Evolution and Biodiversity:

The evolutionary basis of biodiversity and its potential for adaptation to global change

Report of an electronic conference, March 2010

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The changing landscape (Peyresq, southern France). Allan Watt, CEH Edinburgh.

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Mallorca, 13-15 April 2010

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Preface

Research on biodiversity is essential to help the European Union and EU Member States to implement the Convention on Biological Diversity as well as reach the target of halting the loss of biodiversity in Europe by 2010.

The need for co-ordination between researchers, the policy-makers that need research results and the organisations that fund research is reflected in the aims of the European Platform for Biodiversity Research Strategy (EPBRS), a forum of scientists and policy makers representing the EU countries, whose aims are to promote discussion of EU biodiversity research strategies and priorities, to exchange information on national biodiversity activities and to disseminate current best practices and information regarding the scientific understanding of biodiversity conservation.

This is a report of the E-Conference entitled Evolution and Biodiversity: The evolutionary basis of biodiversity and its potential for adaptation to global change preceding the EPBRS meeting to be held under the Spanish EU presidency in Palma, Mallorca, from the 12th-15th April 2010.

Introduction

Joachim Mergeay, E-Conference Chair

We are facing global changes that are unprecedented in the history of humanity, but that we have caused ourselves. We have created a world where the influence of a single species is omnipresent in all realms and ecosystems. Pollution, overexploitation, habitat loss and fragmentation, invasive species and climate change are the main causes of global change, and as a corollary, current biodiversity loss. Jointly they form a multitude of stresses on life on this planet.

The main question is not whether life on earth will adapt to global change, because it will. Life inevitably finds new pathways to cope with change. The issue is rather how this will happen. What does a relatively sudden and massive interference into such ecosystems do with the stability and functioning of these ecosystems, and what is the role of evolution in the responses to global change?

In contrast to the dynamic evolutionary flux that characterizes life, our view on biodiversity and ecosystem functioning has mainly been a static one, trying to conserve biodiversity as it is, and preferably, as it was. Given the pace and magnitude of global change we are imposing onto our world, we need to be able to predict how life will change as a result of our own actions. We will still need the same ecosystem functions and services tomorrow, so we will need to know if and how these will be altered by our actions. That is a serious challenge.

In the "United Nations international year of biodiversity" we should get to the evolutionary sources of biodiversity itself, and rethink biodiversity in all its aspects. We need to understand how evolution shapes diversity, from genes to ecosystems. How diversity originates, how functions originate, and how they are affected by change. How biotic interactions originate and how we can maintain the ecosystem services we badly need in spite of the changes we impose on life.

We live in an era where science policy makers and science funding agencies are focusing more and more on direct applications and short term return-on-investment. But for science to provide solutions to the biodiversity crisis and its associated social and economic consequences, we first need to understand the processes that generate and maintain biodiversity in the face of global change. This was the key issue of this e-conference.

The e-conference covered three main topics, one per week of the e-conference:

Session 1: The evolutionary basis of biodiversity - strategies to manage and preserve evolutionary processes, and their likely impact on biodiversity
This first session focused mostly on the lowest levels of biodiversity (genes and individuals). We started by considering the role of evolution in biodiversity from a human perspective, and then looked in more detail at:

- New genomic techniques and their applications in conservation biology
- The genetic basis of phenotypic evolution
- Non-genetic inheritance mechanisms (epigenetics)
- Genetic and genomic studies of a biodiversity hotspot
- How rapid evolution affects invasive species as well as species in invaded biota

Session 2: Evolutionary responses to global change
This session focused on how populations respond to global change, and how this affects relatively simple biotic interactions. In particular it addressed:
- Landscape-level impacts on ecological and evolutionary change
- Genetic consequences of habitat fragmentation on populations
- Past climate change and the reconstruction of its effects
- Present-day rapid evolutionary responses to climate change, and predicting evolution
- The challenging task of accurately distinguishing evolutionary responses from other confounding factors

Session 3: Evolution in complex systems and co-evolutionary networks: managing complexity in the face of uncertainty
This session aimed mostly at understanding evolutionary dynamics in communities and ecosystems, and the feedbacks between ecological and evolutionary processes. In particular it focused on:
- How we should tackle the interaction between ecology and evolution at various levels of biotic organisation
- How we can learn from non-biological complex networks to better understand the evolution of biotic complexity, and try to find general patterns into complex multi-species interactions
- How ecological processes influence evolution and vice-versa
- Coevolution in complex environments
- The theory of geographic mosaic of coevolution
- How to manage biotic complexity in the face of uncertainty

The keynote contributors to this e-conference were globally distributed, and came from a wide gamut of scientific backgrounds, including social, life and environmental sciences, with geneticists, ecologists, evolutionary biologists, palaeontologists and philosophers. We hoped to bring a broad and interdisciplinary view on evolutionary research, with new ideas, challenging perspectives and urgent research needs. Above all, we hoped this e-conference would be intellectually stimulating, interesting and fun.

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Summary of contributions

Joachim Mergeay and Fiona Grant

Summary for week 1: 'The evolutionary basis of biodiversity'

The evolutionary basis of biodiversity was discussed in the first week of the e-conference. A central question inherent to this topic was what should motivate society to conserve biodiversity. Stefaan Blancke and Felix Rauschmayer put forward the need to conserve biodiversity for moral reasons. Stefaan Blancke also emphasised the need to conserve biodiversity for the ecosystem services that it provided to human society. François Bonhomme, however, argued that there was a risk that the latter view would dominate science policy and political and economic decisions.

As mentioned in Stefaan Blancke's keynote, viewing biodiversity in evolutionary terms was a step forward with regards to the rather static view that had dominated our perspective in the past. This view had also led to a fixed systematic view on biodiversity that was rightly questioned by Pierre-Henri Gouyon, thereby honouring again the legacy of Charles Darwin. We have long thought of evolution as an extremely slow process, and have too often only regarded it on a macro-evolutionary scale: the origination of a new species and the loss of species through extinction. Nevertheless, the rate of species loss greatly exceeds that of the origination of new species. We cannot solve or compensate for the loss of species that we have caused in the past, and rapid evolutionary responses are not going to help in any way, as argued by François Bonhomme. In addition, many other species are facing extinction, and may purely survive temporarily on extinction debts. Can we use evolutionary processes and principles to save them from extinction?

Maybe we can, but as indicated by Pierre-Henri Gouyon, we are only fighting the symptoms because the underlying evolutionary processes that constantly create new evolutionary variants are disrupted and disturbed. However, one can argue that in general genetic variation (instead of creation of new variation) is more important for short term evolutionary changes (Frankham et al., 2009), which puts the focus again on the conservation of present-day genetic variation for safekeeping evolutionary potential.

Joop Ouborg highlighted the promise of genomic tools in the study of biological conservation. He argued that the development of new genomic techniques could make it possible to progress from the correlative and retrospective inferences of conservation genetics, based on neutral genetic markers, to a causal, mechanistic and prospective understanding, based on functionally important genetic variation, in a conservation genomic approach. These approaches could be used to investigate in non-model organisms and in organisms that could not be subjected to experimental approaches the functional genetic basis of adaptation, of inbreeding depression, genetic drift and so on.

Some caveats and questions were raised by Joachim Mergeay, who warned against the oversimplification of underlying genetic processes. Some of his questions were answered in

the next keynote contribution, by Virginie Orgogozo. In her essay on the genetic basis of evolution, she focused on two observations: Firstly, the variation between species was driven mostly by a subset of the variation within species, because within species variation was often caused by loss of function of a gene due to mutations in that same gene, whereas across species (the evolutionary changes that were eventually conserved) this was more often due to differences in regulatory elements. Secondly, mutations contributing to phenotypic variation were often homologous across species, and tended to affect selected genes. She argued that the rapid progress in molecular biology gave us hope that we might soon be able to draw a list of sensible candidate genes for many phenotypic traits.

This could give the impression that knowing and understanding the genetics of evolutionary changes could allow us to predict these evolutionary changes. Already in the opening statement of the e-conference it was mentioned that we needed to be able to predict evolutionary responses to global change. Ferdinando Boero argued that genetics alone could never be used to make any kind of predictions if we did not know the ultimate causes of change, which were ecological. This therefore required a much better understanding of the underlying ecological processes to understand evolutionary changes. But even then, he argued, we would only ever be able to reconstruct past evolutionary responses. Eventually, ecological processes and biotic interactions, except in the simplest systems, were likely to be too complex to allow for any sound evolutionary predictions, according to Ferdinando Boero.

Russel Bonduriansky emphasized in his keynote the role of non-genetic inheritance in adaptation. These could be acquired through learning processes, phenotypic plasticity, and through epigenetic inheritance. Especially the latter were novel, and although genomic tools could increase our understanding of the role of epigenetics (silencing of functional genes through methylation of Cytosine bases), we needed ecological studies to complement our knowledge of epigenetics in laboratory conditions.

Another way to understand circumstances that resulted in rapid evolutionary change was by studying biological invasions, which was addressed in Richard Shine's keynote contribution. He explained that invasive species were themselves subjected to new selection pressures, including intraspecific competition in an invasion front of cane toads that led to differences in dispersal rates among invasive cane toads. Secondly, invasions were good laboratories to study responses of species to selection pressures from exotic species. The invasion of cane toads in Australia showed that different species tended to react differently to cane toads: some by phenotypic evolution, physiology (resistance to toxins), behaviour, but also by non-genetic mechanisms, such as learning not to eat toads. This again highlighted the unpredictable nature of evolutionary responses mentioned by Ferdinando Boero. With regards to management of invasive species, it showed that management itself should include the possibility of evolutionary responses.

Eviatar Nevo wrote a fascinating keynote about hotspots of evolutionary changes, located in so-called evolutionary canyons in Israel. Using an integral approach that included detailed studies of ecology, physiology, geography, genetics and genomics, and over a wide range of taxa, his research revealed a number of generalities of evolution on both micro- and macro-evolution driven by microscale differences.

In the final keynote of the week, Timo Vuorisalo focused on the legal instruments for the conservation of biodiversity in Europe, such as the Habitats Directive, the Natura 2000 network and the Convention on Biological Diversity. He highlighted the lack of a European long-term perspective on the preservation of evolutionary potential, and on the lack of separate management for different evolutionary significant units. Although this may be intended in the term "genetic isolation" of the Habitats Directive, genetic isolation was not necessarily a result of functional evolutionary adaptations, because genetic drift and inbreeding could also lead to strong genetic isolation, cases in which further isolation should be avoided. Elena Bukvareva further commented on the conservation of evolutionary potential in Europe, with a focus on the different roles of intraspecific and interspecific biodiversity in relation to environmental stability. She argued that we should not necessarily focus on maximizing biodiversity, but rather on optimal levels, and explained the principles underlying this concept.

Summary for week 2: 'Evolutionary responses to anthropogenic pressures'

Hans Van Dyck opened discussion by outlining the importance of incorporating evolutionary dimensions in conservation management strategies and called for a better insight and understanding of patterns underlying evolutionary processes. Hans-Peter Grossart agreed with these points and emphasized the need to take the complex interrelationships between organisms, populations and ecosystems into account when trying to understand evolutionary processes and changes in biodiversity.

Kuke Bijlsma outlined a major threat for the persistence of biodiversity: fragmentation. He argued that from a population genetics perspective, fragmentation of populations resulted in small, isolated populations that were subject to genetic drift and inbreeding and that these processes tended to cause decreased fitness, decreased tolerance to environmental stress and impeded adaptive responses to changing and stressful environmental conditions. On the other hand, Ferdinando Boero suggested that fragmentation was not necessarily detrimental to biodiversity; he argued that fragmented populations were conducive to evolutionary change, in both an anagenetic and cladogenetic fashion. Similarly, Francois Bonhomme agreed that it was possible for fragmentation to, on occasion, promote local adaptation and the rise of evolutionary novelties. Pablo Goicoechea developed these ideas further, highlighting that the scale of fragmentation was an important factor to consider, as was the species and the mobility of its gametes.

Discussion then ensued on the topic of John Stewart's keynote contribution: evolutionary processes during past Quaternary climatic cycles. He outlined that ecological community make-up was affected by climate change in the Quaternary and that this was probably both the cause of, and caused by, evolutionary processes such as species evolution, adaptation and extinction of species and populations. Jan Jansen agreed with this and highlighted the need to also study evolutionary processes that were triggered by historic land use practices in socio-economic and political-administrative settings. Martin Sharman responded with a very provocative contribution, which sparked a great deal of debate around the issue of the burden human-kind impose on our planet. Gernot Gloeckner and Balint Czucz agreed with Martin Sharman, but Balint reasoned that ecologists had an important role in communicating to society about how to create resilient systems. Martin Sharman called for future research on understanding how we could stop the loss of biodiversity. Arturo Arino stressed the importance of assessing what biodiversity was being lost and how it was being lost in order to be able to attempt to establish a sustainable relationship with the world we live in.

