



BIODIVERSITY AT THE ECOSYSTEM LEVEL – PATTERNS AND PROCESSES

Proceedings of the 2nd DanBIF conference
26-27 April 2006, Aarhus University

NERI Technical Report no. 741 2009



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Henrik Balslev (ed.)¹

Flemming Skov (ed.)²

¹Faculty of Sciences, Aarhus University

²National Environmental Research Institute, Aarhus University



Data sheet

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Authors: Henrik Balslev¹ and Flemming Skov² (eds.)
Departments: ¹Aarhus University, Faculty of Sciences and ²Aarhus University, National Environmental Research Institute

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Abstract: This publication contains the presentations and discussions from the second DanBIF conference, entitled Biodiversity at the Ecosystem Level – Patterns and Processes. The questions asked at this conference were: What is biodiversity at the ecosystem level? How is it related to biodiversity at other levels of organization? How may GBIF (Global Biodiversity Information Facility) deal with ecosystem level data and informatics? The conference had two important goals. The first was to present an overview of contemporary research related to ecosystem level biodiversity and the second was to help GBIF formulate a strategy for dealing with biodiversity above the species and molecular levels and make data available for the end-users.

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Contents

Introduction 5

Henrik Balslev, Faculty of Science, Aarhus University, Denmark

Flemming Skov, National Environmental Research Institute, Aarhus University, Denmark

Acknowledgements 8

Global Biodiversity Information Facility (GBIF) and ecological data: a global perspective 9

Meredith Lane, Global Biodiversity Information Facility secretariat, Denmark

Biodiversity: a European perspective 10

Gordon McInnes, European Environment Agency, Denmark

Biodiversity: a Danish perspective 11

Ulla Pinborg, Danish Forest and Nature Agency, Denmark

Definition and relevance of biodiversity at the ecosystem level

What is ecosystem diversity - and how does it relate to other levels of biodiversity? 12

Speaker: Robert J. Whittaker, School of Geography, Oxford, Great Britain

Discussants: Jens-Christian Svenning, Aarhus University, Denmark

Carsten Rahbek, University of Copenhagen, Denmark

Biodiversity for small and for large organisms 16

Speaker: Tom Fenchel, University of Copenhagen, Denmark

Discussants: Valery Forbes, Roskilde University, Denmark

Andreas Schram, Aarhus University, Denmark

Chemical change and biodiversity through time 19

Speaker: Don Canfield, University of Southern Denmark, Denmark

Discussants: Kjeld Ingvorsen, Aarhus University, Denmark

Peter Westermann, BioCentrum-Technical University of Denmark

Classification and quantification of ecosystem level biodiversity

A framework for the surveillance and monitoring of biodiversity in Europe 22

Speaker: Bob Bunce, Complutense University, Spain

Discussant: Johannes Kollmann, Royal Veterinary & Agricultural University, Denmark

Gitte Petersen, University of Copenhagen, Denmark

Natural drivers of ecosystem diversity patterns 25

Speaker: Jukka Salo, University of Turku, Finland

Discussants: Koos Boomsma, University of Copenhagen, Denmark

Erik Jeppesen, National Environmental Research Institute, Aarhus University, Denmark

Applications: Ecosystem diversity and ecosystem function

Main drivers of ecosystem change in Europe 27

Speaker: Marc J. Metzger, Wageningen University, The Netherlands

Discussants: Vibeke Hørlyck, National Environmental Research Institute, Aarhus University, Denmark

Isabel Calabuig, Danish GBIF node DanBIF, Denmark

Modelling and mapping compositional pattern in ecosystem-level biodiversity and its application to conservation assessment 30

Speaker: Simon Ferrier, NSW Dept. of Environment and Conservation, Australia

Discussants: Volker Loeschke, Aarhus University, Denmark

Rasmus Ejrnæs, National Environmental Research Institute, Aarhus University, Denmark

Ecosystem services as affected by diversity 32

Speaker: Jan Bengtsson, University of Agricultural Sciences, Sweden

Discussants: Jon Fjeldså, Danish Natural History Museum, Denmark

Beatriz Torres, GBIF secretariat, Denmark

Tools and techniques for biodiversity e-Science 35

Speaker: Andrew C. Jones, School of Computer Science, Cardiff University, UK

Discussants: Juan Carlos Bello, Coordinator Ark 2010 Project, Denmark

Mihail-Constantin Carausu, DanBIF secretariat, Denmark

Conclusions 38

Speaker: Martin Sharman, European Commission, Bruxelles, Belgium

Henrik Enghoff, Danish Natural History Museum, Denmark

References 40

National Environmental Research Institute

NERI technical reports

Introduction

When the Global Biodiversity Information Facility (GBIF¹) was planned in the late 1990'es and started in 2001 it was decided to focus on so-called primary biodiversity data, *i.e.*, the 1.5–3 billion specimens in the World's natural history museums. This inevitably gave a strong focus on the organismic level of biodiversity, a focus which would make the project more feasible given the available resources, and also a focus which would distinguish GBIF from other related activities that were concerned with biodiversity research and informatics. When the group behind the Danish participant node of GBIF (DanBIF) applied for funding to the Danish Natural Science Research Council, it pledged also to explore the relationship between biodiversity informatics at the organismic level and other levels of biodiversity, such as the molecular level and the ecosystem level.

Consequently, DanBIF² has arranged a series of conferences. On 11–12 March 2004 the first of these conferences, dealing with *Molecular Biodiversity* was held at the University of Copenhagen. The main questions of that conference were: What is molecular biodiversity? What is the connection between molecular biodiversity and other levels of biodiversity? How do we manage molecular biodiversity? What might be gained by combining the different fields of biodiversity sciences? The main conclusions of the conference were that the science of molecular and organismic biodiversity is one science. Despite differences in methods used, the research questions are quite similar. Moreover, the two approaches are complementary and one approach does not make sense without the other

This publication contains the presentations and discussion from a second DanBIF conference, entitled *Biodiversity at the Ecosystem Level – Patterns and Processes*³, held 26–27 April 2006 at Aarhus University. The questions asked at this conference were: What is biodiversity at the ecosystem level? How is it related to biodiversity at other levels of organization? How may GBIF deal with ecosystem level data and informatics?

The conference had two important goals. The first was to present an overview of contemporary re-

search related to ecosystem level biodiversity and the second was to help GBIF formulate a strategy for dealing with biodiversity above the species and molecular levels and make data available for the end-users.

To set the scene for the presentations and discussions we asked the Global Biodiversity Information Facility (GBIF) to present its view of biodiversity informatics from a global perspective, and in particular its understanding of how ecosystem-level data can be integrated with organismic-level data in web-based information systems such as that of GBIF. We also asked the European Environment Agency (EEA) to provide background information about how an agency — charged with coordinating international biodiversity management — handles the integration of different levels of biodiversity. Finally we asked the Danish Forest and Nature Agency to provide a perspective of how different levels of biodiversity can be integrated in concrete management plans.

On the background provided by these brokers and users of biodiversity information the scientific programme set out to explore fundamental aspects of biodiversity at the ecosystem level and how it relates to biodiversity at other levels of biological organization. This was done in three sessions, each with a few expert presentations followed by discussions. We asked two discussants to analyse each expert presentation and moderate the discussion so that it would contribute to the goals of the conference: to define biodiversity at the ecosystem level and provide operational suggestions for how ecosystem level biodiversity data can be handled in conjunction with data relating to other levels of biodiversity.

The presentations and discussions were presented under three themes.

1. Definitions and relevance of biodiversity at the ecosystem level

In his opening lecture Robert Whittaker (Oxford) reminded the audience of Tansley's definition for the term *ecosystem*, which involve both the organism-complex but also the interrelationships between organisms and their environment, and we were also

¹ www.gbif.org/

² <http://www.danbif.dk/>

³ www.danbif.dk/conference2006

remindend of how this definition encompass systems that vary in size from very small ones to very large ones. The problem of scale was discussed and also how, at the larger scales, the ecosystem concept is not clearly separated from other concepts such as biome, life zones or ecoregions. Not surprisingly then, *ecosystem diversity* appears not to have an agreed on definition but when discussed usually cover such features as diversity of species assemblages or the variety of ecosystems or habitats in a region. Therefore when discussing ecosystem diversity it is important to clarify what we measure and the spatial scale of application. The richness of the system affects our capacity to study it; the richer the system the more difficult it becomes to obtain even simple measures such as species richness at landscape level. In conclusion ecosystem diversity remains a concept without clear and agreed on definitions and the design of experiments and analyses and interpretation of data remains a challenge.

Tom Fenchel (Copenhagen) drew the attention to important differences in population structure and biogeography of large and small organisms. Most species measure about 1 cm and larger and smaller species are less numerous. The low number of large species is accompanied by low population sizes and higher extinction rates, whereas smaller species in general have very large population sizes and therefore remain more resistant to extinction events. Large species also tend to be narrowly distributed whereas small species have much wider ranges. At the ecosystem level this translates into a situation where the small species are less specific to the ecosystem, whereas the larger ones tends to be more specific. In the discussion, conservation aspects of these differences were emphasised concluding that the larger species would be more threatened and in need of conservation measures.

Donald Canfield (Odense) painted the grand picture of evolution of life on Earth, reminding us that organisms and ecosystems as we know them today have only existed for relatively short time, and that early biodiversity in many cases depended on energy sources that were quite different from the dominating oxygen producing photosynthetic organisms we know today. Species definition in extant prokaryotes remain difficult and often depend on molecular rather than morphological differences. This raises questions concerning the definition of ecosystems and ecosystem diversity when it involves microbial biodiversity.

2. Classification and quantification of ecosystem level biodiversity

Following the first section's focus on definitions of ecosystem and biodiversity and various problems related to this, Bob Bunce (Wageningen) turned to the more practical aspects of surveillance and monitoring of ecosystem biodiversity across different scales in time and space. Much work in Europe is related to various international initiatives such as EU's Habitat Directive and Natura 2000 and often depend on data gathered for different purposes and in different contexts. Hence scalability and consistency in the data are major hurdles to using them but much progress has been made, and some of it is represented in the *Handbook for Surveillance and Monitoring of European Habitats* which was authored by the speaker and his colleagues.

In many parts of the World the diversity of ecosystems may be difficult to appreciate due to strong anthropogenic alterations of the vegetation. The western Amazon basin and the eastern slopes of the Andes may be the only large-scale orogeny and foreland where vegetation patterns are still in a natural condition and where the shaping of a megadiverse complex of ecosystems can be studied. Jukka Salo (Turku) described the intricate processes which, over the past 20 Ma have created a mosaic of ecosystems and habitats that may be the richest on Earth. The richness of the system provides methodological constrains on designing appropriate studies, and the enormity of the complex of ecosystem makes it logistically challenging, especially considering the low number of researchers available for its study. Nonetheless, the past 25 years have shown that the early 20th century notion of one large uniform Amazonian ecosystem can no longer be upheld.

Global Change affects ecosystem and their diversity, both the diversity of their component organisms and the diversity of ecosystems themselves. The drivers of these changes vary over time as explained by Marc Metzger (Wageningen) and in the UK, for example, the main driver in the 1980s was habitat fragmentation but in the 1990s changed to eutrophication. Scenarios suggest that land use change will become a significant driver that causes change in European ecosystems. Modelling remain difficult and even more difficult is it to provide interpretations of the models for the policy domain. Available baseline data remains inadequate when it comes to species information. This becomes a relevant challenge for organisations such as GBIF when making

their information available for ecosystem research and management.

3. Applications: Ecosystem diversity and ecosystem function

Conservation assessment and planning are both practical applications in which profound understanding of the ecosystem diversity and function are crucial. Simon Ferrier (Black Mountain) demonstrated how spatial modelling of biodiversity at the ecosystem level may be a very useful tool in biodiversity management, combining data from multiple species and producing information on spatial patterns in the distribution of biodiversity. This includes predictive mapping of community types, species groups, axes or gradients of compositional variation and macroecological properties such as species richness.

One of the most frequently mentioned applications related to ecosystem diversity is the exploitation of ecosystems for the good of humans, the so-called *Ecosystems Services*, which have been widely heralded, not least after the appearance of the *Millennium Ecosystem Assessment*. Jan Bengtsson (Uppsala) discussed this and criticized the simplistic view that there is a direct correlation between the diversity of organisms in a system and the amount of ecosystem services it provides. Still the questions of how biodiversity and ecosystem services are related and what it means to human welfare remains an important research topic, not least given the rate of land use change and potential loss of biodiversity we are facing. It was suggested that GBIF could be an im-

portant player in maintaining focus on this and similar questions.

The study of ecosystem and ecosystem biodiversity lends itself to being done with computer-based tools, especially considering the often very complex nature of the systems. At the same time increasing amounts of data are becoming available in digital form. Nonetheless, the boom in computer software and data has often made it more difficult than before to secure the accuracy of the data and the analyses carried out. The building of integrated workflow systems that can use a variety of tools and databases across heterogeneous data is barely emerging. Andrew Jones (Cardiff) presented some recent finding in the field and also some of the big challenges that remain, one of them being the naming of organism in which one often finds a diversity of scientific opinion and competing taxonomies. Solving that and other similar problems will be crucial or the implementation of workflow systems in the study of ecosystem diversity.

