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Introduction

Biological diversity in a changing world

Anne E. Magurran[1,*] and Maria Dornelas[2,3]

[1]*School of Biology, University of St Andrews, St Andrews, Fife KY16 8LB, UK*
[2]*CESAM, Department of Biology, Universidade de Aveiro, Campus de Santiago, Aveiro 3810-193, Portugal*
[3]*ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia*

From the pioneering explorations of Joseph Banks (later a President of the Royal Society), to the present day, a great deal has been learnt about the extent, distribution and stability of biological diversity in the world. We now know that diverse life can be found even in the most inhospitable places. We have also learned that biological diversity changes through time over both large and small temporal scales. These natural changes track environmental conditions, and reflect ecological and evolutionary processes. However, anthropogenic activities, including overexploitation, habitat loss and climate change, are currently causing profound transformations in ecosystems and unprecedented loss of biological diversity. This series of papers considers temporal variation in biological diversity, examines the extent of human-related change relative to underlying natural change and builds on these insights to develop tools and policies to help guide us towards a sustainable future.

Keywords: biodiversity; species richness; time; threat; speciation; extinction

1. INTRODUCTION

Ecology is in essence a quantitative discipline. It is underpinned by careful observations of the natural world, revealing for example that insect species richness is higher in tropical habitats than in temperate ones (Bates 1863), and that ecological communities invariably have a few common and many rare species (Darwin 1859). Ecologists use these data to understand how populations and communities are structured and to make predictions about how ecological systems might change over space or time, or in response to external forces. As May (2010) has recently pointed out, these sorts of investigations were largely absent in the first hundred years of the Royal Society. It was only through the pioneering endeavours of researchers such as Joseph Banks, who was President of the Royal Society from 1778 until 1820, that data on natural patterns began to be assembled. Banks was a remarkable man (O'Brien 1987); politically well connected, he was an influential supporter of groundbreaking scientists such as William Herschel and Humphrey Davy (Holmes 2009). However, it was botany that was Joseph Banks's first love. Banks joined the *Niger* in its voyage to Newfoundland in 1766, when he was 23, and although his primary goal was cataloguing and collecting plants, he often noted whether a species was abundant or scarce, as well as recording the similarities between this flora and the one he was familiar with in England.

Banks's approach, and the journals he wrote, presaged the work of Darwin, Bates and Wallace and subsequent generations of researchers. While Darwin is rightly celebrated for his contributions to evolutionary biology, he also made significant contributions to what we would now call ecology through his comments on issues such as the relationship between range size and abundance. Like other early researchers, Darwin was primarily concerned with documenting patterns, but also willing to consider process. For example, in the *Origin of Species*, he reflects that:

> ....we forget that each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food; and if these enemies or competitors be in the least degree favoured by any slight change of climate, they will increase in numbers; and as each area is already fully stocked with inhabitants, the other species must decrease.
>
> (Darwin 1859, p. 84)

At the time of Banks's voyages, the world's population was somewhere in the range of 700 million (http://www.census.gov/ipc/www/worldhis.html), and an order of magnitude less than the current level. It was also a time when human technology had a relatively modest impact on the environment. Explorers could find regions and even continents that were essentially untouched. The contrast with today is marked and, as Chown (2010) makes clear, the imprint of our species on natural landscapes is substantial. Indeed, Chown points out that so-called 'anthropogenic biomes' now cover over 75 per cent of ice-free land, and human activities affect even those few remaining 'wild areas'.

We still have a very incomplete record of the biological diversity of the planet. Mammals and birds are reasonably well documented, plants, amphibians,

* Author for correspondence (aem1@st-andrews.ac.uk).

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reptiles and fish less so, many invertebrate species remain to be described, while microbes are a largely unexplored frontier. However, there is no doubt that this biological diversity is under threat as a result of anthropogenic change. Widespread concern about the extent of habitat and species loss led the United Nations to declare 2010 as its International Year of Biodiversity (http://www.cbd.int/2010/about/) while governments and non-governmental organizations recognize that the conservation of biological diversity is a major policy issue.