Joachim Mergeay advised that the role of biologists was to clearly document and study the loss of biodiversity, and to come up with scientific evidence for the role of biodiversity in ecosystem services and ecosystem resilience to disturbance. Rasmus Ejrnaes agreed with this, but also highlighted that while optimal resource exploitation could conserve ecosystem services, it could also lead to the loss of biodiversity; he used the examples of managed forests and organic farming. Ferdinando Boero warned that to solve the biodiversity problems imposed by global change, it was necessary to tackle the ultimate causes (i.e. human overpopulation) rather than focussing only on proximate causes. He also argued that ecosystem goods and services were provided by few species, when compared to the whole of biodiversity. He argued, therefore, that it was not enough just to concentrate on preserving 'useful' species, but that there was a need to make politicians understand that the economic values of biodiversity were not the only reason to preserve it. This view also shared by Pablo Goicoechea.

Luisa Orsini and Joachim Mergeay gave examples of how neutral and selective variation in natural populations along extended time axes could be used to unravel patterns of adaptation to global change. They highlighted the value of dormant propagules as a way to reconstruct past evolutionary changes. On a similar topic, Katalin Török, Gabriella Kutta and Geza Kosa used the Pannonian seed bank as an example of conserving the genetic basis of evolution of vascular plants. Viktor Kotolupov stated that all biological systems had common

characteristics within the framework in which they evolved. An example of a biological system was given by Adrianna Vella and Noel Vella, who presented a case study as an example of how genetic diversity influenced fish evolution and conservation in the Mediterranean.

Mark Visser emphasized the importance of assessing the adaptation potential of two major climate change induced shifts: changes in phenology and range shifts. He argued that the rate of adaptation was mainly set by the rate of micro-evolutionary responses. Pablo Goicoechea suggested Mark Visser's contribution showed a good way to link climate change with biodiversity loss, and he further argued that micro-evolutionary responses would be driven by standing genetic variation (instead of by new mutations), thereby highlighting the importance of genetically diverse populations with high evolutionary potential. Equally, Vladimir Vershinin argued that as a result of this it was the pre-adaptive features of species and populations that played a critical role in their survival. Similarly, Stefan Schindler and colleagues highlighted the need to further investigate the plasticity and evolutionary potential of plant and animal species. Their contribution summarized the results of the 2nd annual meeting of the Austrian Platform for Biodiversity Research (BDFA) and highlighted key areas for future research on evolutionary responses to anthropogenic pressures. On the same topic, Sabine Hille focussed on the importance of gaining a better understanding of species life history traits and their ability to respond to phenology shifts in food abundance as a result of climate change.

Francisco Rodriguez-Trellez looked at our current understanding of genetic responses to recent climate change. He focussed his contribution on previous studies carried out on the fruit fly Drosophila. He highlighted the need for a causal link (instead of a mere correlation) to be established between climate and certain genetic traits such as chromosomal inversions, and the need to gain a better understanding of the genetic architecture underpinning the 'climate-sensing' character set.

Summary for week 3: 'Evolution in complex systems and co-evolutionary networks'

The week started with a keynote from Andrew Hendry, who examined the interactions between ecology and evolution in contemporary time. He outlined three examples at the population, community and ecosystem level and highlighted the need to further understand how contemporary phenotypic changes influence ecological variables on similar time frames. In response, Martin Sharman proposed that future research was required to gain a better understanding of the evidence for and against critical transitions in ecosystems and to characterise the tipping points. Simona Mihailescu used the Romanian Natura 2000 network as a case study for maintaining biodiversity in complex ecosystems. She called for future research to evaluate the impact of human activities on species, habitats, landscapes and ecosystems. Peter Bridgewater questioned how useful protected areas were for evolutionary potential. He considered the possibility that protected areas may lead to the decay of complex systems, while evolution was forced to continue in urban systems. Andreas Tribsch and colleagues provided another detailed list of research recommendations, which came out of the 2nd annual meeting of the Austrian Platform for Biodiversity Research, focussed on this week's topic of evolution in complex systems and co-evolutionary networks.

Pedro Jordano introduced the topic of multi-species interactions; he argued that they were the key to understanding evolution and the consequences of species losses in order to ensure the persistence of the whole ecosystem network. Luis Santamaria and Miguel Rodriguez-Girones highlighted the need to understand the labile nature of multi-species interactions and to predict their dynamics. They argued that pollination and dispersal networks should be used as a model to investigate co-evolutionary responses to landscape and climate change. In response to this contribution, Ferdinando Boero stressed the need for further knowledge on species interactions and emphasised that the intricacies of both positive and negative interactions required detailed knowledge of species natural history. Edit Kovacs-Lang emphasised the importance of studying functional diversity to gain a better understanding of the functioning of complex biological systems.

The topic of metacommunities was covered by Mark Urban who highlighted the need for future theoretical models to incorporate multi-species interactions in order to be able to assess species responses to climate change. Luc De Meester continued this discussion by outlining the concept of evolution in metacommunities as an integration of evolution, community ecology and space. He highlighted how eco-evolutionary dynamics could impact on species composition and trait changes across environmental gradients in space and time. Rasmus Ejrnaes and Hans Henrik Bruun outlined their hypothesis of the community-level birth rate (CBR) in the process of evolution in plant communities and highlighted its importance for the build-up of species over time during the assembly of a community and for the build-up of the species pool by migration and speciation. Yiannis Matsinos summarised the concept of Population Viability Analysis (PVA) as a management tool used in conservation biology to evaluate risk of extinction. He examined how the role of uncertainty on extinction probability affected PVA predictions.

The week ended with two keynote contributions that focussed on the 'Geographic mosaic of co-evolution' framework. Michael Hochberg examined co-evolutionary patterns and processes and called for future research to establish how complex environments affected genetic and species biodiversity in tightly and loosely coupled interactions and networks. John Thompson highlighted the importance of developing a science of applied co-evolutionary biology and emphasised the need to gain a better understanding of the ecological underpinnings of the co-evolutionary process. On a similar topic, Tiiu and Kalevi Kull summarised the development of contemporary research on coevolution, focussing on the concept of consortium.

Research priorities

Fiona Grant, Joachim Mergeay & Juliette Young

1. Research needs to evaluate the evolutionary basis of biodiversity:
Genetic techniques and mechanisms:
- Gain a better understanding of genetic and genomic processes underlying biodiversity dynamics, functional genetic variation and adaptation
- Investigate the role of genetic versus non-genetic and epigenetic mechanisms in phenotypic change and evolution
- Further understand how non-genetic inheritance might contribute to adaptation in rapidly changing environments
- Better understand the genetic basis of phenotypic change by including genomic techniques in non-model organisms
- Further understand why inversion frequencies change directionally in the long-term

Biological invasions:
- Better understand evolutionary responses to disturbance using biological invasions as natural laboratories
- Further understand the role of phenotypic plasticity versus rapid evolution in invasive species
- Further understand the circumstances that result in rapid evolutionary change in some species, but not others using biological invasions as natural laboratories
- Assess the evolutionary potential of alien and native hybrids and the consequences of introgression of natives and taxonomically related aliens into gene pools of native species

Management and preservation of evolutionary processes:
- Assess the minimum viable population size needed in order to make conservation status nationally favourable
- Further explore the evolutionary potential of refugial populations and populations along environmental gradients by analysing functional genetic variation
- Chart the phylogenetic distribution and inter-taxon variation in trans-generational responses to factors such as temperature
- Further understand how trans-generational responses might contribute to population growth and persistence
- Investigate the role and potential of evolutionary change in specialist versus generalist species

2. Research needs to assess the evolutionary responses to anthropogenic pressures:
Response to global change:
- Interpret patterns of change and understand the ultimate and proximate mechanisms behind these patterns

- Further understand the relationship between evolution at the species level driven by global change and the cascading effects of this evolutionary change on communities and ecosystems
- Better understand impacts of global change on future biota by studying non-analogue past communities
- Further understand the relationship between ecological and evolutionary change in response to environmental change using long-term monitoring data (time series, paleogenetics, museum specimens)
- Understand how individualistic responses to climate change alter species distributions and food web structure
- Further study the adaptability of species to different climate regimes in a given study area
- Further understand shifts in species phenology as a result of environmental change

Anthropogenic pressures:
- Identify evolutionary processes and selection regimes in urban environments
- Further understand the factors that affect ecosystem resilience, resource constraints and their internal dynamics
- Identify critical transitions in ecosystems, and characterise, where possible, the tipping points
- Further develop models to study the persistence of biodiversity under anthropogenic stress, taking into account the genetic consequences of population fragmentation
- Investigate the plasticity and evolutionary potential of organisms in relation to changes in land use

Fragmentation:
- Assess the role of fragmentation in reducing or enhancing evolutionary responses
- Further understand the consequences of changes in population fragmentation on gene flow and genetic drift
- Further understand the adaptation plasticity of populations that are genetically eroded due to habitat fragmentation

Plastic and evolutionary adaptation:
- Identify evolutionary significant units, including phylogeographical methods
- Assess the impact of evolutionary change on phenotypic change and/or phenotypic plasticity
- Further understand neutral and selective variation in natural populations along extended time axes (paleogenetics, time series, museum specimens) to explore patterns of adaptation
- Determine nature conservation units, especially with regards to inbreeding and disruption to local adaptation and enhanced evolutionary potential
- Understand the effect of functional redundancy in ecosystems on the rate of adaptation in populations, and ecosystem resilience
- Further understand the genetic architecture underpinning the 'climate-sensing' character set of Drosophila
- Better quantify immigration and adaptation rates in local populations using neutral and genomic markers

3. Research needs to identify evolution in complex systems and co-evolutionary networks:

Multi-species interactions:
- Further develop theoretical models that incorporate multi-species interactions, regional dispersal and evolutionary dynamics
- Establish how complex environments affect genetic and species biodiversity in tightly and loosely coupled interactions and networks
- Quantify metacommunity structure of organisms across landscapes
- Further understand the labile nature of multi-species interactions and the processes that govern them

- Establish which factors drive the assembly and structure of mutualistic interaction networks
- Further understand interrelationships between organisms and populations/ networks, particularly those that are disrupted by anthropogenic actions

Co-evolution:
- Understand the generalities of coevolution in complex multi-species networks with the use of models
- Develop models of the distribution of co-evolutionary networks and its comparison with single species responses
- Further understand the ecological underpinnings of the co-evolutionary process
- Better understand how mega-diverse assemblages co-evolve
- Further understand cryptic co-evolutionary networks in order to establish loose mutualism from symbiosis and true co-evolution

Traits:
- Understand the evolution of quantitative traits across natural landscapes
- Assess trait selection in populations under depressed reproduction
- Establish whether communities and ecosystems are indirectly affected as a result of changes in population dynamics, or directly affected by the evolution of traits.

Complex systems:
- Understand how complex self-organising systems interact with ecosystems
- Determine when true feedbacks occur between ecological processes and evolution
- Further understand how feedbacks between ecology and evolution change biota across all hierarchical levels of biological organisation
- Further develop climate envelope models to explicitly take dispersal limitation into account
- Further understand the role of structural and functional diversity in the performance of complex biological systems
- Further understand the role of community-level birth rate in order to assess the impact of communities and environments on evolution
- Further understand how contemporary phenotypic changes influence ecological variables on similar time frames (evo to eco)

4. In order to achieve the above research needs the following enabling actions are necessary:

General:
- Improve knowledge of the natural history of populations, species, communities and ecosystems
- Acknowledge that biodiversity in all its aspects is too complex to allow for detailed predictions about future biodiversity change
- Gain long-term datasets
- Adopt a multi-disciplinary approach to research

Communication and education:
- Translate evolutionary insights into workable formats and language for policy makers and conservation practitioners
- Develop open-access databases of evolutionary and genetic research
- Improve university education in the basics of 'organism biology', namely identifying species, monitoring, biology of species, animal behaviour etc
- Explain and encourage valuation of biodiversity that transcends the ecosystem services argument

Conservation management strategies:
- Incorporate an evolutionary perspective and take into consideration adaptive genetic processes
- Target not only extant diversity, but also the processes and environments promoting a high community-level birth rate

- Protect communities with optimal natural diversity, i.e. natural communities with low diversity may be as important as those with high diversity
- The nature protection strategy should take into account both species and intra-species diversity as an interconnected system
- Use data on genetic diversity of multiple species in order to systematically design conservation areas and compare the resulting conservation networks with existing ones
- Focus on endemic and IUCN listed species as these are often located in refugia and will lead to data for targeted conservation efforts regarding these species

List of contributions

Session I: The evolutionary basis of biodiversity

Human perspectives on biodiversity

Stefaan Blancke, Department of Philosophy and Moral Science, Ghent University, Belgium

Not only does evolutionary theory have a massive impact on our modern understanding of biodiversity, but also on our reasons for valuing it.