To finalize the conference we had asked two generalist biodiversity workers, a research scientist and a high level biodiversity bureaucrat, to summarize their understanding of the presentations and discussions.

Each speaker was asked to write an extended abstract of his or her presentation. These abstracts and a brief summary of the discussion that took place after each presentation are presented in this booklet.

Henrik Balslev & Flemming Skov

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To plan the scientific content of the conference we were privileged to have the help from a *scientific committee* that through email correspondence and discussion commented on its themes, approaches, emphasis, and orientation. The members of the scientific committee were: Rudolf Amann (Max-Planck-Institut für Marine Mikrobiologie, Bremen), Isabel Calabuig (DanBIF secretariat, Copenhagen), Donald Canfield (University of Southern Denmark, Odense), Gitte Petersen (University of Copenhagen), Henrik Enghoff (University of Copenhagen), Bruce Stein (NatureServe, Washington), Jacqueline McGlade (European Environmental Agency - EEA, Copenhagen), Jon Fjeldsaa (University of Copenhagen), Johannes Kollmann (Royal Agricultural and Veterinary University, Copenhagen), Kai Finster (Aarhus University), Rudy Jocque (Royal Museum for Central Africa, Bruxelles), Tom Fenchel (University of Copenhagen), Volkmar Wolters (Justus-Liebig-University, Giessen).

The organization of the conference was done by the secretariat the Danish node (DanBIF) of the Global Biodiversity Information Facility (GBIF), specifically Isabel Calabuig, Lotte Endsleff and Mihail Carausu. Logistics was arranged by staff and students from the local hosts for the conference, Aarhus Univer-

sity, Faculty of Science and the National Environmental Research Institute: Inger Juste, Annie Laursen, Sten Andersen, Jesper Bladt, Anne Sandal, and Lone Hübschmann. Heidi Klixbüll from Kongreskompagniet arranged hotels and conference fees. Joanna Karlsen and Rania Spyropoulou represented the European Environment Agency (EEA) in the organisation, and Else Maggaard took notes of the discussions following each presentation.

We are grateful for economic support for the conference from the European Environment Agency (EEA), the Danish Forest and Nature Agency (DFNA), the Global Biodiversity Information Facility (GBIF), the Danish Natural Sciences Research Council (DNSRC), and the National Environment Research Institute (NERI). Aarhus University provided the conference venue and the needed technical facilities for which we are thankful.

Finally, we wish to thank the invited speakers who agreed to share their insight within a very fixed conference framework, and also to the group of discussants who carefully analysed the views submitted by the speakers and guided the discussions following each presentation.

Global Biodiversity Information Facility (GBIF) and ecological data: a global perspective

Meredith Lane

Global Biodiversity Information Facility secretariat, Denmark

GBIF is an international mega science project designed to make the world's biodiversity data freely and universally available via the Internet, and especially to share primary scientific biodiversity data for science, society and a sustainable future. When GBIF began, it was focused almost exclusively on species occurrence data as documented by specimens in natural history museums and the like. Now, its information architecture is ready to be expanded to allow interconnectivity with other information domains.

The species level links together the other two levels of biodiversity – molecules and ecosystems. Molecular data are already largely digital and open-access, but most species- and specimen-data are not yet in digital form. Data from ecology lies somewhere in between – more of it is digitized than species-level data are but not as much as of molecular data, and the openness of access is not as great as in that discipline. One of GBIF's two main tasks is to promote digitisation of legacy data, and the other is to facilitate linkages among data from all levels while promoting open access to scientific data.

If these many fragmented sources of information could be linked via a flexible, modular, adaptable and scalable information infrastructure, it would maximise the return on investments that society has made in research and information management in all these fields of biology. Such a thing has the potential to advance by orders of magnitude our ability to exploit the Web's power, to give society true, worldwide, manipulable biodiversity information-at-our-fingertips, and thus to contribute to scientific

innovation and progress and towards a sustainable society.

The web-services based information architecture that GBIF is building can in fact provide the linkage mechanisms needed to achieve such an information system. It uses common standards for data and metadata, and common web protocols, markup languages and services, all of which are also employed by, for example, GenBank and various ecological information initiatives. Partnerships with these other organizations and entities are paramount in GBIF's operations. In building this infrastructure, GBIF contributes directly to science, policy and applications.

As GBIF expands its scope of work to include building the linkages to other information networks, it is important to understand the needs of ecological researchers: What are the ecological data sets that need to be linked into the system? What are the desired characteristics of the user interface? How can GBIF best promote open access in the area of ecological and ecosystems data? How can ecological researchers be encouraged to use GBIF-mediated data? GBIF is already interacting with MarBEF, ALTERnet, LTER and NCEAS – what other partners should GBIF seek in the ecological information domain?

GBIF looks forward to the outcome of this conference and the advice that we will receive from the many ecologists who are making presentations here. We hope that this will be the beginning of a fruitful interaction with the ecological community.

Biodiversity: a European perspective

Gordon McInnes

European Environment Agency, Denmark

Biodiversity includes ecosystems/ecology, species, molecules/genes in all their variability on Planet Earth and needs to be considered and managed at appropriate scales and by various stakeholders, e.g.:

- global level <> Global society; Convention of Biological Diversity
- regional level (e.g., Europe) <> EEA
- national level <> Countries
- local level <> Everybody.

Facing such complexity a number of questions arise: How can biodiversity possibly be assessed – let alone biodiversity loss?! What is done at the European level? And how does the European Environmental Agency (EEA) fit into this context?

The European biodiversity policy is stated in a number of Directives, strategies and action plans among which the most important are:

- EU Birds and Habitats Directives (Species/site/habitat protection)
- EU Biodiversity Strategy (Action Plans, Message from Malahide, Sector integration)
- Pan-European Biological and Landscape Diversity Strategy (Kiev Resolution and Action Plans, Pan-European Ecological Networks, Commission Communication on Biodiversity, Biodiversity in the European Union, The EU and global biodiversity, Biodiversity and climate change, The knowledge base).

In order to monitor the actual state of biodiversity and to evaluate development trends, EU has developed a number of Headline Biodiversity Indicators based on the four focal areas of the Convention of Biological Diversity:

- Ecosystem integrity, goods and services (marine trophic index, connectivity of ecosystems, water quality)

- Sustainable use (forest, agriculture, fishery, aquaculture)
- Status and trends of components of biodiversity (for selected biomes, ecosystems and habitats)
- Threats to biodiversity (Nitrogen deposition, invasive species, climate change).

The HIPPO test

EEA plans to assess progress towards the 2010 target mainly through an integrated land-use and ecosystem accounting. This includes, among many other initiatives, spatial assessments using the Corine Land Cover data base and inventories of plants and animals. In EEA, biodiversity assessment is carried out within the DPSIR conceptual framework (Drivers-Pressures-States-Impacts-Response). The purpose of the DPSIR framework is to ensure that not only the symptoms of biodiversity degradation are recorded, but also the main causes and the ways in which society may respond. Along this line of thinking, the so-called HIPPO test may be applied to ensure that the major threats to biodiversity are considered. (HIPPO ~ Habitat destruction + Invasive species + Pollution + Population + Overharvesting or the alternative HIPOC test ~ Habitat destruction + Invasive species + Pollution + Overharvesting + Climate change).

Concludingly, Biodiversity in an EEA context is mainly about:

- All ecosystems and species (and genes) in Europe or affected by Europe's activities
- Information to support European policy development, implementation and assessment
- Integrated ecosystem approach using best available information including indicators
- A focus on main drivers and their impacts.

Biodiversity: a Danish perspective

Ulla Pinborg

Danish Forest and Nature Agency, Denmark (DFNA)

The Danish effort to protect biodiversity is based on global, European and national conventions and policies (e.g., the Rio Declaration, the Convention on Biological Diversity (CBD), EU biodiversity policies and programmes and national targets and regulations). The Danish Forest and Nature Agency is part of a wider Danish context within the Ministry of Environment and collaborates with sectoral ministries and other administrative units.

Is there a clear Danish ecosystem approach in national policies and practices? The short answer to this question is no, at least not only for the sake of ecosystems. Forests, fresh water and marine policies are mainly based on sustainable development for continued production and lower environmental impacting, but are slowly approaching the use of ecosystem-like concepts.

Farmland policies mainly argue for sustainable development for the same reasons as mentioned above. Nature protection policy aims for sustainable development to ensure continuous and high indigenous diversity of natural/semi-natural habitats and ecosystem types.

What can DFNA gain from this conference? We hope to gain a better understanding of the functionality of ecosystems, the importance and meaning of biodiversity patterns and their dynamics and insights into the drivers and causes of change. Such knowledge will be of utmost importance to develop guidelines for management and restoration, to build models and develop scenarios and to enhance sectoral integration and collaboration. Furthermore, it would strengthen the recognition of the functional importance of the wider countryside and the more common species.

On the long term the Danish Forest and Nature Agency will continue a close collaboration on the European level on, e.g., priority species and habitats, biodiversity friendly regional development, adaptation to climate change, impacts of invasive

alien species and generally on how to integrate biodiversity concerns into policy-making.

What is ecosystem diversity - and how does it relate to other levels of biodiversity?

Robert J. Whittaker

School of Geography, Oxford University Centre for the Environment, United Kingdom

The Convention on Biological Diversity defines biological diversity (aka biodiversity) as “the variability among living organisms from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems.” Diversity within species refers to genetic variation, and can be measured by techniques such as mtDNA, and allozyme electrophoresis, to provide quantitative measures of affinity and variability among populations. Diversity ‘between species’ might mean the diversity of interactions and degree of connectivity between species, but is perhaps more generally taken to refer to metrics such as species richness, and relative abundance, or to the possession by areas of unique (*i.e.*, endemic) species. This leaves diversity of ecosystems to be considered.

In addressing the question of ‘what is ecosystem diversity’ we might first remind ourselves what the term ecosystem implies. The term as defined in Arthur Tansley’s seminal 1935 paper, is an expression of the interrelationships between organisms and their environment, fundamental to which is the continual transfer of energy and chemicals between the organic and inorganic component parts. Tansley (1935) wrote (p299) of the ecosystem in these terms: “...the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome – the habitat factors in the widest sense... the basic units of nature on the face of the earth...and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic.”

Notwithstanding the power of Tansley’s concept, the spatial delimitation of ecosystems is problematic for those wishing to operationalise the term for use in biodiversity assessment. Indeed, it is generally accepted that an ecosystem can be any size, from a pinhead to the whole biosphere (Collin 1988). In

fact, Tansley’s definition tied the term ecosystem to Clements’ earlier term ‘biome’, which refers to a major type of natural vegetation occurring extensively across a region. The fundamental controls on biome distribution are water and energy regimes (and edaphics), and they are characterised by distinctive life forms (*e.g.*, tundra, boreal coniferous forest, savanna, *etc.*). Typically, biome schemes recognise between 8 and 10 biome types. If we follow this approach, we would assess ecosystem diversity at a fairly coarse spatial scale.

From a quick scan of search engines and environmental science dictionaries and encyclopaedias on my own book shelves, the term “ecosystem diversity” does not appear to be well used or broadly discussed. Pullin (2002) writes simply “...community or ecosystem diversity; measured as the number of different species assemblages.” The most prominent mention I found in an encyclopaedia was the following 50 words of a 1300 word article on biodiversity: “Ecosystem or ecological diversity is the variety of ecosystems or habitats in a region. Measurement at this scale is not easily adapted to the common, fine scales of ecological studies. Ecosystem diversity is particularly relevant in larger-scale investigations, such as those relying on remote sensing and to conservation” (Matthews *et al.* 2001). The article did not elaborate on how ecosystem diversity is relevant to conservation.

Hence, whilst ecosystem diversity could mean almost anything, those attempting to define it appear to weigh in with usages described in terms either of the number of different species assemblages or the number of habitats, and referenced to spatial scales from the landscape up to the region. We thus have to consider both the metrics involved and the scale of application.

In following this approach, the next step is to consider how we classify landscapes and regions into more or less discrete habitats and/or species assemblages, in short, what are the units of nature? As

stated in Groombridge (1992, p248), 'The world encompasses an enormous range of terrestrial and aquatic environments.... The classification of this immense range of variation into a manageable system is a major problem in biology..' Over the last 100 years, a number of different ways have been developed towards that goal. We might crudely classify them as either functional or compositional. Functional approaches include Clements' biomes (major vegetation types) or Bailey's Ecoregions scheme, both of which can be more finely subdivided on physiognomic grounds. The Holdridge Life Zone classification, is another such system, which relates the distribution of major ecosystem types to gradients of annual precipitation and energy regime. Compositional approaches to subdivision can include the world's biogeographical regions at a coarse scale of analysis, down to very fine scale subdivisions into different vegetation associations. In practice, vegetation scientists have found it expedient to develop schemes that combine both physiognomic and floristic information. A good example is the USGS - NPS Vegetation Mapping Program. At coarse spatial scales this is a physiognomic scheme, working down through a hierarchy of levels to the level of the formation (*e.g.*, evergreen needle-leaved forest with conical crowns). This provides a mappable unit, but one which itself is comprised of a variety of recognised forest types on compositional grounds. These types or alliances, are themselves made up of associations or 'communities' (*e.g.*, the *Abies lasiocarpa/Vaccinium scoparium* association) based on subdominant or associated species with similar ecological processes.

