreational benefit. When harvest rates are high or select for particular phenotypes, populations may crash or otherwise undergo change in ways that make them less useful to humans. Some of these unfortunate changes are the result of evolution.

Bighorn sheep *(Ovis canadensis)* on Ram Mountain, Alberta, provide an example. These sheep are hunted as trophies, and hunters are only allowed to take individuals with the largest horns. This generates strong natural selection against individuals whose horns grow particularly fast. A consequence is the rapid evolution of smaller horn size, which then reduces the value for hunters (Coltman *et al.* 2004). Another example of undesirable evolutionary change caused by harvesting is the evolutionary decrease in size at maturity in Atlantic cod *(Gadus morhua)*, which may have contributed to the collapse of this fishery (Olsen *et al.* 2004).

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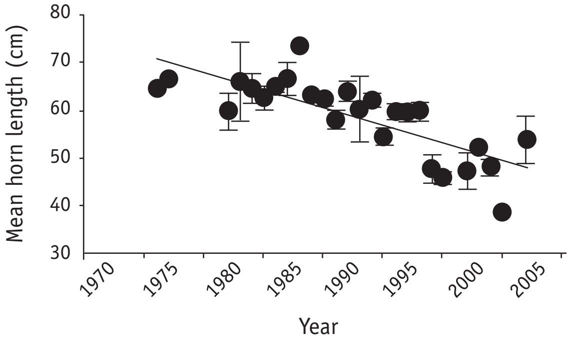


FIG. 14.1. The horn size of bighorn sheep rams has decreased during the last 30 years of selective harvesting. The plot shows phenotypic change, but additional work has shown that this has a genetic basis (from Coltman *et al.* 2003).

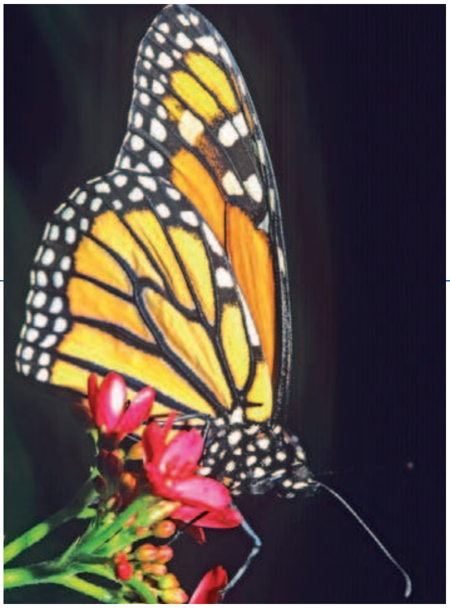
FOCUS 3.
Evolution, biodiversity, and human well-being

The United Nations World Summit on Sustainable Development (2002) identified a set of key objectives: biodiversity and ecosystem services must be maintained (or restored), food security must be improved, and global population health must be enhanced. Moreover, the development of renewable energy is seen as crucial in view of the adverse consequences of global warming on society. Further, security from biological threats – from the spread of debilitating diseases to the possible use of deadly bioagents – is an increasing concern. The bioGENESIS Core Project will bring an evolutionary perspective directly to bear on these pressing issues, to identify new uses for evolutionary knowledge in conserving biodiversity and promoting human well-being.

In general, research in evolutionary biology is playing an increasingly important role in addressing these key societal objectives. Advances across a number of evolutionary disciplines (e.g., comparative genomics) provide a necessary foundation for addressing numerous challenges. For example, the rapid identification of emergent diseases now depends directly on molecular phylogenetic methods, as does the identification of their bio geographic origins (Box 6), the prediction of spread, and the design of appropriate responses (including vaccines). The same is true of introduced species more generally, where effective management of invasive organisms often depends critically on knowledge of evolutionary relationships and processes.

As noted above (Task 2.4), recent work on eco-evolutionary dynamics is providing profound insights into how organisms will respond to anthropogenic environmental changes. In fact, we now recognise that human impacts, including pollution, land-use change, climate change, agriculture/aquaculture, and introduced species, may be among the most important drivers of modern evolutionary change (Palumbi 2002). In each of these cases there are a range of evolutionary consequences, from the erosion of genetic diversity, to the evolution and spread of diseases, and even human-induced speciation. Analyses of such evolutionary responses are critical to the development of a truly predictive biodiversity science that can provide a sound basis for ecosystem management.

The emerging field of metagenomics – the use of genomic tools to probe environmental samples (from a gram of soil or a drop of sea water) for microbial biodiversity – relies directly on evolutionary analysis for the identification and characterization of what now appears to be a vast reservoir of uncharted biodiversity (Box 1). Predictions based on the phylogenetic relationships of these unknown organisms provide the first step in understanding their possible ecosystem-level functions and global impacts. Phylogenetic studies also provide the basis for sound "bioprospecting", focusing attention on the close relatives of organisms that produce medicinally useful chemicals or that may be important in the development of sustainable energy. Recent studies of endophytic fungi living inside of tropical plants, for example, have provided a glimpse of the enormous biological and chemical diversity that remains to be discovered and potentially harnessed for human purposes. Some of these fungi produce entirely novel bioactive compounds, and a few have even been found to produce octane and may one day provide the basis for new biofuels (Box 2).



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While Focus 1 concerns the discovery and documentation of biodiversity, and Focus 2 deals with the causes and consequences of diversification, Focus 3 addresses evolutionary management and conservation. DIVERSITAS, through bioGENESIS, can play a significant role in promoting these areas of investigation, by providing a focal point for identifying and tackling evolutionary questions of immediate relevance to managing biodiversity. bioGENESIS can help to coordinate the development of an integrated system for evolutionary ecosystem management aimed at mitigating the effects of climate change, combating emerging diseases, and conserving threatened species and their evolutionary potential. Through its working groups and activities, bioGENESIS will promote the application of new tools and the exploration of creative new ways to harness evolutionary biology in the service of biodiversity and sustainability.

TASK 3.1 Evolutionary ecosystem management

To prevent biodiversity changes undesirable for our own existence, we need increasingly to manage the protection of threatened species, the eradication of invasive species, and the restoration of native ecosystems. Current practices in what has become known as "ecosystem management" generally undervalue evolutionary considerations. A bioGENESIS working group in this area will promote new approaches to the science of ecosystem management based on evolutionary biology. Retrospective approaches can help us to understand how our activities have impacted ecosystems during human evolution, migration, and population expansion. Complementary prospective approaches enable us to project how humans are likely to affect ecosystem functions and how we might mitigate against deterioration.

Homo sapiens has continuously expanded its population since moving out of Africa around 80,000 year ago (Hawks *et al.* 2007). During the human journey, our species has had profound impacts, locally and globally, through the use of fire, the development of agriculture, the processing of metals, the construction of cities, the expansion of trade, and the development of science and technology. These activities have driven extraordinary biodiversity change, including the evolution of weeds, pests, and pathogens, and the mass extinction of wild species. Historical analyses of how biodiversity and ecosystem services have been changed by human activities provide unique insights into the effects of such changes on human well-being. The first aim of Task 3.1 is to facilitate the integration of various retrospective approaches to reconstructing the history of biodiversity change in order to develop better models to predict long-term trends.

The second aim of Task 3.1 is to provide an analysis of the on-going evolutionary responses of both native and alien species to recent environmental perturbations. One important class of outcomes entails the rapid evolution of invasive species which results in their even more rapid spread (e.g., the cane toad in Australia, Phillips *et al.* 2006; Box S10). In other cases, hybridization can result between native and introduced species, possibly promoting rapid hybrid speciation and cycles of further invasion and ecosystem disturbance. Such gene flow between natives and non-natives may be quite common in some groups of organisms, and could have devastating consequences (e.g., Kim *et al.* 2008; Box S11). Also of concern are cases of the rapid spread of aggressive genotypes through invasive populations, as appears to have happened in the reed grass, *Phragmites*, in North America (Box 15). In some cases, hybridization or selective sweeps appear to be associated with major changes in breeding system, such as shifts to self fertilization or asexual reproduction. Likewise, there may be significant impacts on predator-prey, host-parasite, or host-pathogen dynamics and evolution with the introduction of new species into a system (e.g., Schwarz *et al.* 2007; Box S9).