Although there are very strong indications that the current rate of species extinctions far exceeds anything in the fossil record (Lawton & May 1995; May 2002), a major challenge is assessing the extent of short-term and often local changes in ecological communities relative to the underlying or baseline change that all communities experience. This is essential because the human population, through its resource use and technology, can cause rapid changes in ecosystems. Additionally, conservationists working over short time scales need to know whether the practices they have implemented have made a difference. There is no question that large-magnitude events such as glaciations, vulcanism and sea-level rise profoundly affect the organisms involved, but less appreciation of the fact that ecological communities naturally vary through time. Darwin, in the quote above, considered the species rearrangements that might occur as a result of ‘any slight change of climate’, while MacArthur & Wilson’s (1967) influential ‘theory of island biogeography’ is underpinned by the observation that immigration and local extinction are not just universal, but also play a major role in structuring communities. Both environmental variability and the continuous colonization and extinction of communities create natural variability of biodiversity in space and time. Despite this, there is a pervasive view that habitats and assemblages are unchanging rather than acceptance that some change, including local species loss, is inevitable. Separating anthropogenic change from the ongoing baseline change is not always easy, not least because we have a limited understanding of how communities vary through time, and the processes that are involved in this variability.

This volume, and the accompanying discussion meeting, examines biological diversity in a changing world. We take the lead from a classic ecology paper by Watt (1947) by first considering patterns of change, and then exploring the processes that are involved in shaping these patterns. The final set of papers address the policy issues linked to natural and anthropogenic change.

(a) *Pattern*

The study of pattern forms the backbone of ecology. Knowing how species are distributed in space and time is the first step towards understanding how these patterns arise, and any model or theory of biodiversity must, of necessity, be able to reproduce these empirical distributions of organisms. There is an extensive literature relating to spatial patterns such as latitudinal gradients of diversity (Willig *et al.* 2003), species area relationships (Arrhenius 1921) and range size distributions (Gaston 1996). In contrast, less attention has been paid to temporal patterns of biodiversity (though studies of succession are a notable exception). One reason for this is that long-term investigations of ecological assemblages, particularly with the goal of monitoring background turnover, are not especially attractive to funding agencies, and do not fit neatly into grant cycles, or even the career span of a single researcher. There are notable exceptions of course, including the Park Grass Experiment (Silvertown *et al.* 2006), and the Continuous Plankton Recorder (Richardson *et al.* 2006), and an upsurge in new long-term monitoring projects such as the Long Term Ecological Network (www.lternet.edu) and the National Ecological Observatory Network (www.neoninc.org). Researchers often use spatial patterns as a surrogate for temporal ones—but these are not necessarily equivalent. There is an urgent need to develop a fuller understanding of temporal patterns of diversity and to devise improved methods of assessing these. This is the subject matter of the introductory group of papers.

Ever since R. A. Fisher, who proposed the first ‘index of diversity’ (Fisher *et al.* 1943), researchers have been developing metrics that can be used to summarize the biological diversity of an assemblage or sample. Traditional measures focus on species richness and the relative abundance of species, but these approaches make no distinctions among the species involved. Many investigators and conservation managers would like to use an index that takes the taxonomic status, or phylogenetic relatedness, of species into account and a growing number of measures are being developed to meet this need. Our issue begins with a paper by Anne Chao and co-authors (Chao *et al.* 2010) who introduce a new class of phylogenetic diversity measures sensitive to species abundances and phylogenetic distance, and that can be applied over any time interval of interest. These measures have the potential to uncover shifts in the phylogenetic structure through time, for example in response to a change in management practice. This could be particularly crucial in cases where species richness has not changed through time.

Although it is clear that individual species abundances can vary quite markedly, there have been relatively few attempts to track temporal patterns in ecological assemblages as a whole. Magurran & Henderson (2010) examine a three-decade time series of estuarine fish and show that individual species abundances fluctuate asynchronously through time. The overall structure of the assemblage, in terms of its relative abundance distribution, is however maintained through this period. Simulations reveal that this distribution remains stable across a wide range of temporal turnover scenarios. An interesting finding is that metrics that track species ranks appear to be more sensitive to changes in community structure than diversity measures that ignore species identity.

Gotelli *et al.* (2010) are also interested in temporal trends in assemblages, and develop a novel bootstrapping procedure that can be used the identify sets of species that are either increasing or decreasing—as well as those that remain constant in abundance.

These approaches are tested using long-term data collected on stream fish and grassland insects, and reveal marked temporal reorganization—even in the assemblage (of fish) that experienced no obvious physical changes. Importantly, these methods take account of incomplete sampling and imperfect detection and thus address one of the most difficult issues in biodiversity assessment.