Different physiognomic types, formations, and associations typically have differing average values and ranges of species diversity. They provide useful units for ecosystem management and mapping purposes. But, how useful are these systems in assessing biodiversity? In one sense, they 'do what it says on the can', *i.e.*, they provide a measure of the num-

ber of more or less distinctive ecosystems and/or assemblages to be found within a landscape or region. On the other hand, ecologists are typically more concerned with either (i) the amount of biodiversity at species or sub-species level that might be held within these landscapes, and/or (ii) the functional health or integrity of these ecosystems. Focus on the latter has led to a variety of approaches under the general header of ecosystem management, a term that has itself been claimed for a variety of rather different approaches and conceptualisations of the problems at issue (Yaffee 1999).

If we are concerned with summing the number of ecosystem elements across landscapes, then it will often emerge that certain types of cultural landscape turn out to be amongst the most diverse. I am thinking here in particular of areas of mixed use agriculture intermingled with semi-natural or natural habitats, providing of course that we recognize the inherent physiognomic and floristic diversity of orchards, meadows, and grazed chalk grasslands in our classification system. Yet, the extent to which such landscapes hold, or permit the passage of, native species of plants and animals, can vary dramatically, for example, in relation to the use of herbicides and pesticides.

Of course, it is not just the intensity of agriculture but also how different landscape elements are configured spatially that matters (reviewed in Whittaker and Fernández-Palacios 2007). For example, if we are concerned with the conservation of woodland species, how fragments of woodland are embedded within complex landscapes containing roads, towns, cities, rivers, and many forms of agricultural activity can be crucial to the functional connectivity of the woodland species populations. As a first example, countless thousands of birds are killed each year through collision with motor vehicles and with overhead power cables. Research has shown that deaths through collisions with cables

Spatial scale	Diversity phenomena	Variables predominant	Temporal scale
Local	Richness within communities	Fine-scale biotic & abiotic interactions, habitat structure, fires, storms	~1 – 100 years
Landscape	Richness between communities (turnover)	Soils, topography, altitude, drainage	100 – 1000 years
Regional	Richness patterns over large extents	Water-energy dynamics (climate), peninsular effects	Last c. 10k years
Continental	Differences in species lineages across continents	Aridification events, Pleistocene climate change, Mountain building	1-10 mill. years
Global	Differences reflected in biogeographic regions (<i>e.g.</i> , mammal family distributions)	Tectonic plate movements, sea-level change, long-term climate change	10s mill. years

can be greatly reduced by consideration of important flight paths during construction, by design features of the gantries, and by attaching a variety of objects to the cables to enable birds to sight them. Second, there may be greater opportunity for dispersal between two distant reserves linked by a river and its adjacent riparian corridor, than between two similar but closer reserves separated by a mountain barrier of differing habitat type. For butterflies, differences in landuse as subtle as switches from one woodland type to another can significantly influence the passage of butterflies from one favoured habitat patch to another. While more research into the ways in which linear features function would be beneficial, what is required is that such information is integrated into improved management of whole landscapes. This is important on two fronts: first, in terms of the functional integrity (*e.g.*, dispersal services) of native plant and animal populations, and second, in terms of ecological goods and services (*e.g.*, pollination of valuable crop plants by native animals), which can be of enormous economic importance (Ricketts 2004, Daily *et al.* 2003). It is not clear to me how we build such detail into assessments of ecosystem diversity that take the form of counting assemblage types. Hence, alongside quantifying number of ecosystem or community types, we should be looking at ways of measuring functional aspects of ecosystems, *i.e.*, of assessing both diversity and health of ecosystems.

At the outset of this discussion, I distinguished two main themes: these were respectively what we measure and the spatial scale of application. I would like to address the latter in respect of the next tier down in biodiversity assessment: namely species diversity. The table below, from Willis and Whittaker (2002), is intended as a schematic for organizing ideas about diversity pattern and process from the local scale to the global. The table points out that the aspect of diversity that we measure typically differs as a function of scale. For instance, at fine scales of analysis, alpha scale or local scale assessments might be measured by a snap-shot survey based on a temporary plot or a point count, whereas on a coarse scale of analysis, we are more likely to be using herbarium or museum records, assimilated into species range maps, and representing spatial and temporal generalizations as to species presence. In turn, these differing phenomena typically appear to be responsive to different controlling biotic and abiotic variables, which themselves have differing temporal signatures.

An important implication of this line of argument is that in comparing the diversity of two ecosystems, it

is crucial to control for variation in area between the systems being compared. This can be done either post-hoc, by statistical manipulation, or prior to data collection, by using equal area (or equal effort) sampling systems. The latter is much to be preferred (Whittaker *et al.* 2001) but does not of itself eliminate the possibility of statistical artefacts (*e.g.*, data quality problems, spatial autocorrelation, *etc.*) entering analyses of patterns of diversity between different ecosystems.

Unfortunately, the problems involved in comparing diversity tend to be more acute the richer the system, in part this is due to incompleteness of taxonomic knowledge (the so-called Linnean shortfall) and in part to the paucity of distributional data for many taxa. Even for well-known taxa, such as birds, when working in highly diverse parts of the tropics, the problems involved in obtaining adequate samples to allow reliable estimates of species richness at landscape level appear almost intractable. For example, an analysis by O'Dea *et al.* (2006), of an Ecuadorian cloud forest system for which the overall richness was reasonably well-known, showed that 'industry standard' species richness estimates gave little basis by which to assess landscape-level diversity.

In this short abstract and presentation, I have sought to open up two sets of questions for debate and discussion: what is ecosystem diversity - and how does it relate to other levels of biodiversity? Whilst it is easy to appreciate the ecosystem diversity matters, it is a non-trivial task to work out an agreed, standard interpretation of what we really mean by ecosystem diversity. Moreover, once we work this out, significant challenges remain in terms both of how we collect data and perhaps as crucially, how we analyse and interpret such data.

Discussion

Following the lecture the reality of communities or ecosystems was discussed. Are ecosystems 'real' or are they merely convenient classification artefacts? And, even if their reality may be disputed, may such classifications still be useful and is it possible objectively to standardise methods and approaches to develop and describe them? Most participants at the conference agreed that ecosystems do not exist as static units in nature, but are in constant change due to natural and anthropogenic processes. Nevertheless, an ecosystem approach was still considered useful, partly as a conceptual framework for organising and structuring knowledge, partly as a tool to

help manage and conserve biodiversity. The issue of ecosystem health was discussed and the need for clear and objective definitions was emphasised. Also, several participants emphasised the necessity to incorporate dynamics and flows of nutrients and energy into the description of ecosystems. Finally, the potential role of GBIF was discussed. What kind of existing data on ecosystem diversity could it be useful to provide access to from GBIF? Among the suggestions were: vegetation plots and relevé data, *e.g.*, from the Natura 2000 network or the North American VegBank project⁴. Discussants: **Carsten Rahbek** (University of Copenhagen, Denmark) and **Jens-Christian Svenning** (Aarhus University, Denmark).

⁴ <http://vegbank.org/vegbank/index.jsp>

Biodiversity for small and for large organisms

Tom Fenchel

Marine Biological Laboratory, University of Copenhagen, Denmark

The spectrum of body size-species numbers is one of the striking large scale patterns of biodiversity. On a global scale most species seem to measure about 1 cm while larger and smaller species are less numerous. Robert May was the first to draw attention to this. As far as very large organisms are concerned this pattern can be understood from their relatively low absolute population sizes. Small populations are prone to high local, regional, and global rates of extinction so that species turnover is relatively high over geological time and species numbers equilibrate at a relatively low level. As far as the decreasing number of small species is concerned, May suggested that this may be an artefact: many small species remain undiscovered and also, perhaps, species taxonomy is coarser in the case of small organisms.

A local survey of aquatic organisms will, however, reveal many more small species (unicellular eukaryotes, meiofauna) than macroscopic organisms. This accords with the observation that most unicellular appear to have a cosmopolitan distribution. This was observed already in the late 19th century by Darwin and Ehrenberg and again in the 20th century by, e.g., Schewiakoff and Kahl. Similar claims were made in the early 20th century for prokaryotes by Beijerinck and later by Baas Becking who coined the dictum: *Everything is everywhere – the habitat selects*. This means that the distribution of microbes is determined solely by habitat, while – in contrast to macroscopic organisms - historical contingencies over geological time do not play a role for the distribution of microbes. To be sure there exist protists that have been found only in warm climates and others occur only in porous sea ice, but these then tend to have pantropical and bipolar distributions, respectively. Evidence for the existence of endemic protists is regularly published, but due to under-sampling, such claims are difficult to prove or disprove. But it is a generally accepted fact that most species of unicellular eukaryotes can be recovered worldwide.

Fenchel and Finlay (2004) and Finlay and Fenchel (2004) attempted to identify all eukaryotic organisms in a 1 ha pond in the English Lake District and in a 2 ha marine shallow-water habitat in Denmark. Both locations harbour about one thousand species and the great majority measure less than 1 mm in size. It could be shown that the fraction of species with a cosmopolitan distribution increased continuously with decreasing body size and that in both localities the fraction of the global pool of species within different taxonomic groups increased continuously with the characteristic size of members of these taxons.

The explanation offered for this pattern is essentially one of absolute population sizes. These are huge for small organisms: a 1 ha aquatic habitat will roughly harbour about 10^{18} bacteria, 10^{16} protozoa, and 10^{11} representatives for the meiofauna (animals measuring <1mm). Everything else being equal, the ability of dispersal will be proportional to population size. Also, local extinction becomes an extremely rare event. The huge number of species of macroscopic organisms is primarily due to endemisms: thus mountain ranges, small oceanic islands, and old lakes harbour endemic species. Nothing similar occurs for small organism. A corollary is that microbial species (phenotypes) have a low species turnover over geological time.

So far we have considered a classical species concept – that is based on phenotypic and especially morphological traits. Some unicellular organisms show a richness of morphological detail (e.g., ciliates) and others less so (e.g., naked amoebae). It has therefore been suggested that there are cryptic species: species that cannot be distinguished in terms of morphological traits, but may be genetically distinct and by implication show phenotypic (e.g., physiological) specialisations – and that these genotypes may show some sort of real biogeography (for a discussion on species concepts for protists, see Fenchel 2005 and Fenchel and Finlay 2006).

Many protists groups harbour sexual outbreeders, whereas others include only asexual species with clonal evolution. In the latter case, there is no theoretically based species concept. In the 1940's and 50's, breeding experiments with certain ciliate outbreeders (especially *Paramecium aurelia* and members of the *Tetrahymena* species complex) proved the existence of such sibling species. Many of these have been shown to have a worldwide distribution, but whether this applies to all such strains is unknown and to prove or disprove this will require a substantial effort.

More recently gene sequencing has opened for new approaches, and in particular rRNA genes ("ribotypes") have been studied. It has been found that – like in bacteria – genetic distances within nominal species are very large (e.g., in the above mentioned *Tetrahymena* complex genetic distances for rRNA-genes is comparable to that of all mammals). Studies on isolates of asexual protists have shown that every new strain that has been sequenced seem unique. The null hypothesis is that the recorded genetic differentiation is selectively neutral – that is, neutral mutations have accumulated over long geological periods, but natural selection has maintained particular phenotypes that represent some sort of adaptive peaks. However, in some euryhaline "species" a correlation between certain clades and salinity preferences has been shown. But it has not been possible to show that any correlation between geography and genotype is evident.

Several other studies have indicated that ribotypes within nominal species may show a global distribution. Notably, this has been shown for certain protozoa with bipolar distribution by Darling and co-workers and by Montresor and co-workers).

A recent study of the ciliate *Cyclidium glaucoma* (Finlay *et al.* 2006) included 54 isolates collected worldwide, and they represented 31 distinct genotypes. No evidence of biogeography was found; thus one particular genotype was sampled in Argentina, Peru, Morocco, Russia, and Ukraine, and another one in Australia and Denmark. *Cyclidium glaucoma* occurs in all salinities spanning from freshwater to hyperhaline lakes. In the phylogenetic tree, one clade included only sea- and brackish water isolates and within this clade, a subgroup included all hyperhaline isolates. Another clade included exclusively freshwater isolates, while a third clade included marine as well as freshwater isolates. In experiments, all strains proved to be rather euryhaline: saltwater isolates could grow at all salinities (including freshwater), while freshwater isolates

could not grow at salinities exceeding about 20 ppt; the saltlake isolates could grow at all salinities down to very dilute brackish water, but it could not grow in freshwater. The data therefore suggests a certain correlation between salinity preference and genotype, but this is all not quite clear. Certainly, the data indicate that the actually existing number of ribotypes must be very high, and so a complete picture of the correlation between ribotypes and phenotypes may be difficult to obtain.

The conclusion that can be drawn so far is that while it is true that nominal microbial species represent a large genetic differentiation, there is no evidence that these genotypes do not have any biogeography in the sense it applies to large organisms.