To achieve the aims of Task 3.1, bioGENESIS will bring together relevant evolutionary biologists around these issues, especially where clear connections can be made to other DIVERSITAS Core Projects and Cross-cutting Networks. For example, there are obvious links to the maintenance of agricultural biodiversity and food security, and we envision an activity focused on the evolutionary impacts of genetically modified organisms (GMOs) on non-target species.

Research Objectives and Activities

- Facilitate studies on the history of biodiversity change as a function of human evolution, migration, and population expansion.
- Coordinate a synthetic analysis of the impacts of introduced species on rapid evolution, hybridisation, and speciation involving native species.
- Promote an analysis of the potential evolutionary impacts of GMOs on non-target species.


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BOX 15. Invasion of the reed grass, *Phragmites australis*: genetic analysis of a "sleeper weed"

Invasive species pose a major threat to the maintenance of native biodiversity, and in some cases have enormous ecological and economic consequences. Therefore, it is important to understand why and how they spread. Evolutionary analyses are increasingly being applied to this problem.

The rapid spread of the common reed grass, *Phragmites australis*, in northeastern North America (and beyond), provides an example of the application of molecular genetic techniques in tracing the history of invasion. Until the beginning of the 1900's a native form of this species remained limited in distribution in North America. Since then, *P. australis* has spread rapidly, and expanded into many freshwater habitats, choking out the native vegetation. Analyses of several chloroplast genetic markers, both from living plants and from herbarium specimens going back over 100 years, demonstrated that a non-native strain of *Phragmites* moved into North America from Eurasia and has rapidly replaced the native populations in many areas and greatly expanded the range of the species (Saltonstall 2002). The spread of the exotic genotype also has been documented in Quebec, Canada, where its movement inland appears to have been promoted by the development of the highway system beginning in the 1960's (Lelong *et al.* 2007). The introduction of a new, more aggressive genotype appears to explain the sudden awakening of this "sleeper weed."

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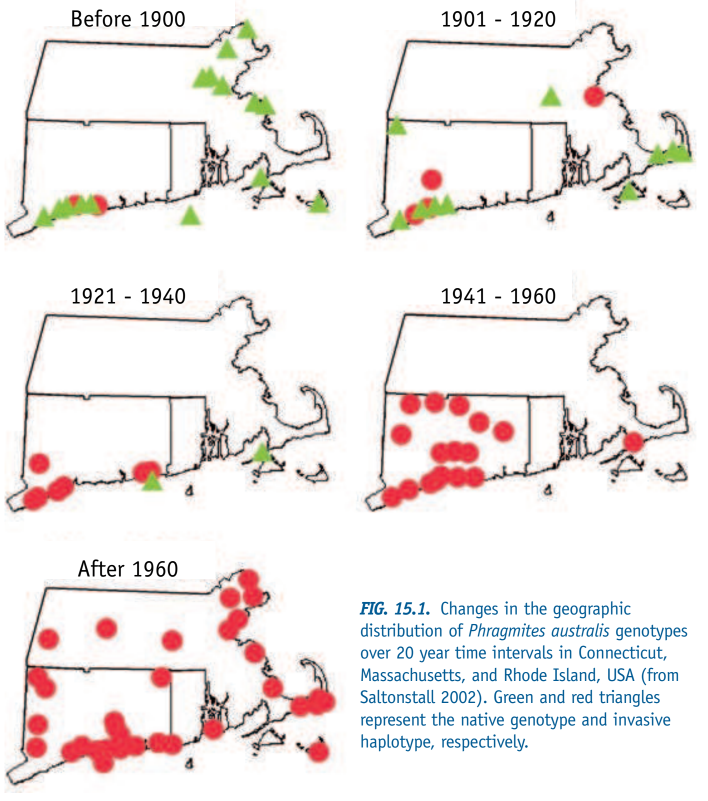

FIG. 15.1. Changes in the geographic distribution of *Phragmites australis* genotypes over 20 year time intervals in Connecticut, Massachusetts, and Rhode Island, USA (from Saltonstall 2002). Green and red triangles represent the native genotype and invasive haplotype, respectively.

BOX 16. Rapid evolution of native species in response to invaders

The invasion of a species into a new geographical location should impose strong natural selection on the invader and on the native species with which it interacts. This might then result in rapid evolutionary change. An example of this phenomenon comes from soapberry bugs – insects that use a “beak” to pierce the fruits of certain plants and then feed on the seeds inside. As larger fruits require longer beaks, and vice versa, evolutionary changes in beak length have taken opposite trajectories in different parts of the world, depending on the relative sizes of the fruits of the native and introduced plants (Carroll *et al.* 2005).

In Florida, the native soapberry bug *(Jadera haematoloma)* feeds on a native plant (balloon vine, *Cardiospermum corindum*) with a large fruit, but it evolved a shorter beak when it switched to an introduced plant with smaller fruits. In Australia, the reverse occurred. There, the native soapberry bug *(Leptocoris tagalicus)* feeds on native plants (*Alectryon* spp.) with small fruits but evolved a longer beak when it switched to a balloon vine *(Cardiospermum grandiflorum)* introduced from the neotropics. The balloon vine is a major pest in Australia and soapberry bugs are the only native species to have colonised it. It has been suggested that the evolution of native soapberry bugs in response to this plant may decrease its spread, averting the need for biocontrol through further species introductions.

FIG. 16.1. The native Australian soapberry bug on its native host (left) and on the invasive balloon vine (right). The larger fruits of the balloon vine have caused the evolution of a longer beak (seen being inserted into the fruit capsule) in these bugs, ©S P Carroll.

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Carroll SP, Loye JE, Dingle H, Mathieson M, Famula TR and Zalucki MP. 2005. And the beak shall inherit – evolution in response to invasion. *Ecology Letters* 8:944-951

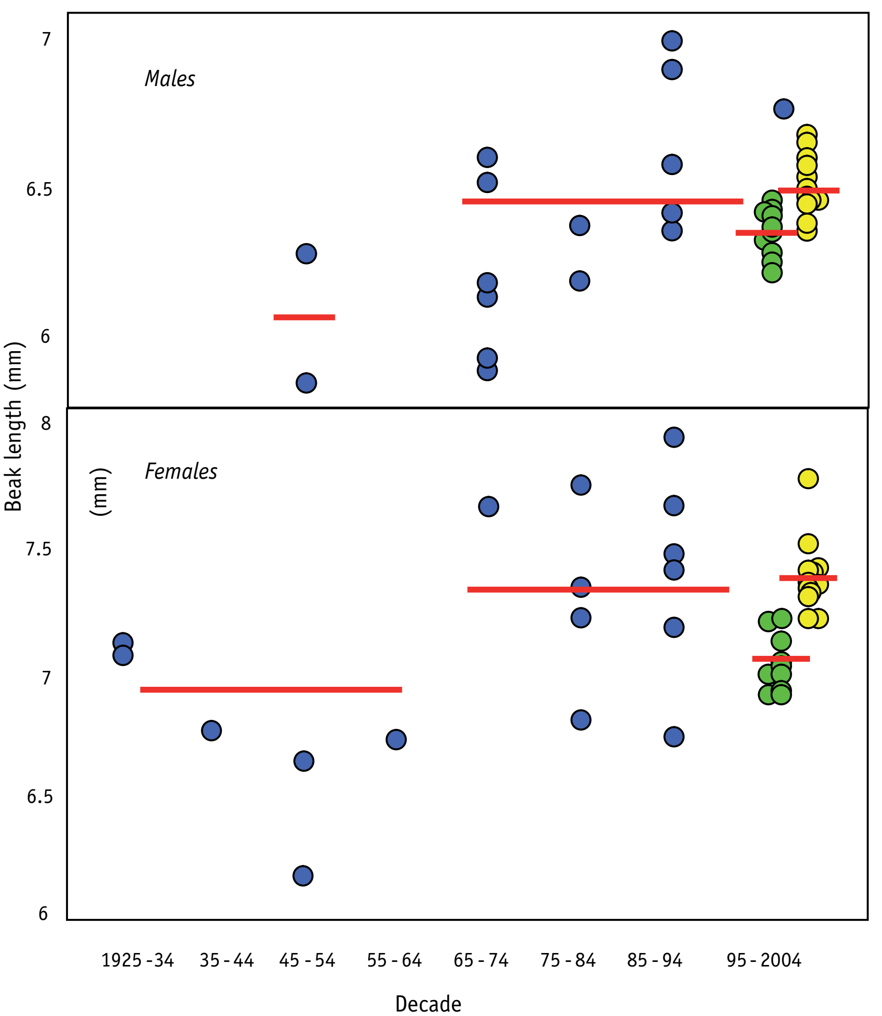

FIG. 16.2. The left-hand part of the plot (circles) shows the smaller beak length of museum specimens before 1925-1964 vs. after 1964-2004 when balloon vine became common. The right-hand part of the figure also shows that soapberry bugs in Australia are diverging into two forms – those adapted to the native plant (diamonds) and those adapting to the introduced balloon vine (triangles) (from Carroll *et al.* 2005).