Of the many conceptual changes brought on by Darwin's theory of descent with modification, there are at least three that have determined the way we look at biodiversity today. First, instead of interpreting species as imperfect images of an ideal type, Darwin was the first to fully appreciate the omnipresence and importance of variations in nature. Since Darwin, we no longer consider species to be immutable units, but varieties that are, as Darwin put it, "strongly marked and well-defined". By constantly providing alternatives or new possibilities, variation allows populations to adapt to a changed or changing environment. Therefore, variation is a condition sine qua non not only for the survival and reproduction of those populations, but, in the end, also for the very existence and the preservation of biodiversity. Biodiversity, which is variation among species, can only occur by means of variation within species. It is the product of evolution.

Second, because populations will continue to vary, to adapt and hence to evolve, biodiversity should be considered to be a dynamic, and not a static, phenomenon. Except for a few isolated voices, people before Darwin tended to think of nature's diversity to be a static order, arranged in resemblance of God's reason. But, today, we realize that biodiversity is in a constant flux. It itself varies continuously, thus indeed providing life as a whole with a strong potential to adapt to new circumstances and to evolve. However, this dynamic character also poses important limits on what kind of biodiversity we can expect to maintain. For instance, if we transplant a species into a different environment in order to rescue it from extinction, the species will adapt to the new conditions and thus change. In general, thinking in essentialist terms about biodiversity – which we do intuitively – would set our hopes too high. We can work hard to preserve nature's diversity, but we cannot expect to keep it as it is.

Third, as species evolve by adapting to the environment, they cannot display any feature that is "formed for the exclusive good of another species". Some of Darwin's contemporaries still cherished the idea that life on Earth was created solely to the service of humans. Darwin realized that if this would be the case, "it would annihilate [his] theory", but, today, his theory still stands. Now, life on Earth might have turned out not to be exclusively created for us, but in the end we are, as far as we can tell, the only species that can value its diversity. And we have two very good reasons to do so. First, how will people later judge our generation if we do not attempt to preserve a minimum of diversity, especially because we know perfectly well how to accomplish this? They would rightly blame us for leaving them with a less interesting and less fascinating world. And second, as species adapt to each other, they form "a web of complex relations", in which too much interruption might have unpredicted but severe consequences for human lives and society. These two reasons alone should be sufficient to make our moral instinct – initially evolved to deal with kin and tribe – encompass nature's diversity.

RE: Human perspectives on biodiversity

Francois Bonhomme, Institute of Evolutionary Sciences, France.

I would like to comment about what should motivate society to support biodiversity research in an evolutionary perspective. Let me first review rapidly some of the statements put forth by Stefaan Blancke and propose that we should make categorical distinctions in the first place.
        "*In general, thinking in essentialist terms about biodiversity, which we do intuitively, would set our hopes too high. We can work hard to preserve nature's diversity, but we cannot*

expect to keep it as it is." OK, let's agree on this point, if we have been good enough to convince the man on the street that biodiversity is a dynamic process, we'll have surely made an important step forward. Nevertheless, in this birth and death process, an important point is that we are dramatically altering the pace by increasing the latter and probably decreasing the former. If we believe the retrospective analyses of Kirchner & Weil (2000), recovery times following extinctions at the family level are on the order of 10 million years to regain a comparable level of taxonomic diversity; that is far beyond any sensible temporal scope. This means that whatever we do, we'll lose things that we may consider valuable, and therefore the question of the qualification of biodiversity we would like to see preserved remains pregnant.

"How will people later judge our generation if we do not attempt to preserve a minimum of diversity..." This "minimum of diversity" is the very devil in the statement. It disserves qualification, as said, and deciding for instance to preserve genetic resources in a series of crop species for future adaptation to climate change, or even setting experiments to promote the understanding of the underlying adaptive mechanisms, is one thing; very different indeed from deciding that we want by any means to preserve, say, the phylum of marine mammals from extinction. Who will chose?

"...especially because we know perfectly well how to accomplish this?" Maybe we know for some crops (although we rarely do it right, do we?), but is it the case for all the rest?

"They would rightly blame us for leaving them with a less interesting and less fascinating world." This sentence and the following one have the merit in my opinion to put side by side the two contradictory issues about the perception of biodiversity and thus raise the question of what we should do about it: *"As species adapt to each other, they form "a web of complex relations", in which too much interruption might have unpredicted but severe consequences for human lives and society. These two reasons alone should be sufficient to make our moral instinct initially evolved to deal with kin and tribe encompass nature's diversity."*

On one hand, one relies on something emotional (interest, fascination, empathy for other creatures…) and on the other hand, one speaks of functional aspects, like food, eco-services... The stock exchanges at the surface of the planet are not so interested by the first aspect unless it is marketable (is it?). Research funding policies are sensitive to public opinion, but in a decreasing order, emotion being less valued than food or health or employment questions. On the one hand, we tend to mainly tackle higher order biodiversity categories; on the other hand, we mostly (but not only) address more micro-evolutionary mechanisms.

I have thus the impression that if we do not confront at the very beginning of this e-conference this dual aspect of biodiversity loss and biodiversity evolution, we'll just produce a basket full of eggs and carrots, and at the end it will still be difficult to "sell" research packages to policy makers...

RE: Human perspectives on biodiversity

Joachim Mergeay, Research Institute for Nature and Forest (INBO), Belgium

There is a great deal of truth in the above comments, which highlight the very ambiguous ways of how we perceive the role of biodiversity in our society, emotionally and functionally.

Focusing on functional aspects of biodiversity, e.g. through ecosystem services, has the merit of making clear to the man/woman in the street that biodiversity has an economic value far beyond his/her imagination. The risk is, of course, that marketers will want to strip biodiversity of seemingly redundant species and genetic variants if they can profit from doing so.

As scientists it is our task to identify processes that affect biodiversity and its evolution, and to convince policy makers to conserve biodiversity in all its facets, and not only for economic reasons.

The notion that we need healthy and diverse ecosystems for human security, welfare, and happiness, and that this requires an integral approach, is seeping through in the global community (IUCN 17/06/2009; IPCC 2009, Millennium Ecosystem Assessments 2006). The 1992 Rio convention on biological diversity, ratified by nearly all nations (except USA, Andorra and the Holy See), set the political basis for why and how we should conserve biodiversity. In the process of implementation of this convention, European policy makers are still debating what the Favourable Conservation Status should be for each species of concern, and at this stage these FCS definitions are still too much a compromise and lack essential input from genetic indicators (Laikre et al. 2010: Conservation Biology). But at least they provide a baseline. As scientists, we need to guard the scientific side of this process and steer it further. But we should also be prepared to cope with changes that we may not like. Changes that have started decades or even centuries ago and that have gained momentum and that are currently being blown in our faces. We cannot immediately stop climate change, pollution, invasive species, etc. So we should find out how to make the best of a bad situation, and try to find out how evolutionary processes have a role in this. And I guess that "making the best of a bad situation" is more or less what was meant by the preservation of the "minimum diversity" in Stefaan Blancke's contribution.

RE: Human perspectives on biodiversity

Pierre-Henri Gouyon, National Museum of Natural History (MNHN), France
Biodiversity is better approached through the diagram Darwin included in "the origin of species" (see appendix) than through any list of species (a vision inherited from the fixist XVIIIth century early systematics). The crucial point is that the evolutionary process constantly produces novelties which eventually go extinct, more or less, rapidly in most cases. This process is healthy if the novelties are potentially more numerous than the extinctions. The problem thus is not that some species are going extinct, which could be corrected by saving some of them, but that the process itself is not working properly anymore.
The clearest example of such a breakdown of an evolutionary process producing biodiversity is the management of crop diversity. Instead of letting all farmers reproduce their seeds and produce constantly new forms, diversity is centralized, at best congealed and in general lost. The whole story started when seed production became the job of a small subset of farmers and is becoming crucial with patenting genes and varieties. The Svalbard solution of pretending that all diversity will be conserved in a gigantic fridge is the exact opposite of an evolutionary, sustainable attitude towards biodiversity.
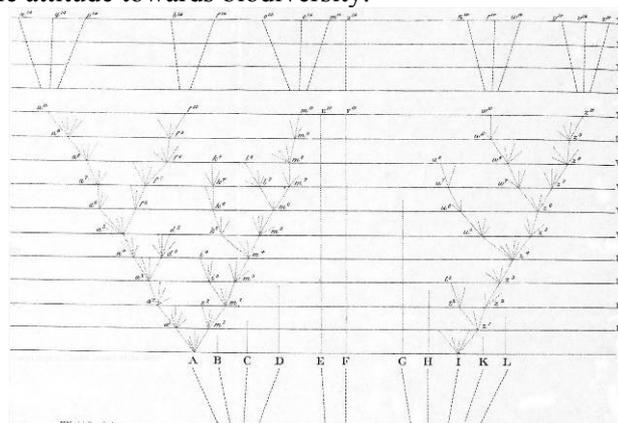
Figure 1 Diagram from 'Origin of Species', Darwin (1859)

RE: Human perspectives on biodiversity

Felix Rauschmayer, Helmholtz Centre for Environmental Research - UFZ OEKUS, Germany

I am puzzled by the last paragraph made in Stefaan Blancke's contribution for several reasons:
Why should a possible judgement of possible future generations be a 'very good' reason for us to value biodiversity? Parfit stated, with his well-known identity problem, (Parfit, 1983) that the problem is that it is not easy to give moral value to the interests, judgments etc. of someone whose identity and even existence depends on one's own action. This means that, intuitively, the participants of this conference very probably agree that future generations very probably would judge us on our current behaviour, but that it is very difficult to make a good, philosophically, and politically valid argument from this intuition.
The second reason is politically caught by the precautionary principle, but we all know how difficult it is to deduce clear values from this. And is it biodiversity that we value here or the insurance value inherent in the (anthropogenically decreasing) redundancy of ecological relations?
The major puzzle is posed in his last sentence, though: What is a moral instinct? Does he mean intuition? Wikipedia says: "Instinct is the inherent disposition of a living organism toward a particular behaviour. ... Instinctual actions ... have no learning curve". Morals refer to right and wrong in a society, either descriptively or normatively. To me, these two words do not fit together and even less in a call for its evolution towards an encompassment of nature's diversity. Here, even intuition does not work, as, in our scientific tradition, only arguments can give good reasons for an enlargement of a concept. And, as said in my first point, this is not an easy task!

RE: Human perspectives on biodiversity

Ferdinando Boero, University of Salento, Italy

I have read the opening messages and I have seen the word "prediction" used in an evolutionary context. Evolution makes up the history of life and evolutionary biology is a historical discipline. A-historical disciplines are ruled by laws and can lead to predictions. Historical disciplines are ruled by laws but, also, by contingencies. Predictions are possible in a-historical domains, once the laws are known. But they are impossible in historical domains, because, sometimes, the laws do not work. Evolution became hyper-reductionistic with the advent of genetics. And this led to enormous advances in understanding the evolutionary process, and even some "laws" have been identified. But genetics has to cope with ecology, where the laws are very feeble (unless you take the ones of thermodynamics, but ecology is not physics).
In the Origin of Species, Darwin wrote:
"Throw up a handful of feathers, and all must fall to the ground according to definite laws. But how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing...."
What is happening now is just history. All the predictions we can make are that, if temperature increases, then species of warm climates will be favoured and will expand, whereas those of cold climates will be pushed northwards, or on the top of mountains or in the depths of the seas. However, some of these species might even evolve, and take advantage of the new situation.
For instance, *Fucus virsoides,* is the only representative of the genus in the Mediterranean Sea, and is confined to the Northern part of the Adriatic, the coldest part of the Mediterranean. I expected it to be negatively affected by global warming but, instead, it is

now a pest in the lagoon of Venice. Instead of declining, this cold water species is increasing. The ctenophore, *Mnemiopsis leidyi*, arrived to the Black Sea in the early Eighties with the ballast waters of US oil tankers, is a temperate species and its establishment led to the collapse of fish populations in the Black Sea. It never left the Black Sea, but in 2009 it was recorded in enormous quantities from Israel and from the Western Mediterranean. Probably it evolved to become tolerant to high temperatures. But such things cannot be predicted; they can only be explained, once they occur.

Right now the Mediterranean biota are going through a period of tropicalization (many tropical species are becoming established) and of meridionalization (the species that usually thrived in the southern parts of the basin are expanding northwards). It is to be expected that temperate species will decline, or that, at least, will be pushed to the depths of the sea. But some might become adapted to the new conditions. The first thing to do, repeating Darwin's statement, is to study "the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing." This is done by Natural History and requires a historical approach. Pretending to predict historical phenomena with the tools of a-historical disciplines is an epistemological mistake. It is like considering nature just as a handful of feathers thrown in the air. Making difficult problems simple does not help much in really understanding what is going on. Darwin understood it very clearly but, unfortunately, his vision has been forgotten, and we are looking for precise laws that will allow us to predict future history.

Evolution, from one side, is a matter of genetics (for the proximate causes) but the ultimate causes are ecological. And we are facing an ecological problem. Ecology and evolution divorced a long time ago (when Elton wrote Animal Ecology and ridiculed natural history) and ecology did not even contribute to the modern synthesis. Evolution is not only genetics, and cannot be predicted (just like history, unless you reason like an economist, but we know the results).