The general picture that smaller organisms tend to have a wider distribution than larger ones as a consequence of larger absolute population sizes accords with "the neutral theory of biodiversity" as developed by Bell and by Hubbell. A recent analysis of data on the regional and global numbers of insect species (Finlay *et al.* 2006) also indicate that this principle applies more generally and not only to microbes.

Discussion

The discussion following Tom Fenchel's lecture touched upon the practical impacts of the different roles of large and small organisms in the ecosystem, and one conclusion was that — for conservation purposes — efforts should focus on the larger organisms because the smaller ones occur everywhere and are much less likely to go extinct. So even if small organisms may have key functions in the ecosystems, these key functions are not threatened because the organisms that secure the functions persist. This principle may be more relevant in natural ecosystems, considering that in some artificial systems microorganisms do go extinct due to, e.g., agricultural treatments. The distinction between free-living and interacting (fungi, parasites, yeasts, *etc.*) microbes is also important to make. Free living microbes have good dispersal and reduced possibilities for speciation but, at the same time, good dispersal lowers the risk of extinction for a species. Interacting microbes have limited dispersal, their speciation and evolution is tremendous, and at the ecosystem level they are very important, also when addressing questions of species diversity. The problem of species concepts in prokaryotes is also relevant to the discussion of their role in the ecosystem;

it may be more useful to use functional classifications of prokaryotes when assessing ecosystem health. Finally the delimitation of ecosystems was questioned, and it was agreed that it depends on the point of view; a lake may be an ecosystem for large organisms but a system of several ecosystems for small ones. This relativity in ecosystem delimitation makes it hard to apply the ecosystem concept to

information systems such as GBIF because it would be very difficult to establish "an electronic catalogue of ecosystems" parallel to the "electronic catalogue of names" which is used in GBIF's efforts to gather biodiversity data about species. Discussants: **Valery Forbes** (Roskilde University, Denmark) and **Andreas Schramm** (Aarhus University, Denmark).

Chemical change and biodiversity through time

Donald E. Canfield

Ecology Group, Institute of Biology, University of Southern Denmark, Denmark

The Earth started as a lifeless planet and is presently teeming with life. Therefore, there is no question that biodiversity on Earth has increased with time. There are a number of possible approaches to reconstruct this history. One approach is to explore phylogenies through the analysis of molecular sequence data. One can also approach the problem logically and consider the possible energy sources available to have fueled early life, and how these energy sources might have changed through time. Finally, the geological record offers some insight into the history of biodiversity. In this talk, I will consider all three approaches.

In principle, phylogenies constructed from molecular sequence data can be used to reconstruct the history of life and the history of biodiversity. The earliest approaches considered the accumulated mutations in DNA that gave rise to amino acid changes in proteins. These changes provided the basis for phylogenetic comparisons. Nucleotide sequences can, of course, also be used, and molecular-based phylogenetic reconstructions became widespread with the utilization of small subunit ribosomal RNA (SSU rRNA) sequences.

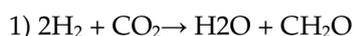
These new phylogenies forever changed our view of the history of life, and the resulting "Tree of Life" demonstrated that the evolution of life on Earth was mostly a history of microbial evolution. Furthermore, the deep-branching, and presumably the most ancient, organisms, were mostly high-temperature adapted. In addition, they were anaerobic, with metabolisms involving the utilization of chemical compounds like hydrogen, sulfide, sulfate and reduced ferrous iron. From this we can imagine ancient microbial ecosystems concentrated in deep-sea and terrestrial hydrothermal areas utilizing reduced chemical compounds originating from the interior of the Earth. Oxygen-utilizing organisms came later, spawning a massive evolution of oxygen utilizing organisms.

This is a good story, but its details are obscured by a number of factors. First, the placement of the deep-

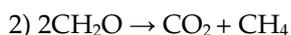
est branches in the Tree of Life is often in doubt, and different treatments of the data often yield different results. More serious, probably, is the reality that over time, genes have been swapped between different organisms. This means, for example, that the defining metabolic trait of an organism (which establishes its place in an ecosystem) may have been obtained by gene transfer, rather than from the linear process of evolution and change. Therefore, if an organism branches deeply within the Tree of Life, we cannot be certain that its defining metabolic characteristic also emerged early.

Life requires energy in order to survive. Presently, most of the energy used to fuel the biosphere comes from primary production by oxygenic photosynthesis. However, oxygen-producing phototrophs did not occupy the earliest Earth ecosystems. Therefore, we must search for alternative energy sources. Indeed, these energy sources came from the Earth's interior and were delivered to the surface environment through volcanic outgassing. Thus, energy sources would have come from subaerial volcanoes as well as deep-sea hydrothermal vents systems. The substrates available to fuel life would have consisted of a variety of oxidizing and reducing compounds including: H_2 , CO_2 , H_2S , SO_2 , SO_4^{2-} , Fe^{2+} , $FeOOH$, NO_3^- and NH_4^+ . This mix of substrates is very similar to the mix of substrates used by modern anaerobic ecosystems. Therefore, based solely on considerations of substrate availability, a rich biodiversity may have existed on the early Earth well before the evolution of oxygen production by cyanobacteria. This biodiversity may have rivalled that of modern anaerobic ecosystems.

We can explore the possible structure of these ancient ecosystems in more detail. Hydrogen gas is a high-energy electron donor of great preference, and it fuels a number of anaerobic metabolisms. These include the reduction of SO_4^{2-} , SO_2 , $FeOOH$, and CO_2 to methane and acetate. Also possible is the phototrophic oxidation of H_2 to H_2O , coupled to the reduction of CO_2 to cell biomass:

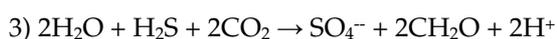


This type of photosynthesis is known as anoxygenic photosynthesis, as no oxygen is produced, and a variety of lines of evidence shows that anoxygenic photosynthesis predated the evolution of oxygenic photosynthesis. We can surmise that an ecosystem driven by this type of anoxygenic photosynthesis would have involved a variety of different players. Other than the primary producers, organisms would also have been engaged in organic matter remineralization. Chief among these was probably methanogenesis, which would have decomposed the organic matter to CO_2 and methane gas:

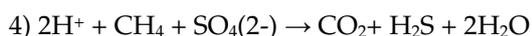


Through atmospheric reactions this methane would have been converted back to hydrogen gas, enhancing the hydrogen available to primary producers. Overall, such an ecosystem on the early Earth would likely have been about 100 times less active than the present marine ecosystem.

Ecosystems involving the cycling of sulfur compounds would also have been possible. Sulfur emerges from subaerial volcanics as well as hydrothermal systems. Those hydrothermal systems on land such as we find at Yellowstone National Park, on Iceland, or the North Island of New Zealand, could have fueled a very interesting and complex ecosystem known as a *sulfuretum*. In such an ecosystem anoxygenic photosynthetic bacteria oxidize hydrothermal sulfide to sulfate:

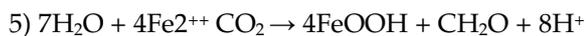


This reaction represents primary production, and the organic matter produced can be reoxidized by a group of organisms known as sulfate-reducing bacteria, which conduct reaction 3) in reverse, using the sulfate produced by the phototrophic bacteria. Other microbial populations could also be active in the *sulfuretum* including methanogens (reaction 2) as well as an interesting microbial consortium which oxidizes methane with sulfate:



The potentially most energetic of all early-Earth anaerobic ecosystems would have been one based on the anoxygenic phototrophic oxidation of Fe^{2+} . Evidence suggests that early oceans contained abundant ferrous iron. We know this because of the occurrence of expansive deposits of Fe-rich sediments known as Banded Iron Formations. In principle,

this iron would have fueled a population of anoxygenic phototrophic bacteria, which produce iron oxides (essentially rust) as their byproduct:



As this combination of iron oxides and organic matter settled into the deep ocean, the organic matter would have been remineralized by a group of iron-reducing bacteria. Overall, this marine ecosystem could have been nearly as active as the one we have at present.

Clearly, a diverse and interesting range of biodiversity likely existed on the Earth before oxygen-producing photosynthesis. However, the evolution of oxygen production would have spurred the evolution of myriads of oxygen-utilizing organisms. This led the way to eukaryotes, and ultimately to higher organisms like animals.

In principle, the geologic record has captured the history of biodiversity through time. Our window into the early history of biodiversity is, however, very limited. As discussed above, the early history of biodiversity is mainly a history of microbial evolution, and microbes do not preserve well as fossils in rocks. In any event, even if they did, morphology alone is not a good indicator of lifestyle. The geologic record does, however, give us some clues. We know, for example, that life existed by 3.8 billion years ago, but the nature of this life is uncertain. If we move forward to 3.5 billion years ago, we have reasonably good evidence for the activities of specific microbial populations including anoxygenic phototrophs, sulfate reducers, and methanogens. Thus, by this time, we have evidence for an assemblage of diverse microbial ecosystems.

A significant question becomes, when did oxygen-producing photosynthesis evolve? As outlined above, this innovation would have promoted the evolution of oxygen-utilizing organisms and would have forever altered the biodiversity of the planet. Here, the geologic record is very stingy. Probably the best evidence for cyanobacteria dates to 2.7 billion years ago, but their evolution may have well predated this. It is quite ironic that one of the most significant biological innovations in the history of life, the evolution of oxygenic photosynthesis, is nearly cryptic in the geologic record.

In any event, as we move forward in time, we begin to see changes in the diversity of marine ecosystems (there was probably only limited life on land, and of this, we have only a very poor record). By 2.1 billion

years ago, we see evidence for the first eukaryotes in the geologic record, although the nature of these eukaryotes is uncertain. The first algae appear around 1.2 billion years ago, and the earliest evidence for animals is seen around 580 million years ago. Indeed, there is much debate about the nature of the earliest fossils we interpret as animal. They lack symmetry and had a developmental plan completely different from anything living today. Their emergence may have been triggered by an increase in atmospheric oxygen levels, and by the Cambrian-Precambrian boundary at 542 million years ago, many recognizable animal forms are found.

Over the next 20 to 30 million years there was an amazing degree of innovation and evolution within the animal kingdom. This time of dramatic evolutionary change is known as the *Cambrian explosion*, and through special windows of exceptional preservation, we observe marine animal ecosystems with nearly all of the principal players we see today.

Discussion

Species concepts for prokaryotes makes definition of their diversity difficult; this must be solved using phenotypical, functional and genetic analyses. This also raises the question about at what time in the history of life it makes sense to talk about biodiversity; do we need to have diversity in kinds of organisms or are we talking about diversity in kinds of DNA strings? And what implications do this have for our definition of ecosystems? Many of the metabolic environments mentioned in the presentation can be realized, but are they ecosystems? or are they microbial ecosystems? They definitely are functional units able to utilize the energy which is available. Maybe they should just be called habitats? It was proposed that the species problem for microbes is not different from the species in other organisms and that it should be possible to make species phylogenies, taking into account that species are not always clear cut. In historical terms no big changes were observed in microbial diversity in connection with the formation of continents 3-4 billions years ago. Discussants: **Kjeld Ingvorsen** (Aarhus University, Denmark) and **Peter Westermann** (BioCentrum-Technical University of Denmark).

A framework for the surveillance and monitoring of biodiversity in Europe

Bob Bunce

Alterra, Wageningen, The Netherlands. (Temporarily at Departamento de Ecologia, Universidad Complutense, Madrid, Spain)

There is a well defined policy requirement for a practical, transmissible and reproducible procedure for the surveillance and monitoring of biodiversity in Europe. This need is linked to many initiatives, such as the Habitats Directive and most recently the Natura 2000 programme. However, it should also be emphasised that not only are checks on the effectiveness of protection in these sites necessary, but also that the majority of the resources of nature conservation are outside these areas; which inevitably cover only a relatively small part of the land surface. The procedure should transcend national frontiers and enable regional monitoring programmes to be placed onto a common framework. It should also utilise satellite imagery, aerial photographs and *in situ* data, *i.e.*, field records, to combine the strengths of each approach.

The present abstract summarises such an approach which has been tried and tested over the last 40 years, mainly in the UK, but also in other European countries. Indeed all the components have been in place for many years - what has not been done is to link them together at the European level. For example many test projects have shown how satellite imagery can be linked with *in situ* data, but still most satellite programmes of work proceed without the added value of combining detailed observations with the census coverage of satellite imagery.

One of the major problems to be overcome is that biodiversity needs detailed local records which inevitably cannot be made at a continental level. In social sciences this dilemma has long been solved by the development of stratification systems and subsequent sampling and conversion of the samples to population estimates. However, field ecology has largely been concerned with descriptive studies based on records at one point in time; *i.e.*, surveillance - for example Tuxen (1937). Monitoring however involves repeated

measurements at specified time intervals. However, individual taxa such as birds and butterflies are well covered by existing schemes often using amateur recorders. The monitoring of changes in assemblages of species or habitats requires rigorous rules, otherwise change cannot be separated from background noise, especially when different groups of observers are involved. For monitoring it is essential to record at the same locations, otherwise larger samples are required and there is a higher degree of statistical error (Bunce *et al.* 1996). Such studies are relatively uncommon, for example, in the UK Bunce *et al.* (1993) found only a few published analyses of vegetation change. Long term strategic studies are being carried out, *e.g.*, Brandt and Agger (1988) and, increasingly, national and regional programmes are being undertaken, although using a variety of methods. Any procedure to integrate these diverse studies must not only be able to place them onto a common reference system but also have rules to derive general categories from diverse available data.