In the next paper, White *et al*. (2010) examine the linkages between spatial and temporal patterns of species richness. They note a strong interaction between species–area and species–time relationships, discuss the theoretical underpinnings of this and emphasize the contribution that an integrated spatio-temporal approach to species richness can make to explaining ecological and palaeontological patterns of diversity and to understanding how natural communities will respond to global change.

As noted earlier, the Earth's biosphere is still very incompletely documented, and when knowledge is sparse, it becomes impossible to document change. One of the least studied realms is the air, which Womack *et al*. (2010) argue should be considered a habitat in itself as it supports a rich assemblage of micro-organisms. They make a strong case from drawing on biogeographic and macroecological approaches and using these to identify and interpret patterns of distribution and abundance in these taxa over space and time.

(b) *Process*

Elucidating the processes that shape the patterns of biological diversity that we find in the natural world is not just an important fundamental challenge but also provides the tools that allow researchers and policy makers to predict and manage change. This goal can be achieved through a range of approaches, including the search for regularities and associations between variables through time, reviewing and synthesizing available information about specific ecosystems and developing mechanistic models to predict how ecological and evolutionary processes affect biodiversity patterns. These different approaches provide complementary insights needed to fully understand how biodiversity patterns are generated.

One way of understanding contemporary patterns is to look back and examine biodiversity in deep time. Benton (2010) explores the origins of modern biodiversity on land and contrasts two approaches to view this issue: a phylogenetic expansion view, which focuses on describing how and when current phylogenies were formed, and an equilibrium view, which focuses on developing density-dependent global scale models as general rules for the origins of biodiversity patterns. The paper argues for the former and points out that most land diversity is due to a subset of groups in which there is an increased rate of diversification, and that the availability of empty ecospace has helped shape current patterns.

Palaeontological investigations shed light not just on diversification but also on shifts in species distributions and on species extinctions. The Late Quaternary represents a natural experiment that reveals how species responded to climate change at a time when glaciers were expanding and contracting. Lyons *et al*. (2010) find that there are no differences in the extent of range shifts between the survivors and victims of the megafaunal extinction that occurred at this time. However, body size, lifespan and topography are linked to range shifts in Late Pleistocene mammals and are factors that should be considered in studies that assess the ecological consequences of contemporary climate change.

Species may also respond to climate change by changing their elevational range to track their optimal environmental conditions. Colwell & Rangel (2010) develop a model to explore the relative roles of ecological and evolutionary processes in range shifts and species richness patterns on tropical elevational gradients along Quaternary glacial and inter-glacial cycles. This model can generate a diverse array of patterns, which a comparison with empirical data reveals are realistic. Model results highlight that species richness profiles are strongly affected by temporal asymmetries in environmental conditions, and spatial asymmetries in area along the elevational gradient. The fact that glacial periods have lasted considerably longer than inter-glacial periods in the recent (geological) past means that current tropical species are better adapted to cope with cooling than with warming climates. This is extremely worrying given the current climatic trends.

Extreme environments provide a complementary set of insights into evolutionary and ecological consequences of climate change. Clarke & Crame (2010) consider the diversity of polar assemblages and note that the much higher richness of tropical communities is due to the presence of large numbers of rare species. Indeed, it appears that this characteristic latitudinal gradient of richness has a long history. Clarke and Crame highlight a major unresolved issue—that is the extent to which the marine benthos was able to survive in refugia at glacial maxima—but also observe that the fact that lineages can be traced back to the Mesozoic points to the survival of assemblages *in situ*. Moreover high-latitude glaciations, through their influence on sea level, have contributed to the diversification of tropical and deep-sea faunas.

Tropical forests are repositories of a large fraction of the Earth's biological diversity. They are also being degraded at unprecedented rates. It is estimated that around half of the tropical forest present at the beginning of the twentieth century has already been lost, with the peak deforestation occurring in the 1980s and 1990s. To date, most attention has been given to species extinctions and the reduction in species richness. However, it is not just the species but also the interactions between them and the networks they form that are important in ensuring ecosystem function. Morris (2010) reviews this important field with particular emphasis on the link between network structure and ecosystem functioning. She stresses the importance of large-scale experiments and improved theory and emphasizes the role that this work will play in ameliorating the impact of human activities on tropical forests.