TASK 3.2 Evolution and climatic change

A rapidly expanding area of inquiry is focused on predicting the impacts of climate change on natural ecosystems, agro ecosystems, and water supplies. The dramatic increase in temperature over the past few decades has been having serious impacts on biodiversity, including local extinction, range shifts, and adaptation to rising temperatures. Phenological shifts (leading to earlier reproduction) corresponding to increasing spring temperatures have now been documented (Box 17), although the genetic bases for such shifts remain uncertain in most cases. In some cases, shifts in timing have resulted in mismatches with pollinators or with the abundance of food supplies, as in the decline of the pied flycatcher in Europe (Both *et al.* 2006).

It is expected that phylogenetic constraints and evolutionary potential will influence responses of various organisms to climatic changes (Reusch and Wood 2007). For example, a recent analysis of the flora surrounding Henry David Thoreau's Walden Pond in Concord, Massachusetts, USA, demonstrated that members of specific angiosperm lineages that had failed to shift their flowering times in response to temperature change are now greatly decreasing in abundance (Box 18).

Here again, insights can be gained from both retrospective and prospective analyses. Retrospective approaches, integrating geological data on climatic change during the Pleistocene and the Pliocene, and even earlier in the Tertiary, with knowledge of phylogeny, help us to understand the relative importance of migration/niche conservatism and adaptive evolution to climate change, and to test the validity of climate envelop models in predicting future changes. New insights are now being provided by modelling environmental factors associated with present geographical distributions using data obtained from specimens in natural history collections and reconstructing past distributions and the evolution of niche parameters using phylogenetic trees. Such studies permit broader comparisons among clades and can be scaled-up to make predictions about ecosystem composition and function in the face of climate change. Finally, the phylogenetic distribution of species at risk of extinction due to climate change can be used to predict the maintenance of diversity (Yesson and Culham 2006; Box S12).


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At the same time, prospective approaches based on the principles and methods of population biology are critical in predicting the demographic and genetic effects of climate change and how populations are likely to respond. Such approaches are particularly important in predicting how the boundaries between different vegetation types are likely to shift under climatic change. At present, however, most evidence of adaptive response to climatic change is indirect and it remains uncertain how large the genetic variance is in wild populations for adaptation to climatic changes. The aim of Task 3.2 is to stimulate productive collaborations between evolutionary biologists and archaeologists, geologists, and ecologists focused on climate change. Here we envision close ties with elements within the bioDISCOVERY Core Project, especially regarding the analysis of geographical ranges and climate niche modelling.

Research Objectives and Activities

- Promote the integration of phylogeny and abiotic niche reconstructions into climatic change research to test and improve climate envelope models.
- Facilitate analyses of short-term evolutionary responses to climate change.
- Coordinate collaborative research on vegetation boundary shifts incorporating the evolutionary responses of populations.

BOX 17. Evolutionary responses to climate change

One of the major global changes over the past few decades has been the dramatic increase in temperature, and this change is expected to accelerate in the coming decades. Since organisms are often adapted to local temperatures, populations will need to either move to new locations or evolve rapidly to remain adapted. Such adaptations are expected to be particularly likely in relation to the timing of reproduction.

Climate warming is expected to be especially acute at high latitudes. In the Yukon, for example, the average April-June temperature has increased by 2° C over the last 26 years, and the production of spruce cones on which the red squirrels (*Tamiasciurus hudsonicus*) depend has come correspondingly earlier. The squirrels have, in response, advanced the date at which they give birth to young (parturition) by almost 26 days. This advance has been accomplished by a combination of phenotypic plasticity and genetic change (Réale *et al.* 2003). Many other examples of shifts in timing are known, but the relative contributions of plastic *versus* genetic responses are less certain. Another case where the response is known to be genetic is the shift in photoperiod in pitcher plant mosquitoes, *Wyeomyia smithii* (Bradshaw and Holzafel 2001).

References

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Réale D, McAdam AG, Boutin S and Berteaux D. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London B* 270(1515):591-596

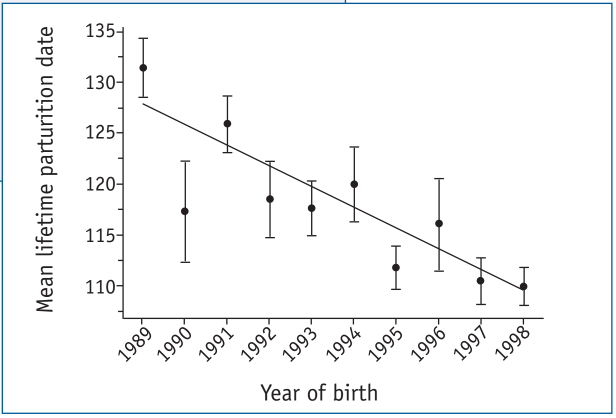

FIG. 17.1. Red squirrels in the Yukon that were born in 1998 reproduced (parturition) almost 20 days earlier (averaged over their entire life) than did those born in 1989. This plot shows phenotypic change, but additional work has established that this phenotypic change has a genetic basis (from Réale *et al.* 2003).

BOX 18. Responses to climate change in Thoreau's woods

It may often be the case that closely related species will respond similarly to climate change, in which case knowledge of phylogeny and clade membership will provide the ability to predict responses and to design conservation strategies accordingly.

A recent example comes from the flora of Walden Pond in Concord, Massachusetts, USA, where it has been possible to track changes over a 150 year period, building on Henry David Thoreau's initial inventory. From the analysis of these data it appears that species that have declined significantly in abundance are also those that have failed to adjust their flowering phenology in response to climate change, possibly resulting in mismatches with pollinators. Furthermore, these species are not randomly distributed in the phylogenetic tree that has been produced for the Walden flora. Instead, they are significantly clumped in particular clades. These declining clades include, for example, significant parts of the Ranunculaceae, Saxifragaceae, Lamiaceae, Asteraceae, Liliaceae, and Orchidaceae. It appears that clade-specific differences in the ability to adapt to climate change are influencing the vulnerability of species and their ecological interactions.