This is a very complex problem, and reductionism, alone, does not work.

RE: Human perspectives on biodiversity

Joachim Mergeay, e-conference chair, INBO, Belgium

Ferdinando Boero is right in stating that we cannot exactly predict evolutionary responses, we even have a hard time in predicting ecological responses in relatively simple ecosystems (see for example, chaotic oscillations in plankton; Huisman and Weissing, 1999). This is what makes anticipating the effects of biological invasions so extremely difficult. But as Virgine Orgogozo states in her contribution, the genetic basis of phenotypic evolution may be predictable to some extent (see also Stern and Orgogozo, 2009).

With regards to the interaction between ecology and evolution, the third session of this e-conference may enlighten us further. "Predicting evolutionary responses" should perhaps not been interpreted literally in a probabilistic sense. But to provide a counter-example against Darwin's "feather metaphor" - throw in a handful of stream sticklebacks in a Canadian lake, and they will have a high probability of adapting to that lake environment and evolve into pretty predictable morphs, and likely even diversify into benthic and limnetic feeders with predictable phenotypes (Gow et al., 2008), and using expected pathways (Marchinko and Schluter, 2007).

So what we can do is investigate through quantitative and functional genetic approaches whether the potential for adaptation (through genetic and non-genetic mechanisms, and by investigating standing genetic variation in populations) to a certain selection pressure is high or low, investigate through which pathways this is likely to happen, and use that information to formulate expectations (instead of predictions).

Ferdinando Boero, University of Salento, Italy

Joachim Meregeay is right: throw a filter feeder in the Great Lakes and it will clean up the waters. That's what *Dreissena polymorpha* did. Predictions can work sometimes, but at other times they do not. Genetic evolution considers genes. But the carrying phenotypes can go through things that their genes cannot predict. Throw a ctenophore in the Black Sea (*Mnemiopsis leidyi*) and it will eat all fish eggs and larvae. But will it be the same in the Eastern Mediterranean, where that species arrived this year (Galil et al., 2009)? The same species also reached the Western Mediterranean, together with a tropical scyphozoan jellyfish (Boero et al., 2009). Can we expect the very same reaction? By the way, along the US East coast *Mnemiopsis* is not reacting the same as it did in the Black Sea. Furthermore, the beautifully adapted genes of *Mnemiopsis* can do little if you also throw *Beroe ovata* in the Black Sea. But then we do not know what *Beroe* will do, once all the *Mnemiopsis* are eaten.

I am sorry folks, but history cannot be predicted. And evolution is history. Evolution is genetics AND ecology.   The example of "throwing a handful of sticklebacks..." is not a counterexample to Darwin's metaphor. It is an attempt to transform natural history into physics, treating the handful of sticklebacks as if they were a handful of feathers.

Sometimes the system might react in a given way, other times it might answer in a completely different way. I have been arguing this in a long series of papers (some recent ones are attached as an appendix) and it is so strange that people continue to pretend to be able to predict history. Putting forward some success and forgetting all the failures (e.g. the management of fisheries...). Maybe this depends on the topic we study. I study jellyfish, and their irregular appearances are ruling the world (sometimes). And even if last year they were all over the place, throughout the world, I will not bet that this will be the case this year.

Bernard Kaufmann, University de Lyon, France

Reading the contributions of François Bonhomme and Joachim Mergeay, I can't fail to notice how most of us (including myself) have a fundamental, irrational urge to "save" biodiversity, and lose as little of it as possible. This urge is shared in part by the general public, albeit a small part. It is akin to a larger number of people's attachment to historical monuments and art. Our countries do not preserve the past and its art because it is profitable or lures tourists, even if that has been a recent factor. Our countries do it because there is a fundamental urge to preserve one's identity, history and culture, and because a large number of people are educated to enjoy art, history and culture. This is true at a national level of course as well as a local to international level. Remember the global emotional outcry when the Buddha's of Bamyan were torn down by the Taleban 10 years ago?

Biodiversity and species conservation somehow works at the same level as conscience arts and monuments do, except much less in the eye of the governing elites and general public, who are rarely educated to nature.

The point of my contribution is that as long as we do not recognize that preserving biodiversity is a patrimonial "duty" that we feel is important, we run the risk of always trying to find utility or economy based arguments that will hold for the governing elites or the general public, that only have long-term consequences. Framing thinking in terms of patrimony naturally leads to evolutionary concerns. The biodiverse patrimony we seek to preserve is the fruit of a 4 billion year evolution that must be left to evolve. The larger the biodiversity base left to evolve, the wider the possibilities of evolution in the face of a rapidly changing planet. Mitigating humanity's impact is the task of conservation biology, as explained in every text book. Now, the question remains how to mitigate impact with the dual objective to preserve evolutionary patrimony and potential.

Towards a mechanistic understanding of biodiversity dynamics

Joop Ouborg, Radboud University Nijmegen, IWWR, The Netherlands

The invention of new genomic techniques and their incorporation in biodiversity research will open the way for a deeper understanding of the mechanisms behind the dynamics of biodiversity.

Attempts to understand the dynamics of biodiversity at the species level have been successfully undertaken within the framework of conservation biology. In the past two decades the emphasis has been placed on the genetic aspects of the demography of populations in fragmented landscapes. Extinction probabilities of local populations were investigated in terms of variation in neutral genetic markers within these populations and in effects of inbreeding on fitness. A limitation of this approach is that no direct insight in fitness effects can be obtained with the use of neutral genetic markers.

The invention of new genomic techniques makes it possible to progress from the correlative and retrospective inferences of conservation genetics, based on neutral genetic markers, to a causal, mechanistic and prospective understanding, based on functionally important genetic variation, in a conservation genomic approach.

The development of next generation sequencing techniques now allows one to obtain large amounts of DNA sequence information of species of interest within a conservation context. The application of this information in transcriptional analyses, where the (variation in) activity of genes is investigated as a function of environmental and population-genetic processes, is becoming available for ecological model species and species that are of conservational interest. Extracting genome-wide information from the vast amount of sequence data enables one to follow a genome-scanning approach, where signs of selection can be investigated in the genome, candidate genes that play a role in adaptation to changing environments can be identified and screening of variation in gene sequence and activity can be possible at the population level. These approaches have great promise to substantially increase our understanding of which factors drive adaptation to changing climates, and how landscape processes may limit this adaptive potential.

There is accumulating evidence that epigenetic processes may play an important role in adaptation. These processes include methylation of DNA and modification of DNA-associated proteins, like histones. Both processes lead to changes in the transcriptional activity of genes and seemingly to 'genetic variation', even in the absence of sequence variation. Several studies have taken epigenetic processes into consideration and provided evidence that environmentally-induced epigenetic marks, such as DNA methylation, can be stably inherited to the next generation. Thus, taking up an epigenetic approach may lead to a better insight in how environment and genetics interact, and what alternatives for adaptation there might be for populations that are genetically eroded due to habitat fragmentation effects.

These approaches can be applied to organization levels beyond single populations, including meta-population dynamics, species interactions (such as herbivory, pollination, predator-prey dynamics, resource competition), and ecosystem processes (including responses to disrupted nutrient cycling and global warming). They provide the framework for a mechanistic understanding of the dynamics in biodiversity, and may considerably increase our ability to predict impacts of environmental factors on future biodiversity.

RE: Towards a mechanistic understanding of biodiversity dynamics

Joachim Mergeay, e-conference chair, INBO, Belgium

This contribution by Joop Ouborg clearly situates the enormous possibilities that genomic tools offer to modern evolutionary research, although he only showed the tip of the iceberg.

Unfortunately, the format of the e-conference does not allow more in-depth presentation in these keynotes, and of how these approaches should be elaborated. However, there is ample room for discussion on "do's and don'ts", so I suggest posting some comments.

The promise of genomics in the conservation of biology and in evolutionary biology is indeed enormous. With the risk of ending with a technical discussion, I have nevertheless formulated a few questions that may be relevant for how we tackle evolutionary functional genomics. I may be wrong, poorly informed and biased, but the floor is open to everyone to enlighten me and other people.

1. Genomics allow us to survey a very large amount of genetic loci underlying phenotypic traits. But paradoxically in such extensive whole-genome scan approaches, the pitfall of reductionism is lurking, simplifying the processes underlying the complexity of gene expression regulation, and determining evolutionary potential. Genome scans and the like will help in identifying candidate genes and mutations involved in certain traits, but how can we grasp the cellular, biochemical and molecular complexity of relevant but often polygenic traits with such approaches? Isn't there a risk of only retaining QTLs, candidate genes and such that only reflect simple linear "one gene for one trait" relations?

2. How does evolution along independent biochemical and genetic pathways, but leading to similar phenotypes, influence functional genomics approaches? Sticklebacks and water fleas, both having fully sequenced genomes and with increasing genomic annotation, provide striking examples of parallel evolution and are excellent study organisms to investigate this.

3. To what extent is our selection of candidate genes biased by our choice of sampling, and can it be transferred to other (distant) populations? Ideally, we can include functional (but variable) genes that are conserved across species.

4. Say we have identified a dozen or so loci associated with a certain polygenic trait, do we need to know their exact function and the biochemical pathways in which they are involved in order to gain insight in the evolutionary potential for that trait in a population? If so, looking at a set of such phenotypic traits in non-model organisms will be pretty daunting.

5. How do we deal with non-coding but possibly regulating genetic regions (cis and trans regulation regions) compared to non-silent mutations in coding genes?

6. When looking for signs of selection in genome scan approaches, there is a serious risk of not detecting false positives (Hermisson, 2009). How to deal with this?

The genetic basis of phenotypic evolution: important results for biodiversity management

Virginie Orgogozo, Institut Jacques Monod, CNRS, France

Recent data suggest that the mutations responsible for phenotypic evolution have distinctive properties. This new finding might ameliorate biodiversity management strategies.

Our understanding of the genes and the mutations responsible for evolutionary changes in phenotype is increasing at an accelerating pace. More than 400 genes and mutations have been identified so far as responsible for domesticated, intra-specific or inter-specific changes in morphology, physiology or behaviour. And approximately four new mutations underlying phenotypic evolution are identified and published each month for multi-cellular animals and plants. From this data emerge two striking results that are important to bear in mind when elaborating biodiversity management strategies.

First, the genetic basis of long-term evolution (variation between species) involves a biased subset of the mutations responsible for short-term evolution (variation between domesticated races and between individuals within a species). Long-term evolution appears to involve a higher proportion of mutations in the cis-regulatory regions of genes, and a lower proportion of null mutations (i.e. mutations that lead to a complete loss of the gene's normal function). For example, numerous populations of *Arabidopsis thaliana* have adapted to warm environments thanks to various deletions in the Frigida gene. However, most Dicot plant species possess a Frigida homolog. Therefore Frigida deletions are unlikely to survive over long periods of time despite their short-term benefit (they might have important deleterious effects in another environment, or reduce plasticity, etc.). Importantly, this suggests that for a given species the properties of the mutations (coding, cis-regulatory, null, etc.) responsible for its phenotypic traits might inform us of its probability of long-term survival. Ideally, conservation genetic studies should thus not only examine neutral markers but also analyze the mutations responsible for species characteristic traits. Fortunately, this task might not be as daunting as it seems, according to the next observation.

Second, the mutations contributing to phenotypic variation do not appear to be distributed randomly in the genome: they tend to affect selected genes. Half of the evolutionary-relevant mutations identified in plants and animals represent cases of independent evolution of similar phenotypes due to changes in homologous genes. One explanation is that most genes within a genome play specialized roles. For example, a change in light wavelength sensitivity is likely to be caused by a coding mutation in a gene encoding a light-sensitive eye receptor; and a change in neck feather pigmentation is likely to be caused by cis-regulatory mutations in a pigmentation gene. Most of the known evolutionary-relevant mutations were found by testing candidate genes. Our rapid progress in molecular biology gives us hope that we might soon be able to draw a list of sensible candidate genes for many phenotypic traits.

Both results have emerged only recently with the accumulation of case studies. It is possible that they reflect biases in current research. Given their potential impact on our current understanding of evolution and biodiversity, it is important to develop an open-access database of evolutionary-relevant mutations.

Non-genetic inheritance and environmental change

Russel Bondurianksy, University of New South Wales, Australia

Trans-generational epigenetic inheritance and other forms of non-genetic inheritance represent a poorly understood but potentially important mechanism that, in theory, can enable populations to respond rapidly to environmental change.

A classic assumption of evolutionary models is that the only information that can be transmitted across generations is the information encoded in the DNA sequence. In particular, it has long been assumed that plastic responses of the phenotype to environmental influences cannot be transmitted to offspring. However, it is now well-established that a variety of mechanisms exist whereby components of phenotypic or environmental variation (including those that are independent of genetic variation) can be transmitted across generations (Jablonka and Lamb, 1995; Jablonka and Lamb, 2005). Such mechanisms include learning and conventional parental effects, as well as recently discovered cellular mechanisms such as trans-generational epigenetic inheritance (Bonduriansky and Day, 2009). From the perspective of biologists seeking to understand how populations may respond to rapid environmental change, these mechanisms are of potential importance for two reasons. First, they can vastly increase the amount of heritable variation present in populations. For example, in addition to DNA sequence variation, populations may harbour heritable epigenetic variation (i.e., variation in patterns of DNA methylation or chromatic structure). Populations also typically harbour considerable variation in condition, behaviour, and micro-habitat or community associations (e.g., with parasites or symbionts) that can be transmitted to offspring. Second, plastic responses in phenotype induced by environmental factors can, in some cases, be transmitted to offspring.