We know that ecosystems are increasingly impacted by a plethora of disturbances, which often have dramatic consequences for biodiversity and ecosystem functioning. Dornelas (2010) develops a theoretical framework to explore how ecological disturbances change biodiversity patterns. In this framework, disturbances are defined by their effects on community dynamics. A simple classification then arises based on which demographic rates are affected by the disturbance. The models developed show that this classification can help predict whether and how biodiversity is changed by a disturbance. The model also shows that disturbance that affects carrying capacity has the most severe and lasting consequences. Moreover, isolated communities are more severely affected by disturbance regardless of its type.

(c) *Policy*

New insights into patterns of biological diversity through time, and the processes that drive these patterns, can help formulate effective environmental policy and foster conservation and sustainable practices. The final section of the issue considers four contexts that highlight the linkages between pattern, process and policy.

Chown (2010) is primarily concerned with terrestrial systems, and he approaches these from a southern Africa perspective. Africa faces particular challenges as it has some of the fastest rates of human population growth, climate change and tropical forest loss, combined with limited science funding. As might be expected, southern Africa is undergoing rapid change, and although there are instances where human activities have been beneficial, in most cases they are associated with substantial degradation of natural habitats and communities. That this should happen in a part of the world noted for its high biodiversity is sobering. As Chown notes, there is a case for allocating all available resources to conservation rather than continuing to document biodiversity change. However, he concludes by arguing that well-targeted studies can result in rapid realignment of policy, and thus aid conservation efforts.

While it is clear that global biodiversity is declining as a result of anthropogenic activities, there can be considerable variation among species and populations in the rate of change, and this may be hidden in summary statistics. The identity of the most rapidly declining species can change through time, as can the causal processes that underlie biodiversity loss. Mace *et al*. (2010) use two large datasets to tease these factors apart and identify species that can be classed as winners and losers. They find that anthropogenic change and associated threats are better predictors of trends than ecological or life-history variables. Efficient and proactive conservation planning needs to take account of these complexities.

Flexibility and ability to adapt are also needed to ensure a sustainable future for world fisheries in face of the challenges posed by climate change. MacNeil *et al*. (2010) review available knowledge to try to predict the consequences of current climate trends. They conclude that tropical fisheries are likely to lose species and yield, temperate fisheries are likely to change their species composition and polar fisheries are likely to increase in diversity and yield. These changes will have to be taken into account in fisheries management, to avoid conflicts between winners and losers. Moreover, tools must be developed to allow human populations to adapt.

The issue concludes with a paper by Jackson (2010), who paints a stark picture of the current state of the oceans. Major changes in the marine environment are nothing new—the fossil record reveals that even small shifts in productivity and climate can be associated with substantial ecosystem change, including mass extinction. What is different today is that a single species is responsible. Exploitation—including overfishing—pollution and the rise in carbon dioxide are individually and jointly fostering what appears to be an irreversible change, and the impact of humanity on the oceans makes another mass extinction seem inevitable. Jackson's paper highlights the biggest challenge of all, and that is the urgent but difficult task of drawing together the growing body of knowledge on pattern and process, and using this to develop policies that can help conserve biological diversity in a world that is changing in ways without precedent.

2. CONCLUSIONS

The planet has always been changing: current patterns of biodiversity are the result of past environmental conditions and ecological and evolutionary constraints (Benton 2010; Clarke & Crame 2010; Lyons *et al*. 2010). However, current rates and sources of change pose scientists and people in general with new challenges (Chown 2010; Jackson 2010). We must incorporate change into the way we view biodiversity, and learn to distinguish between necessary change and change we should aim to avoid or at the very least mitigate. Extinction *per se* is an inevitable (and perhaps necessary) process in the balance of the biological diversity contained in the world. It is the mass extinction currently underway, caused by overexploitation of natural resources, that needs to worry us. Similarly, environmental change has always been prevalent, and has helped shape biodiversity patterns of today. In contrast, never before has a single species driven such profound changes to the habitats, composition and climate of the planet. To deal with the challenges raised by these large-scale and intense modifications of the planet, we need to develop quantitative tools to quantify (Chao *et al*. 2010; Gotelli *et al*. 2010; Magurran & Henderson 2010) and understand (Colwell & Rangel 2010; Dornelas 2010) change; we must document change at multiple scales of space, time and organizational levels (Morris 2010; White *et al*. 2010; Womack *et al*. 2010); and we must develop management tools that take change into account (Mace *et al*. 2010; MacNeil *et al*. 2010).

> *Se vogliamo che tutto rimanga come è, bisogna che tutto cambi!*
>
> If we want things to stay as they are, everything must change!
>
> (Tomasi di Lampedusa, Il Gattopardo)

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