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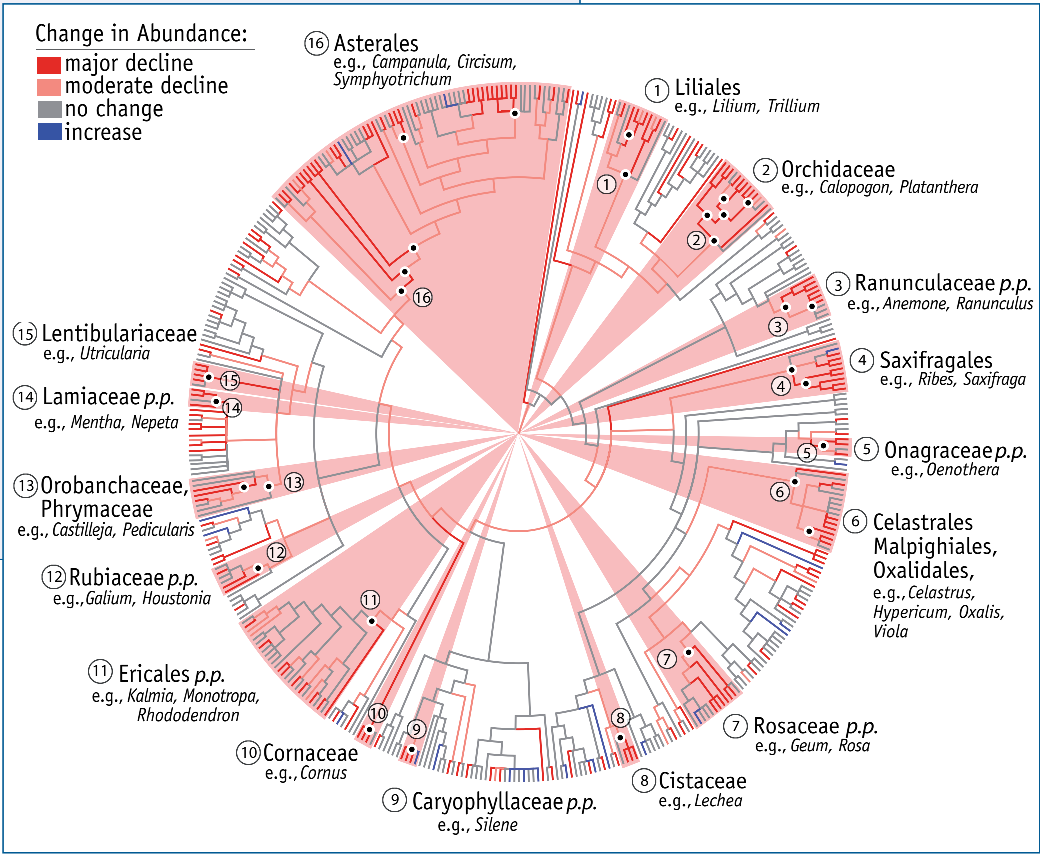

FIG. 18.1. Phylogeny of the plants of Walden Pond, showing those clades in red in which population declines appear to be correlated with a failure to adjust flowering phenology (from Willis *et al.* 2008).

TASK 3.3 Combating disease

Of all biodiversity changes, the migration and evolution of zoonotic pathogens perhaps most directly threatens human life. Because pathogens generally have very short generation times and much higher mutation rates than their hosts, they can quickly adapt to environmental changes, including the antibodies in our immune systems (Box 19). Evolutionary approaches are therefore absolutely necessary for the identification, surveillance, and control of emerging diseases (Box S13, S14, S15).

Many factors have contributed to the emergence of infectious diseases such as West Nile fever and the avian flu, including global human movements, expanded trade in various goods including wild animals, and anthropogenic environmental changes. However, it remains unclear when, where, and how novel pathogens such as HIV and SARS moved from their natural hosts into human populations. Furthermore, for persistent human infections such as influenza, evolutionary approaches provide not only insights into the origins and diversification of the pathogens, but also allow us to make predictions about future outbreaks and anticipated strains (Bush *et al.* 1999). bioGENESIS, in cooperation with ecoHEALTH Cross-cutting Network, will promote integrative studies of such issues, bringing evolutionary biologists together with ecologists, health scientists, and researchers in related disciplines.

The spread of disease in relation to global changes affects not only humans, but other animals and the plants upon which we depend. The migration and evolution of pathogens through wild species often drives dramatic ecosystem changes. For example, migrations of a chestnut fungus from eastern Asia to eastern North America, and of a pine nematode from eastern North America to eastern Asia, caused precipitous declines of chestnut and pine forests, respectively (Box 20). The ongoing loss of hemlock trees in eastern North America due to the introduction of the woolly adelgid from Japan provides another example of this devastating phenomenon. bioGENESIS, again with ecoHEALTH, will facilitate international, interdisciplinary projects aimed at better understanding the migration and evolution of pathogens infecting wild organisms.

Another issue directly relevant to Task 3.3 is the evolution of pathogens resistant to pesticides, herbicides, fungicides, and antibiotics. Uses of these chemicals in agriculture and human medicine have driven rapid and repeated evolution of resistant pathogens. Evolutionary studies of the acquisition of resistance have often revealed unexpected mechanisms such as recombination and the horizontal transfer of resistance genes. Whereas the molecular evolution of resistance has been documented in a few systems (especially viral and bacterial systems), our knowledge of the evolution of resistance remains limited in many pests and weeds. A bioGENESIS working group will play an important role in promoting comparative studies of the evolution of resistance in pathogens brought on by human activities.

Population dynamics of pathogens have been of continued interest in medical science and also in ecology. While classic models describing dynamics without evolution made significant contributions to our understanding of epidemiology, the dynamics of hosts and pathogens is a more complicated process owing to the evolution of resistance in hosts, virulence in pathogens, and drug resistance in pathogens. Thus, evolutionary approaches are critical in developing more predictive models of host-pathogen dynamics. If historical samples are available, past population sizes can be estimated from population genetic theory (Box S14), and inferred population dynamics could, in turn, be used to test evolutionary models. A bioGENESIS working group will coordinate theoretical and empirical studies of host-pathogen dynamics in human and non-human systems that specifically incorporate evolutionary approaches.


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Research Objectives and Activities

- Promote integrative studies on the origin, migration, and diversification of pathogens.
- Facilitate analyses of the mechanisms underlying the evolution of resistance and its consequences for the conservation of biodiversity
- Coordinate evolutionary studies of host-pathogen dynamics in human and non-human diseases in relation to human-induced environmental change.

BOX 19. Drug resistance in HIV

The emergence of drug resistance in HIV has perhaps been the single largest setback in the treatment of AIDS. Once touted as a cure for HIV infection, early drug therapies failed to take into account the rapid evolution of the virus resulting in drug resistant strains. No doubt, the development of highly active antiretroviral therapy (HAART) has greatly extended life expectancy and quality of life for those suffering from AIDS who can access these expensive drugs. The failure as a cure has led to many important lessons concerning our understanding of HIV biology. Using the same phylogenetic approaches developed to investigate evolutionary relationships among species and within populations, we can estimate relationships among viruses isolated from a single patient (Fig. 19.1) using viral sequence data collected over time (both before the start of drug therapy and after the emergence of drug resistant strains). Using the inferred evolutionary history, we can quickly identify the mutations associated with drug resistance that have resulted in wholesale changes in the HIV population through selective sweeps.

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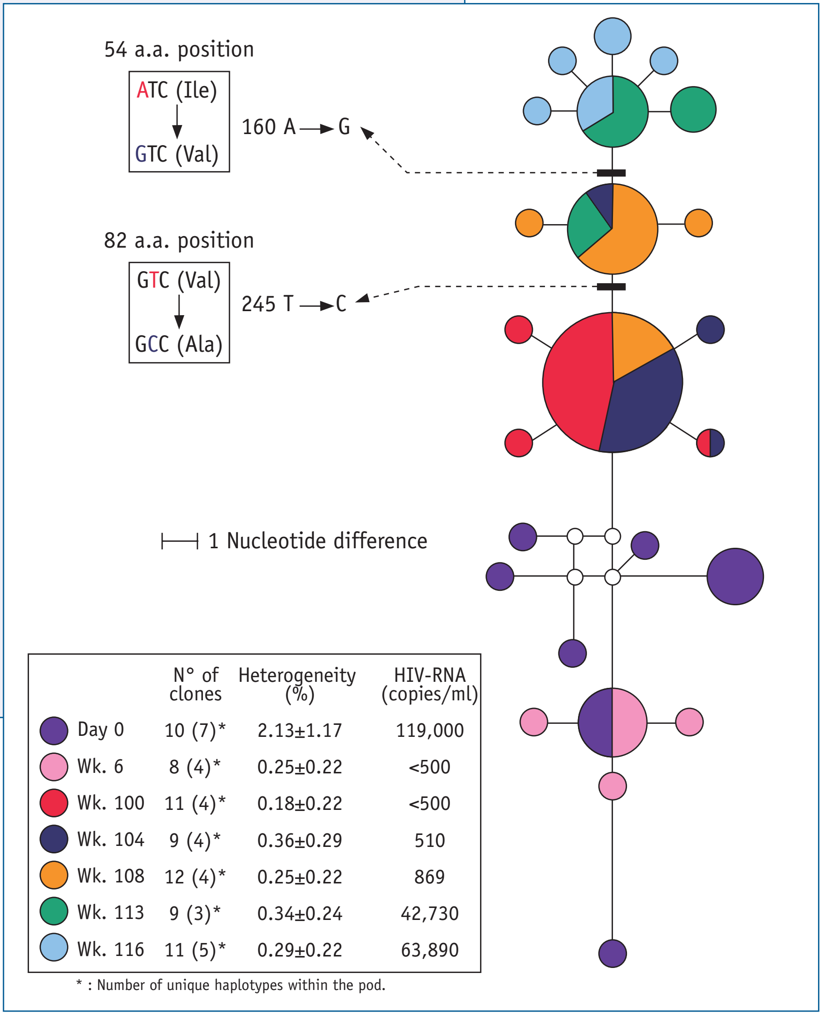