Many aspects of biodiversity are also recorded on different scales, both spatial and temporal, which are then rarely linked together. So, for example, land use or vegetation data across Europe and bird and butterfly records are seldom combined, but the changes that are taking place are likely to be inter-related. Another principle is that local data should be set into a wider baseline: the local resource may make a major contribution to the wider population but, equally importantly, it may be relatively small across the entire domain, but of local significance.

As described by Bunce *et al.* (1996), a stratification system should be based on explicit criteria and must not include features such as biodiversity or land use change for which estimates are required because of statistical considerations. In addition, members of one stratum must not be able to alter

into another stratum during the process of monitoring; otherwise changes cannot be estimated from the baseline survey.

Different procedures have been used for stratification, but as long as they are objective, *e.g.*, Brandt and Agger (1988), they can enable statistical estimates of extent and change to be carried out. Similarly, historic data sets can be used in an opportunistic way to determine change if they are sufficiently well recorded to be re-locatable, *e.g.*, Grabherr *et al.* (1994). Sheail and Bunce (2003) describe how statistical procedures for stratified random sampling from defined populations have been progressively developed in the UK from the late 1960's. The initial work involved sampling woodland vegetation but later environmental strata were constructed, using multivariate analytical techniques which were subsequently sampled for habitats and vegetation. An integrated programme for surveillance and monitoring in Britain was started in 1978; with repeat surveys in 1984, 1990 and 1998; including landscape features, habitats, vegetation, and aquatic invertebrates, as described by Haines-Young *et al.* (2000). Estimates of the extent and change in the parameters were made and a series of papers has been published on the ecological and policy significance of the results.

Whilst it is preferable for the data to be recorded from the same sites, Bunce *et al.* (1993) showed how the environmental strata could be used to integrate studies from different locations for which geographical coordinates were available. For example, data for moths - collected throughout the UK - were linked to the underlying environmental gradient available from the series of samples elsewhere in the UK.

Even in the UK, multivariate analysis of a wide range of environmental data showed that, at a strategic level, climate and altitude were the most important discriminatory variables (Bunce *et al.* 1996). At a European scale, not only have the major divisions been shown to be climatic (Bunce *et al.* 2003) but also data for other parameters, such as soil, are not available consistently at a continental scale. Furthermore, Bunce *et al.* (2003) showed that although boundaries between classes varied in detail, there was a high degree of agreement between national and regional environmental strata, even though different data and analytical procedures were used.

Accordingly, Metzger *et al.* (2005a) developed a European climate stratification at a one km square scale for the whole of Europe, using experience gained from previous studies and involving data from climate, altitude and location. A total of 84 strata were defined, aggregated using statistical rules, into 13 Environmental Zones for summary purposes. These strata were validated by orthogonal regression of the first environmental component with independent data such as soils, potential natural vegetation and satellite land cover. In conjunction with a rule-based system for recording habitats in the field, as described by Bunce *et al.* (2005), these strata could be used to develop an integrated system for surveillance and monitoring for the whole of Europe. Data for a whole range of biodiversity factors from vegetation and plant species to birds, butterflies and mammals, could be linked to the strata, provided that geo-referenced data were available. Statistical estimates of stock and change could then be made using existing monitoring sites that are based on objective strata, *e.g.*, Brandt and Agger (1988) so that changes could be assessed. The framework of the strata would also be used to assess gaps in the present data and to identify where further in situ data were required. Provisional estimates of the time required, based on experience of field conditions throughout Europe have also been made. In addition the strata can also be used to model potential change as described by Bunce *et al.* (1993).

Within Scandinavia there are many such datasets and a combined programme could not only provide an enhancement of the value of national projects but also set regional studies into the European context. A proposal is already underway to carry out a pilot study to link the Swedish landscape programme to the strata, and a similar exercise could also be carried out in Denmark. The procedure described by Bunce *et al.* (2005) has already been shown to be suitable for Danish conditions and a paper is in preparation describing the results. Whilst the European strata are likely to be too broad for small countries such as Denmark, further subdivisions could be made according to local requirements, *e.g.*, on soil, geology or altitude. Such a procedure has already been demonstrated in western Portugal by Jongman *et al.* (2006). Further samples could also be added to better define local variation and give more accurate regional estimates. A test of applicability of the BioHab procedure in Denmark has recently been carried out by Bloch-Petersen *et al.* (2006). It was concluded that the details of the small biotopes recorded by Agger

and Brandt (1988) could be converted to the Bio-Hab categories, which could then enable the data to be coordinated with other extant surveys in the European domain.

Aerial photos could also be used to assess historical change, as in the BIOPRESS project⁵ and, once in situ data were available, these could also be linked to satellite imagery the results could then have added value because the in situ data could be used to assist interpretation of the satellite categories which are inevitably lacking ecological detail. The many sites available with detailed monitoring, as defined within the ALTER-Net project (www.alter-net.info), could then be used to interpret the changes in terms of processes.

It is now widely recognised that in order to achieve adequate data on change to meet the 2010 target and to assess favourable conservation status, an adequate baseline is essential. As far as favourable conservation status is concerned, member states have developed their own recording procedures. What is necessary is a lowest common denominator to link these data onto a common basis for European comparisons. Any procedure must utilise existing data wherever possible, not only to save money but also to enable member states to set their historical data into the European context. Similarly, it is also essential to develop an integrated programme involving aerial photographs satellite imagery and detailed monitoring of sites. The procedure described above would satisfy all these requirements but would inevitably have financial implications. Further work needs to be carried out about the differences between how habitats can be monitored in Natura 2000 sites in different countries because of the variations in size and extent of sites. Also the rare Priority habitats and Annex One habitats may need to be targeted individually.

Discussion

The framework for surveillance and monitoring presented includes detailed methodology and procedures for general ecosystem monitoring that may be implemented throughout Europe and the following discussion naturally focused on issues regarding the practical application of the framework. Much extensive biodiversity and ecosystem data exists in various forms in different countries, but much work and resources are needed to screen these data to provide consistency across national borders and regions. The actual number of categories in the framework and the criteria used to separate them were discussed intensively. The General Habitat Categories were defined based on all possible combinations of Life Forms, defined in the classical literature, supported by other categories, *e.g.*, crops and bare land, resulting in 130 types. The strength of the system is its transparency and scalability. It could be up-scaled to other world regions or more detailed types could be added for local purposes. It was stressed, however, that while names of types are useful for communication and for management purposes, qualifiers are still very important and should be recorded. Finally, it was concluded that the methodologies described in the surveillance framework are ready for implementation and may be used free of charge by GBIF. Discussants: **Johannes Kollmann** (Royal Veterinary and Agricultural University) and **Gitte Petersen** (University of Copenhagen).

⁵www.creaf.uab.es/biopress/background.htm

Natural drivers of ecosystem diversity patterns

Jukka Salo

Section of Biodiversity and Environmental Research, University of Turku, Finland

The western Amazon basin and the eastern Andean slopes form the only remaining large-scale Neogene active orogeny and foreland belt where the vegetation patterns are still in a “natural” condition. Other such belts, like the Siwaliks in Himalayas and the Alps in Europe have faced ecosystem alteration by human action long time ago. The biological diversity of the Andean-Amazonian belt is reflected by the fact that five of the 18 megadiversity countries (Venezuela, Colombia, Ecuador, Peru and Bolivia) lie in this region. The west Andean tectonic dynamics since the Miocene has been poorly understood in relation to the landscape dynamics and biological differentiation patterns. Recent results indicate that the region has been much more active than understood earlier and that these dynamics are crucial in order to understand the ecosystem diversification. The presentation will survey the natural drivers that have had an impact on the landscape ecology of the Andean-Amazon region during the last 20 million years.

The traditional view of the Amazon basin forest as a whole is that of a relatively uniform environment where only a few different forest types can be recognized (Hueck and Seibert 1972, UNESCO 1980, Encarnación 1985, Prance 1989). These categories have been distinguished on the basis of such characteristics as hydrology (non-inundated *vs.* seasonally inundated *vs.* swamp), topography (lowland *vs.* montane) and soil texture (rock outcrops *vs.* white sand soils *vs.* clay soils). The most extensive forest type, *i.e.*, the lowland forest on non-inundated clay soils (*terra firme*), covers more than 50% of Amazonia.

The studies conducted over the past 25 years have revealed that the western Amazon is made up of a mosaic of dozens of clearly delimited ecosystems along the current or abandoned fluvial systems and on non-flooded (uplifted) substrates of lacustrine/brackish and fluvial origins (Räsänen *et al.* 1988, Tuomisto *et al.* 1995). The characteristics of the forests bed have been controlled by the geological dynamics of the Andean foreland belt. These dy-

namics have resulted in a dramatic change in the landscape of the western Amazon since the Miocene: from a large Pebas lacustrine/semimarine depression, the landscape has evolved through various stages, such as possible perimarine wide tidal flats and lacustrine phases into the current riverine ecosystem.

The western Amazon is largely located in the active foreland of the Andes, where long-term uplift and local subsidence have had profound effects on the geographical configuration of the area over the past 25 Ma. In historical times, foreland tectonism affected the landscape dynamics in the area, and it still does so, even today (Pärssinen *et al.* 1996). The modern fluvially dominated western Amazonian landscape evolved through major fluvial reversals in the continental drainage (Hoorn *et al.* 1995) and tectonically controlled evolution of the western Amazon's fluvial systems (Räsänen 1987, Dumont *et al.* 1991, Dumont and Fournier 1994) only some 5-10 Ma ago.

Concurrently with the postulated paleo-environmental changes, the western Amazon fossil record shows notable diversification from 22 Ma to 10.5 Ma onwards for several aquatic taxa (Ostracoda, Bivalvia, Gastropoda and the Sciaenid fish). Molecular findings in avian phylogeny indicate that there has been a major differentiation period from 10 Ma to 5 Ma ago (see Fjeldså 1994), which may indicate profound changes in the landscape. This period coincides with the landscape change from lacustrine to fluvial setting with marked differences between the flooded and non-flooded surfaces which may provide a key approach for the reconstruction of the evolutionary pathways.

For a long time, it was thought that tropical rain forests are the oldest and most stable ecosystems in the world, and that the high species diversity is the result of long-term accumulation of species (Ashton 1969). Amazonia was depicted as a huge sea of uniform rain forest, in which no dispersal barriers apart from the mighty rivers prevented species from mi-

grating anywhere in the entire basin (Wallace 1853). However, analyses of the distribution patterns of birds in Amazonia showed that the species are not distributed evenly in the forest, but that some areas stand out as centers of species richness and endemism. This observation led to the proposition of the Pleistocene Refuge Hypothesis (PRH, Haffer 1969), which postulated that Amazonian climate dried up considerably during the Pleistocene glaciations. As a result, much of Amazonian forest would have been converted into savanna, while rain forest species survived in isolated pockets of rain forest (refugia). By allopatric speciation, some of the isolated populations would have evolved into new species, which maintained their distinctness even after the refugia had been rejoined when moister climate returned. Not all species were able to colonise the whole of Amazonia since the dry periods ended, and therefore the original refugia still stand out as centers of biodiversity and endemism.

By the 1980's, the PRH had gained international acceptance, because it neatly explained both the high species richness of Amazonia and the observed endemism and diversity patterns (see contributions in Prance 1982, Whitmore and Prance 1987). Consequently, most research in Amazonia was planned on this basis, and the results were interpreted in the light of the PRH. However, the PRH was also strongly criticized, because no independent paleoecological, geomorphological, or lithostratigraphical evidence supported the existence of isolated forest patches in ice-age Amazonia (Connor 1986, Salo 1987, Colinvaux 1993, Colinvaux *et al.* 1996). Furthermore, Nelson *et al.* (1990) showed that observed centers of endemism and diversity in Brazilian Amazonia were mainly collection artefacts. In the case of the western Amazon, modern habitat heterogeneity maintained by Andean tectonics may be the underlying factor behind the the postulated climatic refugia.

Recently, an interesting discussion and controversy has emerged about the distribution patterns of western Amazon forest biota. Several authors have documented relative homogeneity of tree communities over large lowland areas and that many Amazonian trees may have much larger range sizes than previously thought (the "oligarch species school" see discussion in, *e.g.*, Pitman *et al.* 1999, Ricklefs 2000, Ruokolainen *et al.* 2002, Condit *et al.* 2002). These observations stress the importance of biotic factors over the edaphic heterogeneity in explaining the observed distribution patterns. On the other

hand, several studies on palms, Melastomataceae and ferns (*e.g.*, Tuomisto *et al.* 2003, Vormisto *et al.* 2004) show linkage between plant community structure and the environmental heterogeneity of the Western Amazon lowlands. Much of this controversy may be a result of poorly documented geological mosaicism of the region – until today no georeferenced maps have been available showing the chronostratigraphic classification of the western Amazon forest beds. In the case of Peru, such a map is currently being processed by the Geological Survey of Peru (INGEMMET) and the University of Turku.