Theoretical analyses have shown that these properties of non-genetic inheritance can enhance the capacity of populations to adapt (both phenotypically and genetically) to rapid environmental change, and thereby avoid extinction (Jablonka et al., 1992; Lachmann and Jablonka, 1996; Pal, 1998; Pal and Miklos, 1999). Whereas conventional phenotypic plasticity can allow populations to adjust rapidly to environmental change (Lande, 2009), non-genetic inheritance can enhance such effects because offspring can be born pre-adapted to the novel environment (Agrawal et al., 1999), and because it may be possible for beneficial phenotypic changes to accumulate over several generations. Most importantly, such phenotypic changes can take place far more rapidly than would be possible through genetic evolution. Although empirical studies have yielded many intriguing examples of non-genetic inheritance, and theoretical analyses have shown that these phenomena can play an important role in adaptation and have interesting consequences for evolution, a great deal of work remains to be done to establish the importance of such effects in natural populations (Bosdorf et al., 2008).

Nearly all of the data available at present come from laboratory studies, and few ecologically-relevant traits have been examined in natural settings. To understand how non-genetic inheritance might contribute to adaptation in rapidly changing environments, it will be necessary to conduct experiments where relevant environmental parameters are modulated and responses are assessed in fitness-related traits. For example, we need to chart the phylogenetic distribution and inter-taxon variation in trans-generational responses to factors such as temperature (Gilchrist and Huey, 2001; Magiafoglou and Hoffmann, 2003; Watson and Hoffmann, 1995), and to understand how such responses might contribute to population growth and persistence. This work will need to be done in ecologically realistic settings. These fascinating and potentially important questions will be a major challenge for ecology and evolutionary biology over the coming decades.

Biological Invasions and evolution

Richard Shine, Biological Sciences, University of Sydney, Australia

Biological invasions – such as the spread of cane toads through tropical Australia - impose strong and novel selective forces, providing an ideal opportunity to clarify the circumstances that result in rapid evolutionary change in some species but not others.

The conservatism of major phenotypic traits through geological time within most lineages, and the strong spatial conservatism of traits within wide-ranging species, both suggest that evolutionary change is a slow process. That conclusion seems inconsistent with Darwinian Theory, which predicts a potential for rapid evolutionary responses to novel selective forces; and also is hard to reconcile with laboratory experiments and captive-breeding projects that report rapid responses to selection in many types of organisms. Biological invasions provide an ideal opportunity to explore this issue, because they involve strong and entirely novel selective challenges; we can then examine how a suite of native species (and the invader itself) responds to those challenges.

My research group has conducted extensive studies on such an invasion, focusing on the cane toad (*Bufo marinus*) in tropical Australia. Native to the Americas, this large and highly toxic anuran has spread over much of the Australian tropics within the last 75 years. Its primary ecological impact has been through lethal toxic ingestion by frog-eating predators. Because Australia has no endemic toads, many native predators are unable to survive exposure to the cane toad's distinctive toxins (Shine 2010). We have found several examples of rapid evolutionary responses within this system; but also, have found little or no evolutionary change in other taxa.

First, cane toads themselves have been dramatically modified by the pressures associated with a rapidly expanding invasion front. Only the fastest animals can stay at the front, imposing continual "spatial selection" for traits that enhance dispersal rates (Phillips et al., 2010). In the case of cane toads, this pressure has resulted in a dramatic increase through time in rates of advance of the invasion front, in relative leg lengths of invasion-front toads, in dispersal rates under field conditions, and in locomotor performance of the invasion-front animals (Phillips et al., 2006; Alford et al., 2009; Llewelyn et al., 2010a). Pressure for more rapid dispersal also may have compromised immune function in these animals (Brown et al., 2007).

Some native predators also have undergone dramatic adaptive shifts in response to the selective forces imposed by toad arrival. For example, some snakes have evolved a suite of traits that facilitate survival in the presence of toads, including changes in morphology (head size relative to body size, thus limiting maximal ingestible toad size), physiology (resistance to toad toxins) and behaviour (propensity to treat toads as prey) (Phillips and Shine, 2004, 2005, 2006). However, other predators (e.g., marsupials, frogs, fishes) have adjusted to toad presence by rapidly learning not to eat toads (a simple taste-aversion response) and hence, do not exhibit shifts in the frequencies of genetically-controlled traits in this respect. Instead, every generation learns anew, albeit with some evidence of a decrease in physiological vulnerability to toad toxins in the decades after toad invasion (e.g., Llewelyn et al., 2010b).

The end result, then, is a mosaic of evolutionary responses. The invading species has evolved rapidly, as have some of the predators most affected by the toad invasion. In other predator taxa, however, behavioural flexibility (through taste aversion learning) has weakened or eliminated the selective forces imposed by vulnerability to toads.

What does this mean for our management of biological invasions? We need to be aware of the ability of natural systems to adapt; the initial impact of an invader may well be worse than its long-term impact, because of the capacity for rapid adaptive shifts (mediated through learning and/or selection) in the native fauna. But equally, invaders themselves will be fashioned by the invasion process, sometimes affecting traits– such as dispersal rates and fecundity – that will make them more difficult to control as time passes. The rapidity and diversity of adaptive responses seen in a single intensively-studied system – the cane toad in

Australia – suggests that conservation planning must incorporate an evolutionary perspective. The entities we study are not constants, and their ability to change through time should be an integral component of any plans to manage biodiversity and especially, to deal with novel challenges posed by human activities.

Research of evolution in action across life at 'evolution canyons'

Eviatar Nevo, Institute of Evolution, Haifa, Israel

Evolutionary processes at the genetic and individual levels of biodiversity are important for future research, both theoretically, with the use of a model, and practically, using natural micro-sites.

Evolution is a system that is affected at all levels from molecular to the biosphere. Certainly, even several generations of inquisitive researchers are not able to register any origin of a new species, in a system (biosphere) that remains relatively stable. But, genetic and intra-specific (individual) diversities are subjected to "visible" evolutionary changes.

Great possibilities to understand many mysteries of evolutionary biology are given by the "Evolution Canyon", Israel. The "Evolution Canyon" has two slopes: a xeric, "African" south-facing slope abutting with a mesic, "European" north-facing slope. The slopes are separated only by 200 meters on average but have very different conditions. The "Evolution Canyon" (ECn) is an excellent micro-site which could potentially reveal many aspects of biodiversity evolution and the genetic basis of adaptation and speciation caused by inter-slope microclimatic divergence.

The long term biodiversity project conducted in the model ECn reveals evolution in action across life from bacteria to mammals at a micro-scale involving biodiversity divergence, adaptation and incipient sympatric ecological speciation. The model highlights diverse taxa species richness, genomics, proteomics and phenomics phenomena by exploring genetic polymorphisms at protein and DNA levels and, recently, genome-wide gene expression and regulation. Genetic diversity and divergence reveal evolutionary dynamics of natural populations exposed to a sharp inter-slope, ecologically divergent, tropical and temperate microclimates on a xeric, tropical (AS) abutting with a mesic, temperate (ES). Four ECns are currently being investigated in Israel: in the Carmel, Galilee, Negev, and Golan Mountains (ECn I-IV), respectively.

We identified 2,500 species in ECn I (Carmel) from bacteria to mammals in an area of 7,000 m2. Local biodiversity patterns parallel global patterns. Higher xerophilous species richness was found on the AS. Mesophilous species richness prevails on the ES. In 9 out of 14 (64%) model organisms across life, we identified a significantly higher genetic polymorphism on the more stressful AS. Likewise, in some model taxa, we found largely higher levels of mutation rates, gene conversion, recombination, DNA repair, genome size, small sequence repeats, single nucleotide polymorphism, retrotransposons, transposons, candidate gene diversity, and genome-wide gene expression and regulation on the more stressful AS. Remarkably, inter-slope incipient sympatric ecological speciation was found across life from bacteria to mammals. The ECn model represents the Israeli ecological analogue of the Galapagos Islands. Microclimatic selection overrides gene flow and drift, and drives both inter-slope adaptive divergence and incipient sympatric ecological speciation at a micro-scale.

Nowadays, with the rapid development of high-throughput techniques of whole genome analysis further genetic and epigenetic research in the sites "pushing on" the evolution is really important. It could potentially clear modern evolutionary processes up including the genetic basis of speciation, and lay a foundation for prediction of future biodiversity trends.

Conserving evolutionary potential in Europe

Timo Vuorisalo, University of Turku, Finland

The Habitats Directive is the key instrument for biodiversity conservation in the European Union. In this directive, maintenance or restoration of natural habitats and populations of wild species of Community interest at a favourable conservation status is defined as an overall objective of conservation measures. The most important practical objective of the Habitats Directive has been the creation of a coherent ecological network called 'Natura 2000'. This network covers the types of natural habitat and wild animal and plant species that are considered to have special importance for Europe. A key criterion of favourable conservation status of a species is long-term viability of its populations. In other words, the population dynamics data must indicate good chances for long-term survival of populations in their natural habitat.

How, then, to conserve the long-term viability of species populations? From the ecological perspective, this question can be divided into several derived or sub-questions. First, what are the minimum viable population sizes (MVPs) for each species, and how do they vary geographically? How big a proportion of local populations need to be viable in order to make conservation status nationally favourable? What are the population structures of protected species? And finally, are the conservation statuses of genetically distinct local populations favourable?

I focus on the last sub-question, which I think has been largely overlooked at the European scale. This may be considered surprising, as the Convention on Biological Diversity (1992) requires that diversity at the genetic level has to be included in conservation targets and monitoring programmes. Genetic diversity within a species also probably correlates positively with its evolutionary potential. In most European countries (admittedly, my experience mostly comes from northern Europe) establishment of Natura 2000 network has been based on local species lists and mappings of habitat types. Genetic studies of local populations have probably seldom been used in justification of new conservation areas. In Finland the best-known exception is the Lake Saimaa seal, a local genetically and morphologically distinct subpopulation of the Ringed seal. Within its range, the Lake Saimaa seal is an important flagship species for conservation.

Although genetically distinct populations within species are not specifically mentioned in the Habitats Directive, site assessment criteria listed in Annex III (Stage 1 B; Stage 2, 2b, 2e) assume that the degree of isolation of Annex II species present in the proposed site is known. Isolated populations may often be genetically distinct for instance due to genetic drift or inbreeding. Annex III specifically requires taking into account of the 'global ecological value of the site for the biogeographical regions concerned' in Community-level assessment of national lists of sites. This clearly supports conservation of local races or subspecies of animal and plant species of Community interest. The greatest obstacle is of course money; financing conservation is not always high in the agenda of national governments.

RE: Conserving evolutionary potential in Europe
Intra-species and inter-species diversity: division of function in the face of human offensive

Elena Bukvareva, Russian Academy of Sciences, Moscow

This message considers the following two main propositions:
1. Viability, adaptability and effectiveness of populations, species and biocenoses are maximum when these biosystems have the optimum diversity (intra-population, intra-species and species diversity accordingly);
2. Intra-species and inter-species diversity "work together" for purposes of adaptation, viability and high effectiveness of wildlife. Diversity at community level (species

diversity) and species-population level (intra-species and intra-population diversity) play a different role in the adaptation of biosystems to environmental changes.

There are the following practical consequences from these propositions:

-   The most useful strategy is to protect communities with not maximal, but with optimal natural diversity; natural communities with low diversity are as important as communities with high diversity.
-   The nature protection strategy must take into account both species and intra-species diversity as an interconnected system.

The principle of optimal biodiversity:

Theoretically, the maximum viability of populations, species and biocenoses corresponds to optimum diversity at population and cenosis levels - i.e. intra-population phenotypic diversity and species diversity – the point $D^*;V^*$ in figure 1. Diversity of undisturbed natural biosystems approximates to the optimum values. In other words the probability of biosystems survival is maximal when they have the possibility to adjust their diversity at optimum levels. Any external factors (both anthropogenic and natural) which change species or intra-population diversity turn biosystems into a suboptimal state and decrease their viability and effectiveness of ecosystem functioning.