	N° of clones	Heterogeneity (%)	HIV-RNA (copies/ml)
● Day 0	10 (7)*	2.13±1.17	119,000
● Wk. 6	8 (4)*	0.25±0.22	<500
● Wk. 100	11 (4)*	0.18±0.22	<500
● Wk. 104	9 (4)*	0.36±0.29	510
● Wk. 108	12 (4)*	0.25±0.22	869
● Wk. 113	9 (3)*	0.34±0.24	42,730
● Wk. 116	11 (5)*	0.29±0.22	63,890

* : Number of unique haplotypes within the pod.

FIG. 19.1. Evolutionary network of HIV sequences from the protease gene collected at different time points (from Crandall *et al.* 1999). Note the evolution of amino acid replacements conferring drug resistance (highlighted in the boxes) and the associated wholesale replacement of the HIV population by drug resistant forms. Circles represent the HIV sequence types; diameters represent the frequency of each type in the population.

BOX 20. Origin and evolution of introduced pests in forest ecosystems

Some of the most dramatic changes in forest ecosystems have been driven by introduced pests. Phylogenetic approaches have been successfully utilised to determine the origin of those pests. In the case of a pinewood nematode, *Bursaphelenchus xylophilus*, that caused epidemics of pine wilt disease and rapid decline of pine forests in Japan (Togashi *et al.* 2004), molecular phylogenetic evidence showed that it is a lineage native to the USA (Mamiya 1988). This American pinewood nematode is not harmful to pines in its native range. Likewise, the native Japanese pinewood nematode, *B. mucronatus*, is avirulent on Japanese pines. It is probable that the nematodes have weakened their virulence to their native hosts during their co-evolution.

To predict the fate of invasive pests, monitoring the evolution of virulence is critically important. It is theoretically expected that a-virulent strains evolve with decreased host density and this is supported by observation in the mixoma virus introduced to Australia in order to control naturalized rabbits. A recent study in *B. xylophilus* showed that its virulence is a heritable trait, with high virulence being closely related to a high rate of reproduction and within-tree dispersal, and less virulent strains of the pine nematode being selected under decreased host density (Togashi and Jikumaru 2006). It is predicted that the evolution of less virulent strains may stabilise the coexistence of Japanese pines and the introduced nematode. Even if this prediction were supported, large area of pine forest have already been lost in Japan; the annual loss of pines reached a maximum value of 2,430,000 m^3 in 1979, and has held steady at about 1,000,000 m^3 since the early 1990's. Eradication in the early stage of colonisation is of primary importance in controlling invasive pests, and phylogenetic knowledge of *B. xylophilus* is now being utilised in surveillance in East Asian countries and in Europe.

FIG. 20.1. Left: A pine forest devastated by an epidemic of pine wilt disease. Right: The pinewood nematode, *Bursaphelenchus xylophilus*, causes pine wilt disease by damaging vessels in the wood and preventing water use, ©K Togashi.

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TASK 3.4 Evolutionary conservation

The knowledge provided by various global biodiversity observations now being integrated by GEO BON (see Task 1.2; Box 3) will need to be integrated with conservation efforts. Evolutionary disciplines, including systematics, phylogenetics, and population genetics, can and must make significant contributions to this effort. A fundamental aim here is to identify strategies for protecting the processes that generate diversity and maintain adaptation; this is crucial to maintain diversity in the face of rapid global change (Stockwell *et al.* 2003; Pressey *et al.* 2007). A further goal is to improve the prediction of spatial patterns of genetic and phylogenetic diversity loss using methods from evolutionary biogeography.

At the ecosystem level, phylogenetic trees of component species enable us to measure the diversity of the system in terms of evolutionary lineages, and to compare this phylogenetic diversity (Faith 1992) among ecosystems, regions, and local communities (Box 21). This information adds an important evolutionary dimension in assessing conservation priorities. Current methods typically focus on measuring and comparing endemism in representative groups, such as birds and plants. Phylogenetic methods are necessary to establish whether endemic species have evolved recently (neoendemics) or represent much older lineages (paleoendemics), and thus provide a more nuanced evaluation of the risks and choices for conservation.

The flip-side of seeking to maximise phylogenetic diversity in protected areas (Box S16, S17) is to identify "evolutionary hotspots" that are geographic areas and landscapes in which species have undergone recent diversification. A fascinating example of an evolutionary hotspot is Lake Victoria where hundreds of cichlid species with extremely diverse morphologies have evolved in less than 15,000 years (Box 7). While phylogenetic diversity is very low in the Lake Victoria cichlids, the evident morphological diversity reflects the divergence of functional genes controlling body colour patterns, spectral sensitivity, jaw morphology and others (Kocher 2004). Additional examples of evolutionary hotspots are found in the Cape Floristic Province of South Africa, which harbours an extremely diverse flora, and in coastal and montane California with concentrations of recently evolved mammals (Box 21).

At the species level, the recognition of distinct taxa is obviously a prerequisite to any conservation effort. Molecular phylogenetic techniques are increasingly used in discovering and properly diagnosing cryptic taxa, and thus in establishing the degree to which evolutionary lineages are threatened. For example, mtDNA sequence data revealed an ancient phylogenetic split within the common carp between the Lake Biwa lineage endemic to Japan and the Eurasian wild lineage (Mabuchi *et al.* 2005). The Lake Biwa lineage is now properly recognised as a threatened cryptic species urgently in need of conservation. Comparative phylogeographic data also serve to identify geographic foci of distinct lineages and their interactions, which can be incorporated into strategies for protecting both pattern and process (Box 21, 22).

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At the level of within-population genetic diversity, it is widely appreciated that decreases in population size can have a variety of deleterious effects and increase extinction risk. Loss of genetic variance in a population restricts evolutionary potential under environmental change. For example, some lowland-rainforest species of *Drosophila* have lost the capacity to respond to selection for desiccation resistance (Kellermann *et al.* 2006), perhaps reflecting severely reduced population size during the last glacial maximum. In plants, mating success is reduced if allelic diversity is lost at self-incompatibility loci. Increased inbreeding is associated with a decrease of population mean fitness due to increased homozygosity of deleterious alleles. The evolutionary analysis of these effects is crucial in devising appropriate conservation measures.

While preserving within-population genetic diversity is important for maintaining viable wild populations, greater genetic diversity is maintained between species, and the functions and processes of ecosystems are largely dependent on this between-species genetic diversity. In view of the rapid loss of ecosystems such as tropical forests and corals, we urgently need to quantify how many genes and alleles are being lost at local, regional, and global scales.

Rapid advances in the efficiency of DNA sequencing have enabled the examination of far larger samples of organisms and genes, which greatly expands our capacity to utilise such data in monitoring biodiversity change and in devising conservation strategies. In some circumstances it may be possible to identify and monitor variation in the genes that determine response to environmental stress (Hoffmann and Willi 2008). A bioGENESIS working group in this area will foster the application of advanced genomic technologies and evolutionary approaches to conservation biology, forging alliances between evolutionary and conservation biologists focused on particular systems and promoting global efforts to monitor biodiversity change by integrating gene-level observations with species diversity and ecosystem function.