Discussion

Amazon biodiversity is very much a matter of scale and generally most lowland Amazon species are widespread and very old, whereas endemism is closely related to the arches between the subsiding basins. There are more endemics in the Andes and more local endemism than we thought, not least in relation to species complexes. Sympatric speciation may well be operational, and heterogeneity in the Amazon may be its driver, but we are still missing detailed explanations. And what about reference data which are especially difficult to obtain when operating at different scales? Yes, we have to remember the complexity of the ecosystems. What is the role of climate and its effect on migration? In the marginal areas climate has to be taken into account more explicitly because of high extinction rates in these areas. How does this relate to sustainable development? In general there is no good protection of biodiversity in the region, but planning efforts now use the various maps which have been produced by scientists, and in Peru there is a national protection plan which will cover the different forest types and forest age-categories. And how do we move from the species level to the ecosystem level when we try to understand Amazonian biodiversity? A lot of field work is needed and training of local researchers must focus on making publications "operational," not in the least by closing the language gap and by increasing the number of ecological researchers interested in the Amazon basin, a group which is, at present, still very small. Discussants: **Koos Boomsma** (University of Copenhagen, Denmark) and **Erik Jeppesen** (National Environmental Research Institute, Denmark).

Main drivers of ecosystem change in Europe

Marc J. Metzger

Environmental Systems Analysis group, Wageningen University, The Netherlands

Many aspects of our planet are changing rapidly due to human activity. Over the past 50 years, humans have changed ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fibre, and fuel (Reid *et al.* 2005). Under current projections of economic development and population growth, such changes are expected to continue into the coming century. Furthermore, there is a growing consensus among scientists and the general public that the climate is changing (IPCC 2001). All these changes, including a growing population and energy consumption, biodiversity loss, land use and climate change are strongly interrelated and cannot be seen in isolation. Because their impacts will influence the entire planet, the combined changes are now commonly recognized as global environmental change, or simply 'global change' (Steffen *et al.* 2001).

The impact of global change on ecosystems and biodiversity is not straightforward to assess at a European scale. However, detailed monitoring programs are able to quantify change in ecological resources (*e.g.*, Agger and Brandt 1988, Firbank *et al.* 2003), and link the changes in biodiversity to specific drivers. For example, Potter and Lobey (1996) and Firbank *et al.* (2000) showed how in the UK landscape fragmentation was the main driver of change in the 1980s, while eutrophication was the main driver in the 1990s. And Grabherr *et al.* (1994, 2000) were able to quantify observed impacts of climate change on alpine vegetation. While such detailed quantitative assessment of change is not possible for Europe as a whole without a common baseline, such as the one proposed by BioHab (BioHab: A framework for the co-ordination of Biodiversity and Habitats⁶; Bunce *et al.* 2005), general insights into global change processes can be used to assess broad potential impacts on ecosystems in the future.

This paper will discuss main drivers of ecosystem change in Europe, based on results of the European Union 5th Framework Program ATEAM (Advanced Terrestrial Ecosystem Analysis and Modelling⁷; a modeling study that focused on ecosystem service supply and human vulnerability to global change in Europe. Principal project results have been summarized by Schröter *et al.* (2005).

Scenarios, providing alternative images of how the future might unfold, form an appropriate tool with which to analyze global change processes. While the possibility that any single scenario will materialize is highly unlikely, a set of alternative scenarios can span a wide range of uncertainty. Within the European Union project ATEAM (Schröter *et al.* 2005) a set of scenarios were developed for future climate and land use in Europe. These scenarios, covering EU15, Norway and Switzerland, are internally consistent and have a spatial resolution of 10 arcmin x 10 arcmin (approximately 16 km x 16 km). The scenarios were generated for four thirty-year time slices: 1961-1990, 1991-2020, 2021-2050, and 2051-2080.

The climate change scenarios consist of monthly climate information based on climatological observations and on outputs from transient coupled atmosphere-ocean global circulation model (GCM) simulations for five climate variables: temperature, diurnal temperature range, precipitation, cloud cover, and vapor pressure (Mitchell *et al.* 2004). In order to provide as full a representation of the uncertainties in projections of regional climate change as possible, climate change scenarios were developed for four alternative greenhouse gas emissions scenarios and four GCMs (for more details see Schröter *et al.* 2005).

These climate scenarios show a general trend of warming. There are, however, considerable differences in changing climate across Europe. Large changes are projected for the Mediterranean, which will become much warmer and drier, including

⁶<http://www.biohab.alterra.nl>

⁷www.pik-potsdam.de/ateam/

large declines in the cooler Mediterranean mountain environments. Similar changes are observed for the Alpine mountain environments, which are projected to resemble more continental conditions toward the end of the 21st century. By contrast, the Atlantic region will stay comparatively stable, with relatively minor changes in temperature and precipitation (Metzger *et al.* 2005b).

The land use change scenarios take into account potential effects of climate change (Ewert *et al.* 2005), but are for the most part dependant on alternative projections of socio-economic developments and world trade, derived from the IPCC SRES scenarios (Nakicenovic *et al.* 2000). Various land use change models were used to estimate aggregate totals of land use change. These aggregate quantities were allocated across the European domain using spatially explicit rules (Rounsevell *et al.* 2006). The scenarios include the major land use classes urban, cropland, grassland, forest and bio-energy crops.

The scenario changes are most striking for the agricultural land uses, with large area declines resulting from assumptions about future crop yield development with respect to changes in the demand for agricultural commodities. Abandoned agricultural land is a consequence of these assumptions. Increases in urban areas (arising from population and economic change) are similar for each scenario, but the spatial patterns are very different. This reflects alternative assumptions about urban development processes. Forest land areas increase in all scenarios, although such changes will occur slowly and largely reflect assumed policy objectives (Rounsevell *et al.* 2006).

Since at a European scale biodiversity patterns is mainly dependant on climatic properties (Thuiller *et al.* 2004, Metzger *et al.* 2005a) climatic change, as indicated by the scenarios, is likely to have a profound impact on ecosystems. The land use changes will more directly influence ecosystems, but the scenarios only give broad classes of land use, and do not convey information about land use intensity, farming practices, or regional landscape structure. Interpretation of the residual impacts of the scenarios on biodiversity is therefore extremely speculative. Nevertheless, just by evaluating the scenarios, it seems evident that both climate and the land use change are drivers that will cause significant change in European ecosystems.

Ecological modeling techniques can be used to evaluate global change impacts in more detail. Thuiller *et al.* (2005) have used niche-based modeling to

study the potential impacts of the climate change scenarios on 1350 European plant species. For each plant species a climatic envelope was calculated based on its current distribution. The climate changes scenarios were then used to evaluate whether its suitable niche changes in the future.

Results show that many species could be threatened by future climate change. Under the conservative assumption that species cannot migrate to new suitable regions, more than half of the species were considered vulnerable or committed to extinction. Under an optimistic, universal migration assumption, results are less severe. Potential impacts are greatest in mountainous regions, where specialized species with narrow climatic niches occur. The southern Mediterranean and Pannonian regions, already characterized by hot and dry summers, show a low species loss. The Boreal region could gain species in a warmer climate. Importantly, even if species numbers in a given region stay stable, a considerable species turnover is projected in all cases (Thuiller *et al.* 2005). Another study, based on the same scenarios, has shown that the current European network of nature reserves is unlikely to ensure longtime survival of all species (Araújo *et al.* 2004). Dynamic reserve-selection methods can help to optimize protection of biodiversity under global change (Araújo *et al.* 2004).

For specified regions, shifts of generic climatic strata can provide a useful summary of projected climatic change. These insights can be combined with ancillary information and knowledge from experts in order to assess the most important drivers of change for a given region. Metzger *et al.* (2005b) have illustrated this for four sample regions, using ancillary data from available European datasets. When available, detailed regional datasets, field observations and local knowledge can be used to make more detailed assessments. Standard GIS operations can then be used to make regional scenarios, useful for evaluating regional or national physical planning and nature conservation.

Considerable global environmental changes are projected for Europe over the coming century. These will include significant changes in climate and land use, which will affect European ecosystems both directly and indirectly. The scenarios developed for the ATEAM project provide a basis for exploring potential changes. They help in understanding the possible magnitude of change, as well as the spatial distribution of changes across the European domain. European policy will have a large influence on future changes in land use, *e.g.*,

through European agricultural policy. As such, there is a strong message towards policy about the importance to evaluate possible effects of socio-economic changes on wider ecological resources. However, the interpretation of the potential impacts of the scenarios on ecosystems remains difficult. Ecological modeling exercises, such as the work by Thuiller *et al.* (2005), provide valuable additional insight and strengthen scientific understanding. Nevertheless, uncertainties in the projections restrict direct interpretation for the policy domain. The broad-brush results are difficult to relate to regional experience and probably too uncertain for the development of targeted policy to prevent impacts on ecosystems.

Uncertainties in projections of global change impacts stem from several sources. Most frequently discussed sources of uncertainty include uncertainties in the storylines behind the climate and land use scenarios, uncertainties in the global climate sensitivity and the regional patterns of climate change, uncertainties in land use change algorithms, and uncertainties in the ecosystem models which use the scenarios. These sources of uncertainty are usually discussed, in the scientific literature describing the scenarios and ecosystem models. An obvious, but frequently neglected source of uncertainty is formed by the quality of the baseline data (Rounsevell *et al.* 2006).

Global change impact studies are generally based on 'the best available data sources.' For Europe, excellent datasets are available for describing broad environmental patterns and gradients. However, biodiversity and ecosystems also greatly depend on regional heterogeneity (*e.g.*, landscape structure, diversity in habitats, management intensity, and disturbance). Unfortunately, that level of detail is not available, or highly inaccurate in European datasets. For example, land use scenarios are usually based on the CORINE and PELCOM land cover databases, which poorly represent landscape structure, and misrepresent minor land cover classes (Schmit *et al.* 2006), which have high ecological significance. In addition, management intensity and ecological importance varies enormously within broad classes such as 'pastures' and 'coniferous forests'. Another example of valuable datasets, with limitations concerning regional heterogeneity are the species distribution atlases, which do not give information about the species abundance, and have a spatial resolution that is insensitive to land use (Thuiller *et al.* 2004). Available baseline datasets therefore frequently introduce considerable uncertainty when

exploring global change impacts on biodiversity and ecosystems.

The scenarios and modeling results discussed here provide alternative images of how the future might unfold. Because we cannot attach probability to any given scenario, they can help stimulate open discussion in the policy-arena about potential futures. It is important to be aware of uncertainty, but even when results are uncertain, general trends between scenarios, or between regions can provide useful information about likely impacts and sensitive regions. Such insights can help focus more detailed research, or stimulate policy developments aimed at mitigation, or adaptation to global change.

Discussion

The discussions following the presentation first dealt with model development and the need for baseline data. Available data sets are still very heterogeneous, but environmental data on, *e.g.*, climate, land use and soils, are being made available on an increasingly finer scale. However, there is still a considerably large gap when it comes to available digitized distribution data for species and ecosystems; and for species, there is a need for more datasets that include abundance data. The GBIF could play a significant role in providing such data for the modelling community. The discussion touched upon the use of models to present complex problems online. It was emphasised, that this approach is dangerous, because end-users may not be aware of the limitations, assumptions of the models. The issue of uncertainties of the models, and how to deal with it, was also debated and it was recommended, that modellers should describe and communicate model uncertainties to avoid misinterpretations of model results. Hence, in many cases, it will be better to publish carefully reviewed analyses based on models, and provide access to the data, including abiotic data, used by the models, rather than making the modelling tools available on-line. Regarding model-based priorities for areas of conservation, these areas should be where the models foresee least changes. Finally, the need to move from static to dynamic models, *e.g.*, for reserve selection and for proactive conservation policies, was stressed. Such models might include, *e.g.*, adaptiveness of species, species dispersal and biotic interactions. Discussants: **Vibeke Hørlyck** (National Environmental Research Institute of Denmark) and **Isabel Calabuig** (DanBIF secretariat).

Modelling and mapping compositional pattern in ecosystem-level biodiversity and its application to conservation assessment

Simon Ferrier

Department of Environment & Conservation, New South Wales, Australia

Conservation assessment and planning require information on the spatial distribution of biodiversity, often across very large regions (Margules and Pressey 2000). Direct field sampling of such regions is typically sparse, with biological survey or collection sites separated by extensive areas of unsurveyed land. Planning therefore often employs remotely mapped surrogates for biodiversity such as habitat (or vegetation) types derived from aerial photography and satellite imagery, or abiotic environmental classes derived from climate, terrain and soil attributes. These surrogates provide better geographical coverage, but the level of congruence between mapped habitat or environmental classes and actual biological distributions may be weak or, in many cases, simply unknown (Ferrier and Watson 1997, Ferrier 2002).

The surrogacy value of remotely generated environmental data can be enhanced by linking this information to available biological data through statistical modelling. The most popular approach to such integration has been to model the presence (or abundance) of individual species as a function of environmental variables, thereby allowing species' distributions to be extrapolated across an entire region of interest (Guisan and Thuiller 2005). Spatial modelling of biodiversity at the ecosystem or community level may, however, confer significant benefits for many applications, including faster processing of large multi-species datasets, increased power to detect shared patterns of environmental response across rarely-recorded species, and enhanced capacity to synthesise complex data into a form more readily interpretable by decision-makers (Ferrier and Guisan 2006).