Figure 1 Optimum value of diversity (D^*) corresponds to maximum biosystem viability (V^*). V_0, a critical value of viability; D_0, a critical value of diversity; the shaded area is a domain of system existence.
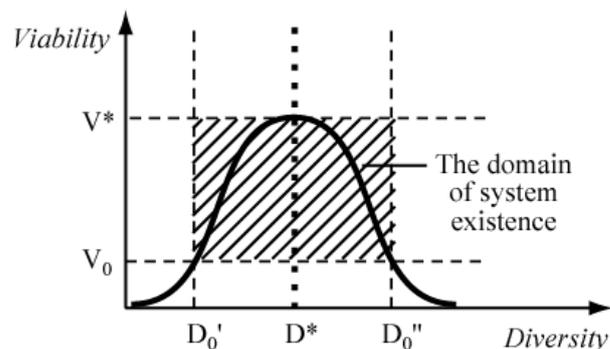
Intra-species and species diversity: interconnection and "division of labour":

Intra-species and species diversity "work together" and play different roles for purposes of adaptation, viability and high effectiveness of wildlife. Our investigations show that reactions of intra-population and species diversity to changes in environment stability are different. Thus, the optimal values of intra-population diversity grow during decreasing environmental stability, whereas the optimal species number decreases. In contrast, the optimal intra-population diversity decreases but the optimal species number grows under increasing environmental stability. Some experiments and field observations confirm that conclusion (see http://optimum-biodiversity.narod2.ru/english_version/).

The opposite reaction of intra-population and species diversity on environmental destabilization displays the difference of their roles in a fluctuating environment. The intra-population diversity is the main adaptation mechanism of populations and communities to environmental instability, and species diversity allows the community more effective resource utilization due to niche differentiation and so we propose to combine both species-population and community levels in the nature protection strategy.

Maximum diversity – may be it a goal?:

The optimum biodiversity principle predicts that natural communities which are adapted to "rich" and stable environments consist of a large number of species with low intra-population diversity (specialists), while communities which are adapted to "poor" unstable environments consist of a small number of species with high intra-population diversity (generalists). In "rich" unstable and "poor" stable environments, we expect the medium level

of species and, consequently, high and low intra-population diversity (see figure 2). These conclusions are made for undisturbed natural systems which exist in a typical historical environment.

Thus, a low level of species diversity (speaking about undisturbed natural systems) is an important adaptation of biosystems to the unstable or severe environment. Therefore natural systems with low diversity deserve no less attention than high-diversity systems.

Figure 2 Assumed levels of intrapopulation diversity as well as the species numbers in communities adapted to different environments.
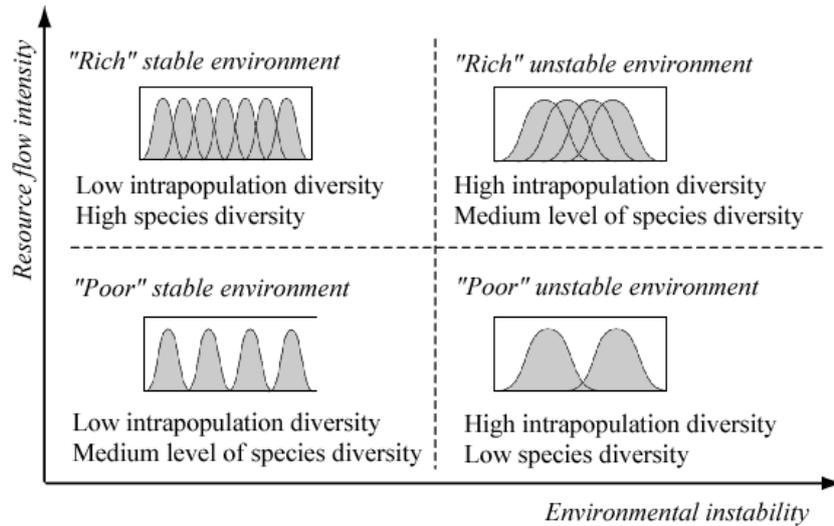
Preserving ongoing evolutionary processes

Andreas Tribsch, Sabine Hille, Matthias Kropf, Günter Gollman, Steven Weiss and Stefan Schindler, Austrian Platform for Biodiversity Research (BDFA), Austria

Outcome of the 2nd annual meeting of the Austrian Platform for Biodiversity Research (BDFA):

Evolutionary responses include changes in the geographical distribution of populations and species. Such changes and resulting evolutionary processes are often related to so-called refugia, i.e. areas, where populations are able to survive climatic instabilities and unfavourable conditions in situ. Refugia hosting reservoir populations are often located in mountain areas resulting in high levels of biodiversity (e.g., endemism and high level of genetic diversity). To get a better insight into these topics, we recommend:
- Carrying out studies of natural populations of all groups of organisms
- Identifying evolutionary significant units (not necessarily species) including phylogeographical methods
- Studying the evolutionary potential of refugia populations by analysing genetic variation and distribution modelling under different climate change scenarios
- Carrying out research focussed on endemic and IUCN listed species that are often located in refugia, which will result in data for targeted conservation efforts regarding these species

Knowledge of the genetic diversity of populations is crucial for understanding adaptive capacities of organisms to changing environments. The mechanisms to understand how fast and effective organisms could deal with it by adaptation and selection is still poorly understood. Especially epigenetic changes in natural (!) populations that result in different evolutionary potentials are unknown. Therefore, we recommend:
- Studying natural populations (e.g., along environmental gradients) by assessing present genetic variation in order to find biodiversity indicators representing future adaptive potential.
- Identifying epigenetic mechanisms as a potential for adaptation

Phylogeographical studies have shown that genetic diversity is often unevenly distributed over a species' geographical distribution. Conservation priorities, however, are usually based on ecosystem and/or species diversity. Given that intraspecific genetic diversity is most relevant for evolution, conservation strategies should also include measures of genetic diversity. Thus, we recommend:
- The integration of genetic variation in conservation measures (as the IUCN demands) and monitoring of populations of target species.
- The use of data on genetic diversity of multiple species for the systematic design of conservation areas and the comparison of the resulting conservation networks with the currently existing ones.

Understanding evolutionary mechanisms, which also include historical changes like environmental change, is important for understanding biodiversity and the evolutionary potential of species. Training in these research areas, especially in identifying wild plants and animals, however, has often been cut down in universities. Thus, it must be guaranteed to:
- Provide an educational basis in evolutionary biology and biodiversity (organism biology) by promoting teaching of these subjects in, but also outside universities.

Evolution and Biodiversity
The evolutionary basis of biodiversity and its potential for adaptation to global change

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Session II: Evolutionary responses to anthropogenic pressures

Changing organisms in changing anthropogenic landscapes

Hans Van Dyck, Biodiversity Research Centre, UCL, Belgium

The author outlines the importance of incorporating evolutionary dimensions in conservation management strategies.

The general aims of conservation biology are twofold: 1) documenting and interpreting patterns of change and 2) providing insights to manage biodiversity in order to alter patterns of change. For the latter, we need to understand the mechanisms behind the patterns. Then, evolutionary ecology is an essential field (Carroll and Fox, 2008). Organisms deal with the environment by their phenotype including morphology, physiology, behaviour and life history traits (e.g. like fecundity, dispersal propensity and ability). These traits have been shaped by evolutionary processes, and they can be under further change by selection or drift. This is not necessarily a slow process. Rapid evolution – i.e. genetic change occurring rapidly enough to have a measurable impact on simultaneous ecological change (Hairston et al., 2005) – is likely to be of significance for several conservation issues.

For several conservation applications species are assumed to have fixed life-history traits (e.g. mobility or fecundity) in changing environments. Although reductionism is an important principle for science, we should not ignore within-species variation for conservation. Focusing on the ecology only (i.e. distribution and population size) and hence ignoring the evolutionary dimension (i.e. significant differences between populations and individuals) leads to different, and arguably less efficient management strategies. This has been demonstrated for fisheries (e.g. Olsen et al., 2004). An evolutionary approach is already incorporated in current text books on (applied) ecology, but we have not yet implemented these important insights and consequences for conservation programs.

In rapidly changing landscapes, different organisms have been shown to make mistakes for habitat-use as they rely on formerly reliable cues that no longer correspond to good habitat (i.e. ecological or evolutionary traps - Schlaepfer et al., 2002). In such cases, data on presence/absence are not sufficient to deal with this; a species can be present with no (or low) reproductive success. This brings us to the significant issue of the extinction debt (Kuussaari et al., 2009).

Species differ in their ability to deal with anthropogenic environments. The 'ecological view' of declining localized habitat specialists – species typically on Red Lists and European directives – versus stable habitat generalists is not reflecting the entire story of the current biodiversity crisis. Several ecosystem functions rely on widespread species with high abundances. Recently, several widespread species have shown strong declines (e.g. Van Dyck et al., 2009; Forister et al., 2010). In conservation we often adopt simplistic ways of deciding what exactly a habitat of a species is (Dennis et al., 2003). Structural habitats through human eyes (biotopes, corridors) are not necessarily functional habitats through other organisms' eyes given their evolutionary history and the ongoing interplay of action-and-reaction of organisms and their environment.

What really makes a species a winner or a loser under anthropogenic environmental conditions, and to what extent we can create new perspectives for current losers, are essentially issues of applied evolutionary biology. Hence, life history strategies, structural verses functional habitat, evolutionary potential, adaptation by genetic and epigenetic effects (e.g. phenotypic plasticity) should be considered key concepts for conservation biology. We are not lacking challenges for the post-2010 timeframe. In line with the general plea for evidence-based conservation (Sutherland et al., 2004), we definitely need greater efforts to translate evolutionary insights in workable formats and language for policy makers and conservation practitioners. This translation requires experts with skills in different fields (evolutionary biology, conservation, policy making, communication).

RE: Changing organisms in changing anthropogenic landscapes
Global change and mechanisms of ecosystem function

Vladimir Vershinin, Institute of Plant and animal Ecology RAS, Russia

With the most common position - the evolution of biodiversity is on the way to maximize the use of environmental resources. The biosphere and all cycles of energy and substance flow are completed, step by step, during the evolution process. This is why the presence of higher biodiversity is one measure that is used to evaluate the stability of an ecosystem. The high degree of biodiversity, at different hierarchical levels of biogeocenoses, is an important factor in ecosystem homeostasis. The other criterion of ecosystem stability is the presence of complete functional blocks – the presence of producers, consumers and reducers guarantees ecosystem sustainability.

We have a lot of examples of functional changes in ecosystems that have occurred as a result of human-induced transformation of natural communities. Examples include food chains of native and invasive species, host-parasite relations, morphogenesis and genetic structure. Genetic structure, morphogenesis and reproductive parameters of populations are strongly influenced by life history canalization and interrelationships with different functional groups in man-transformed communities. Existing environmental changes are defined by long-term vector transformations of communities and population structure as well as the interrelationship of main functional blocks.

Reported changes in these functional relationships may seriously affect the environment-forming activity of biota. It is evident that the balance of ecosystem homeostasis depends on the contribution of the main functional blocks of a community. Transformed ecosystem structure is simplified due to the disappearance of some sensitive species, thus shortening food chains. Therefore, the stability of such systems is maintained by increasing the metabolic rate and energy. In the modern biosphere, along with ancient factors responsible for community's divergence are powerful new factors generated by human activity. Rapid transformation of the modern biosphere under effect of global change leaves no time for evolution, but only adaptation. In this situation pre-adaptive features of some species and populations play a very significant role. With this point of view, the adaptive potential of species and populations depends on their specific genetic structure and their ability to react to change (norm of reaction). This is why complex long-term monitoring is necessary for effective biodiversity conservation.

RE: Changing organisms in changing anthropogenic landscapes

Ferdinando Boero, University of Salento, Italy

I agree with Hans Van Dyck's statement: "The general aims of conservation biology are twofold: 1) documenting and interpreting patterns of change and 2) providing insights to manage biodiversity in order to alter patterns of change. For the latter, we need to understand the mechanisms behind the patterns." But we must distinguish ultimate from proximate causes. Proximate causes affect single species or habitats, and might be buffered in contingent ways (including ex situ conservation, or specific protection at given places, e.g. protected areas), but the ultimate cause is the unbearable anthropogenic pressure on natural ecosystems. There are too many of us, furthermore a part of us (the so called first world) is living in such a way that, if all other humans would live similarly, it would make the world inhospitable for our species. The first thing to do is to reduce the pressure of the first world. We are trying to do this, by simply transferring polluting activities elsewhere (Bhopal?).

Evolutionary ecology teaches us that all species tend to increase their fitness, but the world has no space to contain all these organisms. The most successful species, recognized by the large size of their populations, pose the premises for their own collapse, because their use of resources limits the turn-over of the resources themselves, hence: famine, war and disease.

There is a Lotka-Volterra game between us and the rest of the world. Our curve is going up; the rest of the world is going down. We know already that no species can go up indefinitely. The rest of the world will go up again when we go down. This is the main message that evolutionary ecology can offer to politicians and decision makers. Economists want all indicators to go up. They are preaching infinite growth of our welfare (in economic terms), disregarding the fact that we live in a finite world. We can provide advice on single conservation issues, but this game will not solve the problem. It will cure some symptoms (or remove some proximate causes) but it will not remove the ultimate causes. We can play the game, and ask for some money to study contingent issues. But we know the solution very well. The problem is how to enforce it.