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Research Objectives and Activities

- Promote the concept of protecting evolutionary processes, and the use of measures of phylogenetic diversity in conservation decision making.
- Accelerate recognition and description of cryptic lineages in need of conservation.
- Develop approaches to predicting spatial patterns of genetic and phylogenetic diversity loss.
- Promote global genetic diversity observation by coordinating the application of advanced genomic approaches to biodiversity monitoring and conservation practice.

BOX 21. Phylogenetic diversity, evolutionary mechanisms, and conservation priorities

Biodiversity assessments typically focus on the number of species as the quantity of primary interest, and it is tempting to base priorities for conservation on the number of species that might be protected in different areas. Increasingly, however, it has been recognised that the number of species in an area is not necessarily directly related to the amount of phylogenetic diversity that is represented there. Two areas may have the same number of species, but one might contain species that are very close relatives that originated *in situ* only recently, whereas the other might include distantly related species that represent much deeper splits in the tree of life. The later area encompasses more evolutionary history. Choosing conservation areas so as to maximise phylogenetic diversity (PD) may preserve the greatest "feature diversity", the greatest evolutionary potential, and the greatest number of options for the future use of biodiversity.

One early application of the phylogenetic approach examined the amount of phylogenetic diversity uniquely represented by the mammals endemic to the world's hotspots (Sechrest *et al.* 2002). The phylogenetic clumping of the endemic taxa within hotspots implies that loss of these species would mean that not only terminal branches but also deeper branches would be lost. Thus, loss of the global hotspots would imply a large loss of evolutionary history.

A recent phylogenetic diversity application focused on the extraordinarily diverse flora of the Cape region of South Africa (Forest *et al.* 2007). The western Cape harbours more species but less phylogenetic diversity, in part owing to recent evolutionary radiations in several major lineages within that area. In contrast, the Eastern Cape harbours fewer species, but relatively more phylogenetic diversity. This knowledge of phylogenetic relationships highlights the existence of different, potentially decoupled, objectives for conservation efforts, and will generally promote the development of wiser strategies for biodiversity management.

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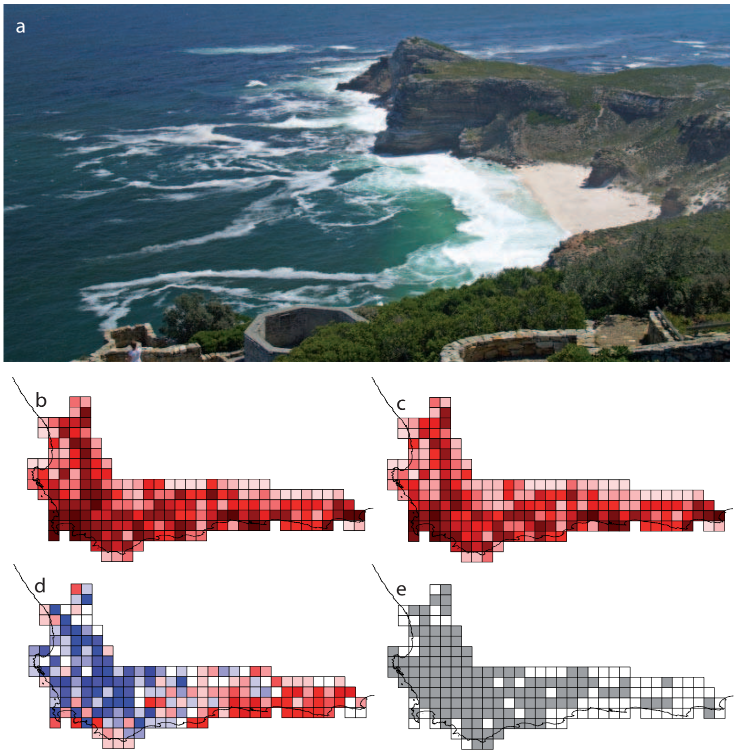
FIG. 21.1. For each quarter degree square within the Cape of South Africa, Forest *et al.* (2007) calculated (b) genus diversity; (c) phylogenetic diversity (PD); (d) residuals from a regression of PD on genus richness; and (e) unusual PD values, where blue indicates significantly lower PD, © F Forest.

a: © istockphoto.com/M Dabell



BOX 22. Evolutionary biogeography and biodiversity prediction

In most parts of the world, especially diverse tropical systems, our knowledge of the distribution of species and genetic endemism is too sparse to inform conservation planning. We need to understand how late Quaternary climate change shaped the current spatial pattern of species and genetic diversity, and how this influences the sensitivity of biotas to future climate change. Such knowledge should improve our capacity to predict biodiversity pattern and protect both the process and products of evolution. One emerging method combines paleo-distribution models with phylogeography (Knowles *et al.* 2007).

Compared to temperate and boreal systems of the northern hemisphere, such studies are only just underway for the tropics. Spatial models of habitats and species under representative paleoclimates in north-east Australia predict strong, long-term contractions of rainforest under cold-dry periods of the late Pleistocene, and for montane species, also during the warm mid-Holocene. Incorporating these climate-driven historical dynamics improved prediction of both species and genetic diversity of low-dispersal species in both this rainforest system (Graham *et al.* 2006), and in the Atlantic rainforests of Brazil (Carnaval and Moritz 2008). In such systems, past climate change concentrated narrow-range endemic species and genetic lineages on mountain-tops, increasing sensitivity to future global warming. It is likely that analogous processes underlie extreme endemism of tropical montane systems in analogous regions elsewhere.

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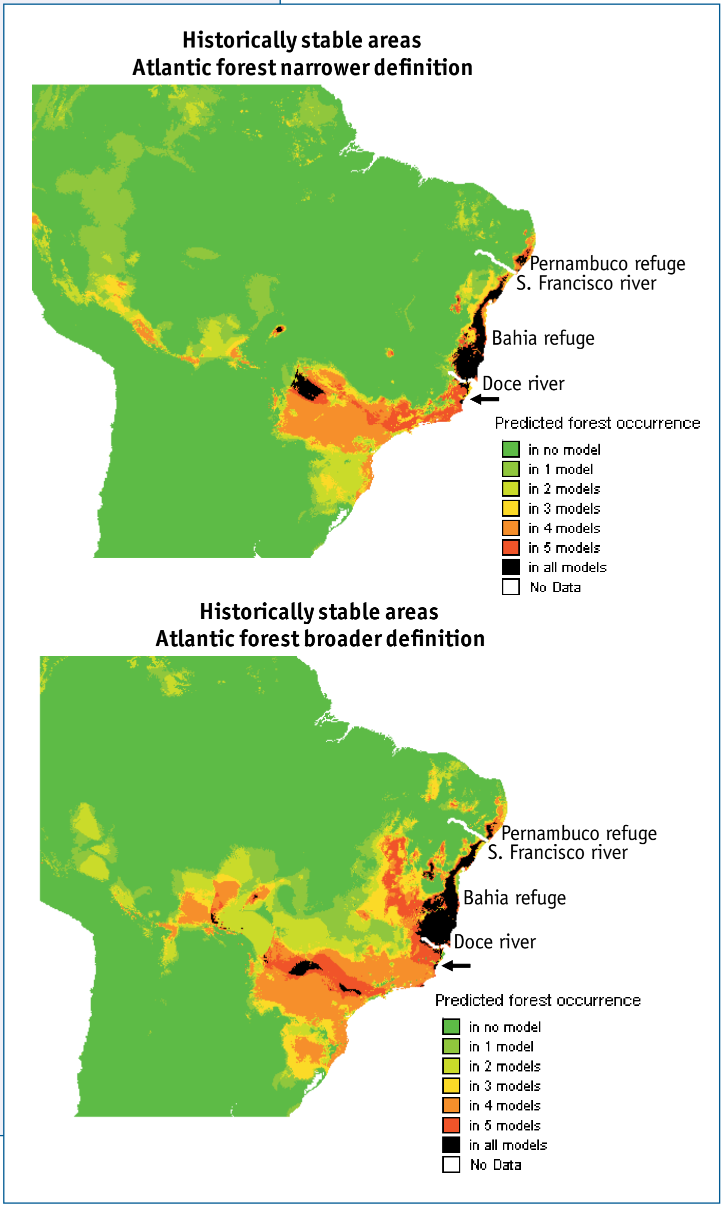

FIG. 22.1. Predicted rainforest refugia in coastal Brazil (from Carnaval and Moritz 2008).