Community-level modelling combines data from multiple species and produces information on spatial pattern in the distribution of biodiversity at a collective community level instead of, or in addition to, the level of individual species. Spatial outputs

from community-level modelling include predictive mapping of community types (groups of locations with similar species composition), species groups (groups of species with similar distributions), axes or gradients of compositional variation, levels of compositional dissimilarity between pairs of locations, and various macroecological properties (*e.g.*, species richness).

Three broad modelling strategies can be used to generate these outputs:

- 1) 'assemble first, predict later', in which biological survey data are first classified, ordinated or aggregated to produce community-level entities or attributes that are then modelled in relation to environmental predictors;
- 2) 'predict first, assemble later', in which individual species are first modelled one at a time as a function of environmental variables, to produce a stack of species distribution maps that is then subjected to classification, ordination or aggregation; and
- 3) 'assemble and predict together', in which all species are modelled simultaneously, within a single integrated modelling process. These strategies each have particular strengths and weaknesses, depending on the intended purpose of modelling and the type, quality and quantity of data involved (Ferrier and Guisan 2006).

I focus on generalised dissimilarity modelling (GDM, Ferrier 2002, Ferrier *et al.* 2002) as an example of one approach to implementing the 'assemble and predict together' strategy. GDM models dissimilarity in community composition (beta diversity) between biological survey or collection sites as a non-linear function of inter-site differences in remotely derived environmental variables and/or

spectral data from various forms of remote sensing. The approach can therefore add considerable value to the types of data currently being generated by revolutionary advances in both remote sensing (Turner *et al.* 2003) and biodiversity informatics (Graham *et al.* 2004). GDM offers a rapid and cost-effective means of mapping spatial pattern in biodiversity across large highly-diverse regions, thereby supporting a wide variety of applications ranging from biological survey design, through reserve selection and land-use planning, to climate-change impact analysis.

In the lead-up to the fifth World Parks Congress in 2003, I was involved in a collaborative project that developed an alternative approach to assessing the representativeness of the world's protected area system, *i.e.*, the extent to which this system includes samples of all elements of biodiversity (Ferrier *et al.* 2004). The approach was intended to complement other assessments based on vertebrate distributions, biomes, and ecoregions. As in those assessments we used coarse-scale surrogates to provide a solid biogeographical foundation for our approach. However, we then added value to these surrogates by using higher-resolution mapping of environmental attributes to predict spatial patterns in biodiversity at finer scales (with a particular emphasis on non-vertebrate components of biodiversity). The link between biodiversity pattern and mapped environmental attributes was calibrated through statistical modelling of available biological and environmental data, based largely around the GDM approach to community-level modelling described above.

This modelling of biodiversity pattern was then used to assess the representativeness of protected

areas by integrating analytical techniques based on the species-area relationship and the 'environmental diversity' approach to conservation assessment (Faith *et al.* 2004).

Discussion

Various issues regarding model development were discussed. For example, it is a problem to model ecosystems that are not in dynamic equilibrium due to, *e.g.*, fragmentation, because it is often difficult to obtain independent survey sites to test the model. Ecosystems models often incorporate measures of species diversity, but it might — in some cases — be useful to include measures of genetic diversity as well. The question of scale was discussed. Most models may be applied on various scale provided the right predictors are available at the scale at question. Many good data sets are available today, but for this specific type of model good soil data are of great importance. The model presented here has — so far — been applied for terrestrial ecosystem, but might be applied for marine environments as well. The more theoretical aspects of whether to model the community as a unit or to model a community as the sum of species it is made up of was discussed. In a stable environment this may not be a problem because species will combine to a fixed community. A carefully selected approach, however, should be chosen when attempting to model community structure in dynamic environments. Discussants: **Rasmus Ejrnæs** (National Environmental Research Institute of Denmark) and **Volker Loeschcke** (Aarhus University).

Ecosystem services as affected by diversity

Jan Bengtsson

Department of Ecology and Crop Production Science, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

Ecosystem services are the benefits that humans directly or indirectly obtain from natural processes in natural or human-dominated ecosystems. Some examples of such processes are plant production, decomposition and nutrient mineralisation, biological control by natural enemies, pollination by natural pollinators (as opposed to feral honey bees), water purification, erosion control, regulation of atmospheric composition, recreation, *etc.* Ecologists usually prefer to discuss ecosystem services in terms of natural processes giving rise to valuable goods. Some economists would rather define ecosystem services as these goods, which can be valued directly or indirectly on the market – hence the ecosystem services in some of the preceding examples would rather be plant biomass or yield, produced by plants or animals, increased by the processes predation and pollination, nutrients, clean water, *etc.* At present, there is no stringent definition of ecosystem services that is unanimously agreed on by ecologists as well as economists. As an ecologist, I am most interested in the natural processes giving rise to valuable products that may or may not be valued on the market, and I will hence use a process-based perspective on ecosystem services.

Ecosystem services can, in theory, depend on diversity in two different ways: Firstly, the rate of a process contributing to the service can be affected by diversity. The simplest example, but also most contested and discussed, is how plant production (and hence yield) is dependent on plant diversity. There are at least three mechanisms behind such an effect — and all three are the subject of substantial controversy. If different plant species utilise different resources in the soil, or have different temporal (seasonal) growth patterns, then because of classical niche differentiation more plant species would entail higher diversity, although the effect is expected to level off (saturate) at fairly low levels of diversity. There could also be positive interactions between plant species, through, *e.g.*, mycorrhiza or nitrogen fixation, that could lead to a correlation between plant diversity and production. Finally, a sampling

effect may result in a higher probability of recruiting the most productive species from the regional pool, the more species are present locally. There is empirical evidence that plant production indeed increases with plant diversity, both in highly contrived experimental set-ups and in more natural grasslands, but it is far from overwhelming. Furthermore, let a goat loose and the correlation between diversity and production may disappear completely. My own interpretation of the available evidence is that processes like plant production, pollination or predation by natural enemies on pests measured under stable conditions will be affected, and yield often increased, by diversity in the organism group responsible for the processes. However, the effect is likely to saturate at low levels of diversity, and changes in trophic structure or presence of particular species may often have larger effects than diversity in itself. To use those studies to argue that overall biodiversity is important for ecosystem services is naive, and in fact few ecologists subscribe to this view.

Secondly, diversity may contribute to ecosystem services by supplying species performing the services under varying environmental and biotic conditions. If years vary in rainfall, some plant species will grow best under wet conditions and others will contribute most to production under dry conditions, because of trade-offs between plant traits and thus different responses to the environment. If a disease attacks the most important pollinator, or predators on the most common natural enemies to pests become common, other species can compensate for such temporal losses in a diverse local or regional community, but not in large-scale monocultures. Hence the response diversity that a diversity of species contributes is likely to stabilise the delivery of ecosystem services. Thus biodiversity can be viewed as an insurance against ecosystem service failures in a variable world.

While this is highly likely, there are several problems that need to be recognised. Most importantly,

since we cannot have full information on future environmental conditions, it is impossible to answer questions such as "which species will be needed?" Hence the insurance hypothesis is extremely difficult to test experimentally. Thus, while this effect undoubtedly is important, it is not very helpful in the particular cases that society wants to have recommendations for. Most politicians and stakeholders in society pay lip service to the "precautionary principle" but other short-term interests usually are given much larger weights when it comes to decisions about management and planning.

In both these cases (process rate effect and insurance effect of diversity) the diversity that is most likely to be important for ecosystem services is the "common diversity" – not the red-listed species that are the main focus of most conservation efforts today, although these species may become important under highly different circumstances. On one hand, this different focus could lead to a controversy among ecologists and conservationists — which species and ecosystems should be of highest priority? On the other hand, the importance of maintaining ecosystem services implies that the focus on red-listed species in set-aside reserves must be complemented with active conservation measures in many managed human-dominated production landscapes. Such an approach focussing on the common diversity may also be more likely to gain support from the public utilising ordinary urban and rural landscapes in their day-to-day activities.

There are a number of examples of diversity at the species or landscape (habitat, ecosystem) levels influencing the delivery of ecosystem services, although the evidence often is circumstantial and indirect. In several instances, a good case can be made for parts of biodiversity producing goods and services that are of economical value for landowners or farmers – usually in terms of marketable yield. Some examples that I will discuss are:

- Natural pollinators increasing yield in strawberries, fruit trees, and coffee, related to the occurrence of natural habitats.
- Natural enemies to pests may increase crop yield, and the magnitude of the effect may depend on landscape diversity.
- Higher plant diversity leading to higher long-term yield in hay meadows.

I am sure that there are other suggestive examples in the literature. However, my main point is that while it is likely that diversity (of what?) can affect ecosystem services (but which?), there is still a pau-

city of good observational and experimental studies (of mechanisms, in different ecosystems) to make the general case that biodiversity (defined as what?) is of crucial importance for ecosystem services and human welfare. The present evidence is not enough to convince not only the believers but also many of the sceptics. Perhaps this research area is at the stage that climate change research was at 20-30 years ago. Given the rate of land use change and potential loss of biodiversity, obtaining good answers to these questions are similarly pressing for society.

Discussion

Temperate zone ecosystems are not in equilibrium, whereas, in other parts of the world people depend on the natural environment. Robustness and resilience of degraded land in tropical areas are very low. At large scales areas with high biological diversity are correlated with areas with high population densities. What does that mean and is there a functional correlation? Maybe this is because of high numbers of endemics but sampling error may also play a role. As for the use of the concept of environmental services, would it not be more interesting to use an environmental damage approach instead of an environmental impact approach? Yes, we should understand these systems better and how they actually provide ecosystem services. How can we make better use of the issue of ecosystem services, *e.g.*, in evaluating the economic impacts and impacts on human well being of flooding and storms in mangrove forests? Maybe a new international convention is needed which would include the impact on biodiversity from climate change, and which would also deal with soil erosion and its control; in this context biodiversity may not be the best gate to demonstrate the usefulness of ecosystem services. What kind of data would be ideal for research on ecosystem services? The best data would be on species distributions, landuse change and data that would allow mechanistic understanding of ecosystem services. The last two presentations have both pointed to a dichotomy between naturalists versus economists which may not be useful - the two should be connected instead of separated. But there is a contradiction between, *e.g.*, population pressure and biodiversity, and biodiversity is the most important ecosystem service. Economists are not interested in the ecological process; they should be because ecosystem services are in decline. If economists do not become interested in an interdisciplinary process, ecology will loose out. The *Millennium Ecosystem Assessment* is an important step in

this direction, but it may be difficult to follow up on this assessment - we need more hard science - and ecologists must learn to talk to economists and to understand their thinking. One example of combining ecosystem services and biodiversity research would be to contribute data on common species;

many such data are collected in a broad collection of monitoring programs, and such data could appropriately be made available through systems such as the GBIF. Discussants: **Jon Fjeldså** (Zoological Museum, Denmark) and **Beatriz Torres** (GBIF secretariat).

Tools and techniques for biodiversity e-Science

Andrew C. Jones

School of Computer Science, Cardiff University, United Kingdom

There is a large variety of computer-based tools that have been developed in order to solve specific problems within biodiversity e-Science, including tools for such diverse tasks as phylogenetic analysis, *e.g.*, PAUP⁸ PHYLIP⁹ and ecological niche modelling, *e.g.*, BIOCLIM¹⁰ GARP¹¹. At present these tools do not generally make sufficient allowance for distribution of data, for its heterogeneity, or for the need to perform complex operations using data and tools from various sources in combination. Ironically, the ever-increasing amount of data available and the range of software that can be used to analyse it has made it more — rather than less — difficult than in the past to ensure that the analyses being performed are based on accurate data, and on accurate interpretations of this data which may be stored using differing resolutions, scientific names, descriptive terminology, *etc.* The amount of effort required to manually prepare data for stand-alone desktop tools is also becoming increasingly unacceptable as data volumes increase. Similarly, as scientists develop new ways of using data of different kinds (*e.g.*, biodiversity data at the ecosystem and at the organismic level), the range of standards and conventions used to represent data that overlaps these domains increases, and mappings between these domains become ever more important.

There is therefore an urgent need for integrated environments that allow scientists to discover distributed, heterogeneous data and software that can analyse this data, and to combine them to perform interesting analyses. There is also the need for a computing infrastructure to support these tasks — middleware that transforms data, reasons with descriptive information (metadata) about the data, *etc.* These environments and middleware need to be as generic as possible, so that they can be applied to a wide range of problem-solving tasks. Here, some recent developments in these two areas (integrated environments and interoperation middleware) are described and, in particular, some of the relevant research the author has participated in is discussed.

In the BiodiversityWorld project¹² (Jones *et al.* 2005) we have been investigating the general problem of providing an integrated environment for biodiversity research, but also providing supporting middleware. We provide a workflow-based user interface, based on Triana¹³ that allows users to discover resources — be it data sources or software that processes and analyses data — and compose them into workflows. These workflows provide a powerful means of capturing scientific processes, and ‘what if?’ experiments can readily be performed, *e.g.*, by replacing a particular analytic tool such as an implementation of GARP by a different one such as BIOCLIM, or by using alternative data sets (*e.g.*, for specimen distributions), or by reorganising the workflow to represent a revised scientific process.