In previous messages I said that predictions are impossible in complex systems. Now I make a prediction: we cannot continue to grow. This is obtained by a gross simplification, reducing the interactors to two: us and the rest of the world. We are the predator; the rest of the world is the prey. We evolve very quickly, with technology. The weakest components of the rest of the world will be affected by our increased efficiency. We will lose the whales, and the panda, and the polar bear, but what we call "pests" will remain. It is a hopeless battle. We cannot win a fight with Nature. Simply because we are part of Nature, and fighting it equals fighting against ourselves. The problem is cultural.

Politicians must stop listening just to economists; they must also listen to evolutionary ecologists. Notice that I use the words "just" and "also". One very simple question: if the laws of economy are in contradiction with the laws of nature, what laws will win over the others? So, ecology and evolution do have a logical primacy over economy. But at the moment it is the opposite. We invented the laws of economy; the laws of nature were there even before us. We must mould the laws of economy into the laws of nature. This is the challenge. Ecological economics is a solution, but just to a certain point. Giving a monetary price to goods and services, or to species and habitats, is not the ultimate solution. And now I will not go into the philosophical distinction between price and value. We cannot solve the problem by using the conceptual tools of insurance companies.

RE: Changing organisms in changing anthropogenic landscapes

Pablo Goicoechea, NEIKER-tecnalia, Spain

I certainly agree with the points of view expressed by Ferdinando Boero in his last post. I further think that one of the main tasks of this taskforce (the EPBRS meetings, people participating to these e-conferences, the BioStrat people, etc) is to make politicians understand that economic value of biodiversity is not the only reason to preserve it. A hint: Just after the last e-conference, Martin Sharman pointed us towards a Nature paper that should be discussed at this forum (probably not this e-conference, which finally talks about the missing part in most biodiversity discussions). We need a clear message, just like climate change people have. And for the moment, it seems we are just arguing among ourselves.

By the way, the moral point of view for preserving biodiversity is fine, but that view can be expressed by any person without a scientific background. I would argue that if politicians ask scientists how and why to preserve biodiversity, they probably expect scientific answers, not moral ones.

RE: Changing organisms in changing anthropogenic landscapes

Hans-Peter Grossart, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Germany

The contribution by Hans van Dyck calls for a better insight and understanding of patterns underlying evolutionary processes. A topic which in my opinion has been greatly neglected is the interrelationship between organisms and populations. In an increasingly anthropogenically

modified world these interrelationships become increasingly altered. That is migration and dispersal not only by abiotic factors but in particular organisms as vectors are increasingly disrupted. For example, more and more aquatic systems become isolated from other aquatic systems or their natural watershed. Hence, many migrating organisms are unable to move between their natural habitats. This does not only result in decreased dispersal of the migrating species but also of species whose life cycles are interrelated with the migrating species. For example, many microorganisms (protozoa, alga, fungi and bacteria) can attach to and detach from migrating organisms for long range dispersal. Additional, higher organisms may be dispersed by other organisms in the form of resting (seeds, eggs) or larval stages.

Hence to understand evolutionary processes and changes in biodiversity related to anthropogenic activities, we need to take the entanglement of organisms and organism networks into account. In microbial ecology we have just begun to realize how important such biological factors are for adaptation and evolution of single species but also for whole populations. For higher organisms many examples have been previously shown. The entanglement, however, also exists between species and populations of different ecotypes, i.e. the watershed does not necessarily reflect the natural boundaries of a lake when migrating organisms lead to import and export not only of organisms but also of organic matter and energy. When managing biodiversity of a given ecosystem we should be very careful in studying the whole extent of interconnectivity between species, populations and ecosystems. This important fact also needs to be incorporated in future modelling approaches.

RE: Changing organisms in changing anthropogenic landscapes

Ferdinando Boero, University of Salento, Italy

The problem of preserving biodiversity has been raised by scientists with the goods and services issue, and with the ecosystem functioning issue (which is a side issue to the services argument). Goods are provided by few species, if compared to the whole of biodiversity. Services might be provided by much more, but we are at present not knowledgeable enough to state what these services are that are provided by the single species. Phytoplankton are important, but are all phytoplankton species equally important? If we do not even know what the species are, how can we say that they are important? The moral issue is important, because the right of existence of species should be guaranteed in spite of their presumed lack of utility (for what purposes, then?). If we keep just the "useful" species the world would be very different from the way it is. The result is the agro-ecosystem.

We often use concepts of ecosystem functioning based on processes that are carried out by bacteria. So our experiments end up showing that biodiversity is not so important for ecosystem functioning. These experiments usually take care of a very restricted number of species of a single trophic level (e.g. 16 species of prairie grasses) and use a general proxy for ecosystem functioning (e.g. plant production). If biodiversity is 16 species and ecosystem functioning is plant production, then we are going to have trouble trying to demonstrate the importance of biodiversity in ecosystem functioning. General messages are very important, and I am very happy if Nature will publish something about these issues. The moral part, however, is not to be forgotten. Sometimes it is the only issue that the general public understand.

By the way, the Pope opened the New Year with a clear cut message: If you want to preserve peace, you must preserve the environment. It would be ironic if the scientific community were less convincing than a religious authority in delivering a message about the importance of the environment.

RE: Changing organisms in changing anthropogenic landscapes

Vladimir Vershinin, Institute of Plant and Animal Ecology, Russia

I agree with Ferdinando Boero and I want to mention that the human population of our planet is not a unified reasonable society moving to common human interests. Unfortunately, we're not a united community, living in harmony with nature.

There is no common humanity living under the laws of collective intelligence which could stop or compel a reasonable limit to technological civilization. The elite of a modern industrial society will not refuse the boons, privileges and profits which it has got due to traditional ways of development of mankind. Changes in people's minds in a technological society is possible, but only for the part that is able to rise above the level of average minds, i.e. those able to voluntarily give up making individual or collective actions that can lead biota to disaster. The emergence of such a change would be an adequate level of significant interspecies differences in brain development. It is necessary to think how to change the minds of those whose whole life is living inside our technological civilization and enjoy all the benefits and privileges of an industrial society. And this is not a role-playing game, which is so abound in all kinds of training.

Fragmentation does impair adaptive responses to environmental stress

Kuke Bijlsma, University of Groningen, The Netherlands

From a population genetics perspective, fragmentation of populations results in small, isolated populations that are subject to genetic drift and inbreeding. These processes cause decreased fitness, decreased tolerance to environmental stress and, most importantly, significantly impede adaptive responses to changing and stressful environmental conditions. This is a major threat for biodiversity persistence.

To meet anthropogenic changes of the environment it is essential that populations can cope with the imposed stresses at both the short-term and the long-term. At the short-term the initial tolerance and the adaptive plastic response (phenotypic plasticity) are decisive parameters. At the more long-term evolutionary adaptive responses are of paramount importance. As we are mostly dealing with short or intermediate time scales, rare beneficial mutations will be uncommon and consequently the evolutionary response will mainly depend on the standing genetic variation. Hence, the ability to cope and adapt to changing conditions will depend both on how well individuals can adjust to the new conditions and on the amount of genetic variation for relevant fitness traits available for evolutionary responses. Here I argue that fragmentation of habitats and thus of populations will strongly impede such adaptive responses.

Destruction of habitats has caused once large populations of many species to become small and fragmented. Subdivision of once large populations into small population fragments (subpopulations) in combination with limited gene flow between fragments (metapopulation structure) will affect the availability of genetic variation greatly. From a population genetics perspective, small, isolated populations are subject to genetic drift, resulting in both loss of (adaptive) genetic variation and an increase in relatedness among individuals (an increase in inbreeding coefficient). This has severe consequences for the adaptive response of such populations to environmental changes (stress).

For normally outcrossing organisms, an increase in inbreeding coefficient (an increase in homozygosity) is generally accompanied by inbreeding depression affecting most fitness components negatively. As a consequence, inbred populations on average do have a lower basal fitness than non-inbred populations. Consequently inbred populations show already a decreased fitness and lower tolerance even under near optimal environmental conditions (see left panel of figure 1). This will significantly increase their extinction risk.

Particularly in agricultural practice, it is well known that many organisms show decreased developmental homeostasis upon inbreeding. As such, inbred populations are more susceptible to environmental perturbations (although the magnitude of it varies considerably among populations) and often they suffer far more from stress than non-inbreds. In other words, inbred populations show a decreased tolerance to stress. Experimental evidence has shown that the fitness of most inbred populations is significantly more affected by extreme temperatures than non-inbred populations, while, at the same time, the tolerance range of inbred populations seems to be significantly decreased (see right panel of figure 1). In conclusion, inbreeding can impair adaptive plasticity.

Genetic drift, random fluctuations in allele frequencies, will upon fragmentation cause the genetic variation originally present within a large population to become redistributed among the remaining small populations. As different alleles will get fixed in different small populations, this will result in substantial genetic differentiation among the populations, where some may lack (fixed for the non-adaptive variants) or have only low frequencies of the adaptive variants while others are (nearly) fixed for the adaptive variants. This will result in large differences in initial tolerance when these populations encounter a novel stress (see left panel in figure 2), and some of these will go readily extinct. Consequently, after several generations of exposure to stress, some subpopulations show a significant increase in stress tolerance while others, lacking adaptive variation, are unable to improve their fitness under stress (see left panel in figure 2). In addition, compared to large undivided populations,

fragmented populations will show lower levels of standing genetic variation and, consequently, their adaptive potential is necessarily decreased. Experimental evidence shows that metapopulations show on average a smaller adaptive response than undivided populations of more or less the same size for several stresses (see right panel in figure 2). In short, both initial tolerance and the evolutionary adaptive response will become impeded after a history of fragmentation.

Summarizing, fragmentation of (formerly) large populations due to ongoing habitat destruction induces genetic processes that will necessarily limit adaptive responses to changing environments, both at the short-term and the long-term. This implies that ongoing fragmentation will significantly enhance the adverse effects of human induced alterations of the environment (like climate change) and does endanger the persistence of biodiversity significantly. Promoting sufficient gene flow between fragments will therefore be an important management measure, as this will, at least partly, restore the adaptive potential. Moreover models built to predict the persistence of biodiversity under anthropogenic stress should preferably take the genetic consequences of population fragmentation into account.
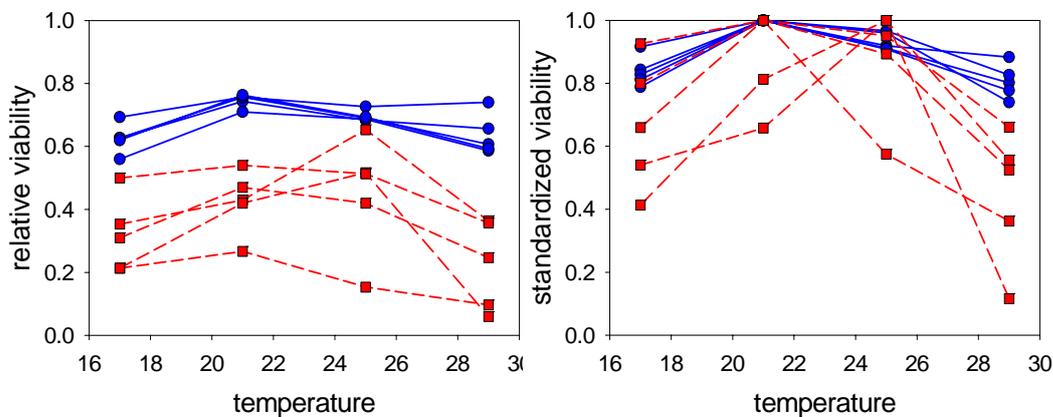
Figure 1 The impact of inbreeding on stress tolerance: viability (egg-to-adult survival) of five inbred (red squares) and five outbred populations (blue circles) of *Drosophila melanogaster* at four different temperatures. The left panel shows that inbred populations have on average a significantly decreased viability compared to outbred populations (inbreeding depression) at all temperatures.