III

Implementation Strategy

Management Structure

The activities of the bioGENESIS Core Project are overseen by a Scientific Committee (SC) with expertise in the evolutionary aspects of biodiversity science. The SC-bioGENESIS is appointed by the DIVERSITAS Scientific Committee. Duties of the SC-bioGENESIS include:

- Providing scientific guidance in the development and implementation of bioGENESIS, especially in stimulating the development of research networks, and identifying funding for, and monitoring the progress of, working groups, and educational activities centred around the focal areas and tasks outlined in this Science Plan ;
- Linking bioGENESIS activities to the other Core Projects and Cross-cutting Networks of DIVERSITAS and to other relevant national and international programmes ;
- Encouraging national governments and regional funding agencies to support bioGENESIS-related research at national, regional, and international levels, and providing expert advice relevant to the formulation of biodiversity policy and conservation management.

International Project Office

The activities of bioGENESIS are supported through the bioGENESIS International Project Office (IPO), currently hosted by the DIVERSITAS Secretariat in Paris, France. Along with the SC-bioGENESIS members, the IPO is responsible for helping to obtain funding for the proposed activities, to organise these activities, and to facilitate links across DIVERSITAS and the wider community, including with relevant national and international programmes. The results of bioGENESIS activities are communicated through reports, publications, and the DIVERSITAS website (www.diversitas-international.org).

bioGENESIS Activities

In its start-up phase (2007-2008), bioGENESIS co-sponsored a set of relevant meetings/symposia as a mechanism to promote its scientific agenda and publicise the existence of the programme. In 2007, these included meetings to **(1)** help coordinate international "tree of life" and "barcoding" activities (USA); **(2)** foster the development of phylogenetic research and applications in China (Beijing); **(3)** promote the development and use of phylogenetic diversity (PD) measures in conservation efforts (New Zealand); **(4)** explore the origin and evolution of the Mediterranean biota (Switzerland); and **(5)** focus attention on the uses of phylogenies in tropical ecology (Mexico). These meetings yielded a variety of products, including publications of symposium proceedings in the Journal of Biogeography and in Evolution and Systematics. SC-bioGENESIS members also participated in pre-meetings of the CBD's Conference of the Parties in Curitiba, Brazil (COP8).

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In 2008, bioGENESIS co-sponsored meetings on **(1)** future trends in taxonomy (Portugal); **(2)** biome boundary shifts (Japan); **(3)** phylogenetic community ecology (Japan); **(4)** the GBIF 2010 Campaign (UK); **(5)** evolutionary applications in conservation (Canada); **(6)** dating phylogenetic divergences (Spain); **(7)** speciation and biodiversity in Patagonia (USA); and **(8)** the establishment of an international regime on access and benefit sharing (Germany). SC-bioGENESIS members also participated in pre-conference events for the CBD COP9 in Bonn, Germany, and in the Global Taxonomy Initiative (GTI) meeting, in Bonn, Germany.

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In its current phase, SC-bioGENESIS members are committed to leading a variety of activities associated to the focal areas and specific tasks described in the Science Plan. Specific areas of responsibility are provided on the bioGENESIS web site. These activities include the formation of working groups and the organization of meetings to stimulate relevant science and outreach activities. The activities of each working group will take place over a specified time period, as appropriate, with new groups being formed as others complete their missions. The SC-bioGENESIS will monitor the progress of the working groups and will entertain requests for support for specific working group activities. As appropriate, these activities will be supported, in part, directly through DIVERSITAS. However, in general, outside funding and partnerships will be sought from national and regional sources, foundations, and non-governmental organizations.

Special efforts will be made to link bioGENESIS with the other DIVERSITAS Core Projects and Cross-cutting Networks, in all cases providing an evolutionary perspective on the problem at hand. Recently, bioGENESIS has engaged with the Global Mountain Biodiversity Assessment (GMBA) to help integrate georeferencing and niche modelling in assessing the past, present, and future of mountain biodiversity. bioGENESIS is also now involved in a working group on the evolution of functional traits in relation to ecosystem function. This project, funded through the Centre for Population Biology (Silwood Park, Imperial College, UK), forms a productive link between bioGENESIS and ecoSERVICES. Similarly, we are engaging with colleagues in bioDISCOVERY to explore the connection between rapid evolution, climate change, and ecosystem function, and an Imperial College, UK, working group focused on "eco-evolutionary dynamics" is working toward the publication of its findings. With bioDISCOVERY we also are involved in the ongoing development of GEO BON, focusing special attention on mechanisms to assess and monitor global genetic/phylogenetic diversity. These connections will be fostered through our active participation in the DIVERSITAS annual Scientific Committee meetings and its Open Science Conferences.

We will continue to encourage and co-sponsor relevant workshops and symposia, and will especially promote activities focused on education and capacity building. For example, we are sponsoring a workshop for Latin American students on phylogenetic methods in relation to biodiversity, organised through the University of Mexico.

bioGENESIS will also provide concrete links between DIVERSITAS and biodiversity organizations such as the Global


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Biodiversity Information Facility (GBIF), the Taxonomic Database Working Group (TDWG), the International Barcode of Life (IBOL), the Encyclopedia of Life (EOL), and the European Distributed Institute of Taxonomy (EDIT). bioGENESIS members have been active in connection with the Convention on Biological Diversity (CBD), especially through SBSTTA activities and the Global Taxonomy Initiative "Coordination Mechanism" (GTI CM). In general, we will actively engage in activities that connect biodiversity science to policy, and will participate in relevant national, regional, and global biodiversity conservation efforts.

Getting involved

There are many ways to participate in DIVERSITAS and to support the activities of the bioGENESIS Core Project, as an individual scientist, through the establishment or participation in a National Committee, or as a funder.

The activities highlighted above are meant only to provide examples of projects that might be carried out in connection with bioGENESIS. We encourage scientists to propose additional activities that support the goals outlined in the bioGENESIS Science Plan including:

- Proposals for collaborative research or educational initiatives
- Meetings, symposia, and workshops
- Synthetic activities and products, including databases and web resources

bioGENESIS also welcomes requests for the endorsement of activities that embrace its goals. Such proposals should be submitted in the early planning stages of the event or initiative. We welcome your involvement in fulfilling the mission of bioGENESIS!

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IV

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V

Acknowledgements

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This bioGENESIS Science Plan and Implementation Strategy is the product of a major co-operative effort.

DIVERSITAS would like to thank the members of the scoping meeting who met 27-30 April 2006, at ICSU, in Paris, France:

Sandra Baldauf, University of York, UK • **Brigitte Bremer**, Bergius Botanic Garden, Sweden • **Elena Conti**, University of Zürich, Switzerland • **Woody Cotterill**, University of Stellenbosch, South Africa • **Joel Cracraft**, American Museum of Natural History, USA • **Jorge Crisci**, National Academy of Sciences, Argentina • **Michael J. Donoghue**, Yale University, USA • **James Edwards**, GBIF • **Daniel P. Faith**, The Australian Museum, Australia • **Catherine Graham**, SUNY Stony Brook, USA • **Christoph L. Häuser**, Staatliches Museum für Naturkunde Stuttgart, Germany • **David Hillis**, University of Texas, USA • **Kent Holsinger**, University of Connecticut, USA • **Anne Larigauderie**, DIVERSITAS • **Susana Magallon**, Universidad Nacional Autonoma de México, México • **Michel C. Milinkovitch**, Université libre de Bruxelles, Belgique • **Craig Moritz**, Museum of Vertebrate Zoology, USA • **Leandro de Oliveira Salles**, Universidade Federal do Rio de Janeiro, Brazil • **Anne-Hélène Prieur-Richard**, DIVERSITAS • **Susanne S. Renner**, University of Missouri, USA • **Isabel Sanmartin Bastida**, Uppsala University, Sweden • **Vincent Savolainen**, Kew Royal Botanic Gardens, UK • **Simon Tillier**, Muséum National d'Histoire Naturelle, France • **Rafael Zardoya**, Museo Nacional de Ciencias Naturales, Spain.