In order for resources to be discoverable and usable in this way, middleware providing some kind of interoperation framework is required. In BiodiversityWorld we provide the Biodiversityworld-Grid Interface (BGI), which provides a standardised interface to resources. For existing resources that do not currently implement this interface, a wrapper is typically created to implement it. A metadata repository stores information about the resources in order that resources can be discovered meeting the user’s requirements, *etc.*

There are a number of related projects, including SEEK¹⁴ and (in a slightly less related application domain) myGrid¹⁵. In particular, these projects have some kind of workflow environment associated with them, and varying degrees of effort are made to provide interoperability. It is becoming increasingly common for facilities to be made available as web services, and some workflow-based systems (including Triana) can interact with these. BiodiversityWorld and these other projects all provide a basis for sophisticated experimentation and computation with various kinds of data, but some aspects of these systems remain fairly crude at present.

⁸<http://paup.csit.fsu.edu/>

⁹<http://evolution.genetics.washington.edu/phylip.html>

¹⁰<http://cres.anu.edu.au/outputs/anuclim/doc/bioclim.html>

¹¹<http://biodi.sdsc.edu/Doc/GARP/Manual/manual.html>

¹²<http://www.bdworld.org/>

¹³<http://www.trianacode.org/>

¹⁴<http://seek.ecoinformatics.org/>

¹⁵<http://www.mygrid.org.uk/>

Although workflow systems provide environments which are to some extent integrated, current workflow environments potentially hinder exploratory experimentation, because of the intellectual overhead associated with designing, constructing and executing workflows. This is not a problem if a particular analytic process is to be repeated again and again, but it is a problem in situations where the user is trying to do something new. We propose that workflow environments be extended to support a more exploratory manner of interaction where, for example, a user might be able to try out some small subtasks and join results together, making use of a record kept transparently (but in a way that can be explored by the user) of interactions and important intermediate results. The system could be supported by a knowledge base and inference mechanism that could anticipate ways things might be combined, making it easier to compose re-usable workflows, and making it possible to generalise or specialise workflows as required. (For more details see¹⁶).

Another area in which work remains to be done is in interoperability, and the middleware needed to support this. It is important to provide interoperability so that systems that are heterogeneous in some aspects can be used together. For example, species data may be stored in a number of different formats and accessed using a variety of protocols. The BiodiversityWorld system provides an interoperation framework, and Web Services also provide a basis for interoperation: a combination of wrappers which present resources according to agreed standards (protocol, data format, *etc.*) and metadata that describes these resources can be effective in achieving interoperation in many circumstances. We have demonstrated this in BiodiversityWorld and in the SPICE for Species 2000 system (Jones 2000). This latter system comprises a federated catalogue of life, where a number of databases holding sectors of the catalogue in a variety of formats are made available to the SPICE common access system via wrappers which transform the data to conform to a common data model. But sometimes it is difficult or inappropriate to define a common data model, or to define the transformations needed between representations. This kind of interoperation (semantic interoperation) is an area where ontologies play an important role, defining terms and relationships between terms. An important development of which we are aware is the BioCASE thesaurus¹⁷, but further work

is required to establish ontologies relating to the various kinds of subject matter (*e.g.*, species-related, climate-related, *etc.*) of interest to biodiversity researchers, and in particular to build links between these ontologies.

We have addressed — and are continuing to address — some issues specific to interoperation of biodiversity data, and the specialised middleware needed to achieve this integration, in the LITCHI and myViews projects. In LITCHI (Embury *et al.* 1999) we have investigated the problem that experts differ in their classification of organisms, and these differences are reflected in the scientific names that are used for these organisms. We have taken advantage of the fact that there are conventions on naming of organisms, many of which are imposed by the codes of biological nomenclature as rules that must be conformed to, in order to develop constraints on what can comprise a consistent taxonomic checklist of species names and synonyms. The result of this process can either be a checklist in which inconsistencies have been removed, or a cross-map between different checklists. The latter is particularly useful, in that it can be potentially used in the retrieval of data that has been stored according to differing taxonomic views: the user's scientific name is mapped onto the one that has been used in a given data set. Others have approached this problem from a somewhat different angle. For example, in the Prometheus project¹⁸ (Pullan *et al.* 2000) and the role that scientific opinion relating to individual specimens in classification is emphasised.

Scientific naming is an example of a more general problem, namely that there is diversity of scientific opinion and this is reflected in the way that information regarding specimens, ecological information, *etc.*, is expressed. In the myViews project Jones (2006a) we are starting to explore techniques for working with data from sources reflecting differing scientific viewpoints and opinions. In particular, in information retrieval we (a) allow users to be selective and (b) transform between users' viewpoints and those underlying the data stored, as far as possible, both for querying the data and (if the user wishes) for presentation of the data to the user. A small prototype has been implemented, and we are currently exploring representational and inferential issues, especially with respect to scalability.

More detailed discussion of lessons learned in the biodiversity informatics projects that the author has

¹⁶http://www.nhm.ac.uk/hosted_sites/tdwg/2005meet/TDWG2005_Abstract_37.htm

¹⁷<http://www.biocase.org/Doc/Results/results.shtml>

¹⁸<http://www.dcs.napier.ac.uk/~prometheus/>

participated in, and discussion of areas for future work, can be found in Jones (2006b). But in conclusion, much progress has already been made towards making biodiversity data available and interoperable, and one of the most important developments has been the emergence of Web Services. Techniques that have been employed only in relation to some aspects of biodiversity e-Science could be extended to deal with other specific problems encountered in biodiversity science at the ecosystems level. It is to be hoped that future developments will be increasingly generic in nature, so that tools for data analysis, data curation, *etc.*, will not so frequently need to be built from scratch. Environments such as BiodiversityWorld are a first step towards achieving such genericity, and towards providing integrated environments and middleware to support biodiversity e-Science.

Discussion

The discussion focussed on the potential benefits the research community may expect from web-based data base technologies. Such systems should, above all, be easy to use and assist the user retrieve and analyse biodiversity data from the intricate network of distributed data bases in various formats. Many tools and a lot of data are already available, but it is necessary to provide links and translations between them. The development of systems should be open and user driven. If, for example, end users wish to make use of Natura2000 data for scenario building, it should be made possible. The key to the success of such systems is their modularity. It is also feasible to build in dynamic quality control in such systems. Here GBIF may play an important role in relation to check of specimens and taxonomy. Discussants: **Juan Carlos Bello** (Ark 2010 Project) and **Mihail Constantin Carausu** (DanBIF secretariat).

Conclusions

Martin Sharman

European Commission, Brussels, Belgium

Henrik Enghoff

Danish Natural History Museum, Copenhagen, Denmark

The main aim of the conference was to answer three questions:

1. What is biodiversity at the ecosystem level?
2. How is it related to biodiversity at other levels of organisation?
3. How may GBIF deal with ecosystem level data and informatics?

1. What is biodiversity at the ecosystem level?

There are two senses of the term 'ecosystem': one relates to nutrient and energy flow and processes, the other to species assemblages and their interactions. The latter, the ecosystem type, seems most appropriate in a GBIF context. But we should remember, that the term 'ecosystem' is both a scientific and a social construct. A social construct allows us to communicate and discuss or to assemble or retrieve data on specimens using key words (*e.g.*, find all specimens of plants collected in rain forests). Social constructs are rarely well defined with exact boundaries as required by scientific constructs that (ideally) possess measurable characteristics that allow them to be unambiguously and repeatably classified. There are not many examples of true scientific constructs in the real world, where classes tend to be fuzzy and gray rather than black and white. This is also the case of ecosystems.

Descriptors of ecosystem diversity may relate to ecosystem composition (species richness, alpha, beta, and gamma diversity, indices of similarity/dissimilarity) or ecosystem function (ecosystem services, ecosystem 'health'). When ecosystem biodiversity deals with species assemblages and their interactions, then availability of basic, organismic level data (specimens, species observations) is essential for scientific understanding and progress. But many other ecological diversity parameters

relate to organismic level data and are useful for understanding species assemblages and their interactions. These include plant life form (trees, shrubs, herbs, epiphytes, lianas, annuals/perennials), grazers, browsers, *etc.*, pelagic, benthic, infauna/epifauna, *etc.*, reproductive strategies (fecundity, generation time, r- vs. K selection, dispersal ability, metapopulation dynamics). When it comes to ecological processes, some relate closely to species assemblages and their interactions, such as predator-prey relations, parasitism, hyperparasitism, mimicry, pollination, seed dispersal, decomposition, symbiosis or commensalism. Others, such as metabolisms (photosynthesis, *etc.*), energy and nutrient flows are less easily connected to specimens and species observations. Finally there are some abiotic-biotic interactions in the ecosystems that are less easily related to species assemblages and interactions such as oxygen production, soil formation and landscape structuring.

It is not possible to compare ecosystems without comparing species and their interactions. Therefore, 'ecosystem diversity' may be confusing and probably not a very useful concept and certainly not a scientific concept. What matters is what questions you want to ask about the species occurrence.

Is the use of 'ecosystem' really necessary? If we are interested in a number of species and have a limited, but reasonable number of records it is possible to use modelling techniques to predict their presence and assemble (or model) the collective biodiversity properties of a system. In other cases we are interested in biodiversity as a whole and may use databases with huge numbers of species, even though each species only may be represented with few records.

2. How is biodiversity at the ecosystem level related to biodiversity at other levels of organisation?

Ecosystems are composed of organisms in a specific physical setting. Ecosystem diversity is related to other levels biological diversity, but the relationship is not a simple, hierarchical one, which may be the reason that ecosystem diversity remains such an elusive concept.

The ecosystem is an abstraction based on the questions you want to ask and of data on species occurrence and their interactions. It reduces options as it involves the establishment of discrete classes, replaces real gradients with sharp edges and produces an irreversible one-way mapping.

3. How may GBIF deal with ecosystem level data and informatics?

One of GBIF's short- to medium-term priorities is to build a species bank that will contain all types of information which can be linked to individual species. Therefore, ecological diversity can "easily" become GBIFed. But GBIFication of ecosystem diversity would be a huge challenge to ecologists and computer scientists.

To make GBIF a data provider that covers ecosystem biodiversity, biodiversity would be needed. This could be based on 'raw' specimen data, but later on they should include aggregated data for communication in the form of ecosystem maps. It would be very important not to lose information in this data aggregation process! More maps of the physical environment (soils, topography and climate) would also be useful. Finally, it would be

important to standardise mapping in order to avoid incompatible assemblages of national maps.

In the context of species data bases: Ecological data are important in order to be able to calculate the niche space of species. Contextual information, both abiotic and biological, generally adds value but such systems should allow users to make their own decisions and data should not be aggregated irreversibly.

More knowledge is needed on the interactions between the distribution of biodiversity and the environment in order to improve modeling. Furthermore, much more focus is needed on the science-policy interface. What are the environmental, social and economic values and benefits of biodiversity? And how may scientific knowledge be translated into useful guidelines for biodiversity protection.

Do not provide modeling tools for public use. Leave the modelling to the specialists. Rather point to where the expertise is found.

We need data, data and more data (species presences, interactions and dependencies, abiotic, etc.)

'Don't neglect the common species' - Ulla Pinborg

'The term 'ecosystem diversity' should be avoided, if you want a message' - Janne Bengtsson

*The biodiversity at the ecosystem level song
There are ecosystems, ecosystems, services, diversities...
and habitats, communities and similar perversities...
and micro-/macro-creatures like bacteria and elephants...
and HIPPO, GBIF, DanBIF, and....
a bunch of nice participants*

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National Environmental Research Institute
Frederiksborgvej 399
PO Box 358
DK-4000 Roskilde
Denmark
Tel: +45 4630 1200
Fax: +45 4630 1114

Management
Department of Arctic Environment
Department of Atmospheric Environment (main address)
Department of Environmental Chemistry and Microbiology
Department of Marine Ecology (main address)
Department of Policy Analysis

National Environmental Research Institute
Vejlsovej 25
PO Box 314
DK-8600 Silkeborg
Denmark
Tel: +45 8920 1400
Fax: +45 8920 1414

Department of Freshwater Ecology
Department of Marine Ecology
Department of Terrestrial Ecology

National Environmental Research Institute
Grenåvej 14, Kalø
DK-8410 Rønde
Denmark
Tel: +45 8920 1700
Fax: +45 8920 1514

Department of Policy Analysis
Department of Wildlife Ecology and Biodiversity

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BIODIVERSITY AT THE ECOSYSTEM LEVEL – PATTERNS AND PROCESSES

Proceedings of the 2nd DanBIF conference
26-27 April 2006, Aarhus University

This publication contains the presentations and discussions from the second DanBIF conference, entitled Biodiversity at the Ecosystem Level – Patterns and Processes. The questions asked at this conference were: What is biodiversity at the ecosystem level? How is it related to biodiversity at other levels of organization? How may GBIF deal with ecosystem level data and informatics? The conference had two important goals. The first was to present an overview of contemporary research related to ecosystem level biodiversity and the second was to help GBIF formulate a strategy for dealing with biodiversity above the species and molecular levels and make data available for the end-users.

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