DIVERSITAS would also like to thank members of the Scientific Committee of bioGENESIS (2006-08), who built upon the work of the scoping team, finalised the bioGENESIS Science Plan and Implementation Strategy, and began its implementation:

Elena Conti, University of Zürich, Switzerland • **Joel Cracraft**, American Museum of Natural History, USA • **Keith A. Crandall**, Brigham Young University, USA • **Michael J. Donoghue**, Yale University, USA, co-Chair • **Daniel P. Faith**, The Australian Museum, Australia • **Christoph Häuser**, Staatliches Museum für Naturkunde Stuttgart, Germany • **Andrew P. Hendry**, McGill University, Canada • **Carlos Joly**, State University of Campinas, Sao Paulo, Brazil • **Kazuhiro Kogure**, The University of Tokyo, Japan • **Lúcia G. Lohmann**, Universidade de São Paulo, Brazil • **Susana A. Magallón**, Universidad Nacional Autónoma de México, México • **Craig Moritz**, Museum of Vertebrate Zoology, USA • **Simon Tillier**, Muséum National d'Histoire Naturelle, France • **Rafael Zardoya**, Museo Nacional de Ciencias Naturales, Spain • **Tetsukazu Yahara**, Kyushu University, Japan, co-Chair.

DIVERSITAS expresses its gratitude to the following institutions or projects which offered funding for the development of this Core Project:

- European Distributed Institute of Taxonomy (EDIT, MNHN; Simon Tillier)
- Japan Society for the Promotion of Science, and
- Kyushu University 80th anniversary memorial fund, Japan (Tetsukazu Yahara)
- BIOTA/FAPESP, Brazil (Carlos Joly)
- Universidade de São Paulo, Brazil (Lúcia G. Lohmann)
- Centre National de la Recherche Scientifique (CNRS; poste rouge to Bruno A. Walther), France
- Yale University (Michael J. Donoghue)

Finally, DIVERSITAS thanks its members who provided core funding:

- Academia Sinica, China-Taipei
- Federal Ministry of Education, Science and Culture, Austria
- French Ministry of Foreign Affairs (MAE)
- French Ministry of Research
- German Federal Ministry of Education and Research (BMBF)
- German Research Foundation (DFG)
- National Council on Science and Technology (CONACYT), Mexico
- National Council for Scientific and Technological Research (CONICET), Argentina
- National Research Foundation (NRF), South Africa
- National Science Foundation (NSF), USA
- Natural Environment Research Council (NERC), UK
- The Netherlands Organisation for Scientific Research (NWO)
- Politique Scientifique Fédérale de Belgique, Belgium
- The Research Council, Norway
- Royal Netherlands Society of Arts and Sciences (KNAW)
- Slovak Academy of Sciences
- Spanish Ministry of Science and Technology (MYCT)
- Swedish Natural Science Research Council (NFR)
- Swiss National Science Foundation (SNF)
- US National Academy of Sciences (NAS).

List of acronyms

VI

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ABS	Access and Benefit Sharing
ATOL	Assembling the Tree of Life
BIOTA	Programa de Pesquisas em Caracterização, Conservação e Uso Sustentável da Biodiversidade do Estado de São Paulo
CBD	UN Convention on Biological Diversity
CIPRES	Cyberinfrastructure for Phylogenetic Research
CoML	Census of Marine Life
CONABIO	Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Mexico)
CTFS	Center for Tropical Forest Science
DIWPA	DIVERSITAS in Western Pacific and Asia
EDIT	European Distributed Institute of Taxonomy
EOL	Encyclopedia of Life
ERIN	Environmental Resources Information Network (Australia)
ESSP	Earth System Science Partnership (DIVERSITAS, IGBP, IHDP, WCRP)
FAPESP	Fundaçao de Amparo à Pesquisa do Estado de Sao Paolo
FIBR	Frontiers in Integrative Biological Research (US NSF project)
GBIF	Global Biodiversity Information Facility
GCP	Global Carbon Project (ESSP)
GECAFS	Global Environmental Change and Food Systems (ESSP)
GECHH	Global Environmental Change and Human Health project (ESSP)
GenBank	NIH (US National Institutes of Health) genetic sequence database
GEO	Group on Earth Observations
GEO BON	Group on Earth Observations Biodiversity Observation Network
GEOSS	Global Earth Observation System of Systems
GISP	Global Invasive Species Programme
GMBA	Global Mountain Biodiversity Assessment
GTI	Global Taxonomy Initiative
GTI CM	Global Taxonomy Initiative "Coordination Mechanism"
GWSP	Global Water System Project (ESSP)
HERBIS	Erudite Recorded Botanical Information Synthesiser
IBOL	International Barcode of Life
ICSU	International Council for Science
IGBP	International Geosphere-Biosphere Programme
IHDP	International Human Dimensions Programme on Global Environmental Change

IUBS	International Union of Biological Sciences
NASA	National Aeronautics and Space Administration
NESCent	National Evolutionary Synthesis Center, Durham, NC, USA
NSF	National Science Foundation, USA
SBSTTA	Subsidiary Body for Scientific, Technical and Technological Advice (UN CBD)
SCOPE	Scientific Committee on Problems of the Environment
TDWG	Biodiversity Information Standards, formerly Taxonomic Database Working Group
TOL	Tree of Life
TreeBASE	Relational database of phylogenetic information hosted by Yale Peabody Museum
UNESCO	United Nations Educational, Scientific and Cultural Organization
WCRP	World Climate Research Programme

Getting involved…


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The success of DIVERSITAS is directly related to the voluntary involvement of scientists and organisations from around the world. The following paragraphs briefly describe the primary means of contributing to this dynamic network of integrated biodiversity science. More detailed information is available in the **Getting involved** section of our web site: www.diversitas-international.org

as a Scientist

DIVERSITAS invites individual scientists to make the Secretariat aware of their ongoing research and to suggest ways to integrate local and international initiatives. The DIVERSITAS Secretariat, as well as the Core Project and Cross-cutting Network offices, welcome proposals for collaborative activities (research projects, workshops, syntheses, etc.) that support the implementation of the DIVERSITAS Science Plan.

as a National Committee

DIVERSITAS encourages the establishment of National Committees as a means of building a truly international network to support integrated biodiversity science. These Committees play an important role in linking national and international programmes, as well as interacting with policy makers and other stakeholders in their home countries.

as a Funder

Funding DIVERSITAS initiatives provides an excellent opportunity for individuals and organisations to demonstrate a strong commitment to conservation and sustainable use of biodiversity – issues that often have strong appeal for their own stakeholders and publics. DIVERSITAS welcomes the opportunity to collaborate with private industry, non-governmental/inter-governmental organizations, foundations and associations.

Our Mission

DIVERSITAS
is an international, non-governmental programme with a dual mission:

- To promote an integrative biodiversity science, linking biological, ecological and social disciplines in an effort to produce socially relevant new knowledge

- To provide the scientific basis for the conservation and sustainable use of biodiversity.

Collectively, DIVERSITAS Core Projects comprise a cycle of discovery, analysis and information sharing that supports the application of socially relevant knowledge. The bioGENESIS Science Plan complements efforts in related areas of:

bioDISCOVERY

Developing a scientific framework to investigate the current extent of biodiversity, monitor its changes and predict biodiversity futures.

ecoSERVICES

Exploring the link between biodiversity and ecosystem functions and services that support human well-being; seeking to determine human responses to changes in ecosystem services.

bioSUSTAINABILITY

Looking at the science-policy interface for ways to support the conservation and sustainable use of biological resources.

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an international programme
of biodiversity science
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Designer Maro Haas - January 2009 – This document is printed on 100% recycled paper, certified by the labels Blaue Engel, Nordic Ecolabel and Ecolabel européen.