To uncover the relation between viability and temperature, the right panel shows the viability of each population relative to the highest viability at any given temperature observed for the same population (standardized viability). The graphs show that viability is the highest for the intermediate temperatures and that it decreases towards the more extreme temperatures. Importantly, this decrease in viability at the stress temperatures is significantly larger for inbred populations than for outbred populations. This shows that inbreeding not only comprises viability, but that the effect becomes greatly enhanced under stress conditions. (R.. Bijlsma, unpublished data, see also Joubert & Bijlsma, 2010).
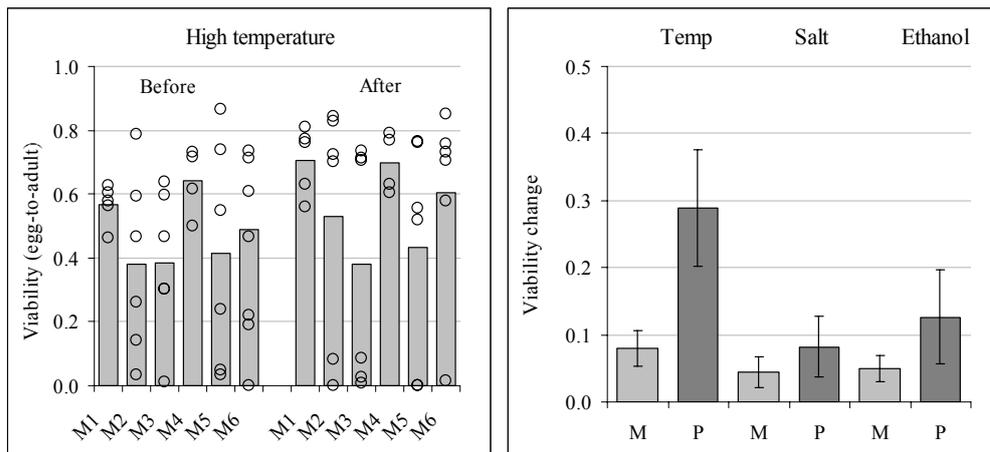
Figure 2 Consequences of population subdivision (fragmentation) for tolerance and adaptive potential of populations

The left panel shows the viability (egg-to-adult survival) at high temperature of six metapopulations (M1-M6, grey bars) before (left set) and after (right set) six generations of adaptation to high temperature. Each of the metapopulations had previously been maintained as a subdivided population with six small subpopulations (open circles) for 40 generations. (For details see Bakker et al. 2010). Before adaptation there is substantial variation among subpopulations within metapopulations with respect to tolerance to high temperature stress as a consequence of genetic drift in the subpopulations. This variation turned out to be due to one or a few recessive deleterious alleles, that when homozygous caused near lethality at high temperature. After adaptation (right set) the distribution in viability becomes highly bimodal: many subpopulations have adapted and show a near optimal viability under stress, but a subset shows a near zero viability. As a consequence of subdivision, the latter subpopulations seem to have lost the adaptive allele(s) and become fixed for the sensitive allele. These are unable to adapt and are expected to go extinct under high temperature stress.

The right panel shows the adaptive response (change in viability) after six generations of adaptation at several stress environments. It shows the average improve of the six metapopulations (grey bars) compared to undivided populations (black bars) that had been maintained as populations of nearly the same population size as the total size of the metapopulations. For all stresses, the increase in viability as a result of the adaptive process is greater for the undivided populations. This shows that fragmentation does decrease the adaptive potential of populations (data from Bakker et al. 2010).

RE: Fragmentation does impair adaptive responses to environmental issues

Ferdinando Boero, University of Salento, Italy

All considerations by Kuke Bijlsma are right. But they can also be read the other way round; especially, but not exclusively, in agriculture. Our experience with pesticides shows that target populations shrink, but this ends up in enhancing their resistance to pesticides, since the survivors are the few resistant specimens that become the founders of new populations. After a while the species becomes stronger. Probably the shrinkage and expansion of natural populations (a rather common pattern) is the most common way in which species evolve in an anagenetic fashion, as envisaged by Carson's flush and crash model. If the connections dividing the fragmented populations after a crash are restored during the flush, the species changes, i.e. evolves. We know from the peripatric speciation model that the formation of side populations is conducive to evolutionary change, also in a cladogenetic fashion. Of

course, like all innovations, evolutionary ones are risky. Population fragmentation is probably the main evolutionary driver.

In a way, humans are a selection agent. The paradox is that we seem unable to eradicate the species that are classified as pests, but the species we care for are very sensitive to our actions. In a way, and this is the basic principle of the EU Habitats Directive, it is tenuous to pretend to conserve single species (e.g. by the construction of corridors) if their habitats are destroyed. The application of the Habitat Directive should take the issues proposed by Kuke into serious account, but they should be enforced at a habitat level. The problem is: what is the maximal fragmentation that a given habitat can withstand before a given percentage of the species inhabiting it becomes endangered? What is the dispersal ability of a species during a flux?

Another issue is the arrival of aliens. Many alien species are now reaching Europe, both on land and in the sea. They usually arrive with a few founders, passing apparently insurmountable barriers, and some can become established in a very dramatic way, so changing the local biodiversity, and even the ecosystem functioning. On the one hand, global change is a threat for species of a cold affinity, whereas it promotes the dominance of species of a warm affinity. Founder effects, inbreeding and low genetic variability seem not to affect the successful aliens. Sometimes they are classed as responsible for the failure of resident species, but they might simply be the substitutes of declining resident species, due to climate change. Again, what are the targets of our action: single species, habitats or ecosystems? Is it feasible to try to save a species once its habitat is destroyed or radically changed? Does conservation mean that nothing has to change?

Natural selection acts through interactions between the organism and its environment. Ecology and evolution must be linked in an indissoluble fashion if we want to understand what is happening, and even more if we pretend to be able to do something to change the trends of environmental change currently on course on our planet.

RE: Fragmentation does impair adaptive responses to environmental stress

Francois Bonhomme, Institute of Evolutionary Sciences, France

We should be cautious of making too general statements. Yes, fragmentation has no doubt many negative impacts, and it corresponds indeed to a change in gene flow regime for the species under consideration. But not all species are high gene flow species, sometimes long range gene flow is detrimental to local adaptation (I would like to recall here the Paradox of Rockall on *Littorina* species – Johannesson, 1988), and in some cases also, moderate inbreeding can help purging deleterious genes. So indeed fragmentation could also promote local adaptation and the rise of evolutionary novelties...

RE: Fragmentation does impair adaptive responses to environmental stress

Joachim Mergeay, e-conference chair, INBO, Belgium

At the onset of this conference and also of this session, we have started to argue that we need a more dynamic view on biodiversity, as populations change due to adaptation to novel circumstances. Probably some of the most striking examples include endangered native species that now entirely depend on invasive exotic species (Van Riel et al., 2000).

However, as indicated by Kuke Bijlsma's contribution (and previous comments on other presentations), the effects of habitat fragmentation and the interaction with other components of global change may well lead to a breakdown of (selective) evolutionary processes, and result in a less dynamic response! This reduction in evolutionary responses may be countered by ecological processes (dispersal, range shifts, competitive displacement by opportunistic species ...).

As Ferdinando Boero commented on Hans Van Dyck: to solve the biodiversity problems imposed by global change, we need to tackle the ultimate causes (human

overpopulation) instead of focusing only on proximate causes. But is this a task for biologists?

RE: Fragmentation impairs adaptive responses to stress

Pablo Goicoechea, NEIKER-tecnalia, Spain

This is a very interesting topic and was very well addressed by Kuke Bijlsma. However, I would like to stress two further points arising from his communication.

The first one refers to scale. How much fragmentation in a landscape is dangerous? What fragment size is dangerous? Evidently, the answers to these kinds of questions depend on the subject (species) we focus on and the mobility of its gametes. The same landscape can be considered non-fragmented for, let's say, wind-pollinated trees and considered as extremely fragmented for small rodents, insect-pollinated plants or soil invertebrates. How should managers address these questions?

The second one, related to scale too, is the size and abundance of corridors. How much gene flow is "sufficient" gene flow? Even outcrossing organisms in a continuous (non-fragmented) landscape tend to show genetic structure as a result of relatedness (i.e.; the probability to mate with others is related to the distance). For many organisms, would corridors be sufficient? Should managers translocate individuals/populations to help gene flow?

RE: Fragmentation does impair adaptive responses to environmental stress

Kuke Bijlsma, University of Groningen, The Netherlands

First of all, I agree with Francois Bonhomme that "We should be cautious of making too general statements". Unfortunately, bringing across a complex matter as I discussed in say 500-600 words does not leave much room for nuancing and refined statements. We all know there are exceptions: some species, particularly plants, are used to high levels of inbreeding and will show little inbreeding depression upon further inbreeding; many species normally live in small breeding units and will be little affected by fragmentation of landscapes; local adaptation can be a problem for reintroductions or genetic rescue, but on the other hand can promote the formation of local races (given the fragment did not go extinct before it evolved); purging of deleterious alleles can alleviate the ill effects of inbreeding, but Darwin already showed that many normally selfing species show highly increased fitness upon outcrossing, indicating that purging is not that effective. Notwithstanding the above, the increasing number of (endangered) species that visibly suffer greatly from genetic and environmental problems show that such arguments are not a permit to ignore the adaptive genetic considerations as I discussed. Boldly stated, adaptive genetic processes should always be one of the issues to be considered when developing management measures. Whether this will lead to specific actions depends on the situation. In my opinion, adaptive genetic measures should be included in a management plan whenever feasible.

I like the examples presented by Ferdinando Boero, as they illustrate in some way what the catch is.

In the pesticide resistance example, a large population (as pests normally show) that through mutation contains a small fraction of resistant individuals (pesticide resistance, disease resistance and metal tolerance are nearly always found to be pre-existent), is subjected to a severe stress. The fraction of resistant individuals survives and can rapidly expand again (pests generally have high growth rates). In the examples I discussed, a population is first bottlenecked by fragmentation for some time, thereby losing the resistant alleles through genetic drift (the lower the frequency of an allele, the higher the probability it gets lost). If this small population is subjected to stress, no resistant individuals are present in the population anymore, and the population goes extinct. (For experimental evidence that initial population size is crucial for adaptation, see Bell and Gonzalez (2010)). Thus the large

population harbours resistant alleles and will persist when stressed, whereas a fragmented population will with very high probability lose the resistant alleles and will go extinct under the same conditions. This is exactly the point I am raising in my contribution.

In the "founder-flush" model of evolution species undergo a bottleneck, but thereafter can expand freely as the species has entered an empty niche where intra- and also possibly inter-specific competition is minimal and, as such, natural selection pressures are greatly reduced (in fact this also holds for the pesticide and the invasion examples). Firstly, the species undergoes a relatively short bottleneck phase, where some variation is lost, but during the expanding phase no additional variation is lost. Secondly, because the natural selection pressures are low, even relative "badly" adapted individuals will survive (also promoting a rapid increase in size), that in the end, because of recombination, will promote rapid adaptation and evolution. Contrastingly, in the situations that I picture, the population is small for an extended time, cannot expand and does experience increased selection pressures. Thus the possibility to persist and to evolve is greatly reduced in the latter situation.

In summary, on the one hand, genetic drift may promote evolutionary processes as it changes and redistributes gene pools and can result in an increase in biodiversity. On the other hand, when populations are permanently small due to habitat fragmentation, the process of genetic erosion will cause a decrease in adaptive potential, impair evolutionary processes and through extinction lead to a decrease in biodiversity. Given the (western) European situation, where habitats are greatly (and most probably permanently) fragmented, the latter scenario, unfortunately, predominates.

Understanding evolutionary processes during past Quaternary climatic cycles: Can it be applied to the future?

John Stewart, Natural History Museum, UK

Climate change affected ecological community make-up during the Quaternary which was probably both the cause of, and was caused by, evolutionary processes such as species evolution, adaptation and extinction of species and populations.

The Quaternary, the last 2.6 million years, with its regular and extreme climatic oscillations at different amplitudes and the accompanying ecological variation would appear to be a likely time for species evolution.

Despite this, it has been claimed that Quaternary climate change has acted in such a way as to decrease the opportunities for species formation rather than be the principle driver of modern species evolution. This is because the differentiation that occurs because of endemism in allopatry during glacials would be undone in subsequent interglacials by the interbreeding of the formerly allopatric populations (Coope, 1978; Bennett, 2004; Klicka & Zink, 1997 versus Avise & Walker, 1998; Lister, 2004). The opinions seem to be driven by the nature of the fossil record of each organism type studied. (For example the difference between two closely related modern birds will often be in their plumage and song which do not preserve and not in their osteology).

In contrast there is much evidence for ecological change during the Quaternary and in particular the existence of non-analogue communities – organisms living together in the past that do not live in sympatry today (Graham, 1990; Williams & Jackson, 2007). These non-analogue communities have also been shown to become less analogue with deeper time (Stewart, 2008). Therefore, it is clear that in each subsequent oscillation the environment did not return to the state it was in at the equivalent stage of the preceding oscillation.

It seems likely that the ever changing mixtures of organisms will have had an evolutionary effect on the organisms making up changing communities. This effect has been called the "New Neighbour Hypothesis" (Hewitt, 1996, 2000; Stewart 2009) and suggests that the Quaternary probably involved more evolution than often claimed. If this is the case the existence of non-analogue communities which become progressively more non analogue with deeper time maybe act in part as a proxy for this evolution that may not be visible in the fossils of certain organisms.

The cause of non-analogue communities is generally believed to be because of the individualistic nature of species. This is that species respond to climate change by expanding or contracting their geographical range and not whole ecological communities of species.

The implication of the individualistic nature of species is important to conservation biology as it implies that species are unlikely to respond as communities in the future. This is already being observed with the arrival in Britain of birds that have never lived here before such as the little egret and the cattle egret (whether caused by climate change or not) (Stewart, 2004) and through the detailed study of woodland ecologies in Southern England (Keith et al., 2009). This in turn suggests that we should expect the unexpected much as it has been suggested that we should expect non-analogue climates in the future (Williams and Jackson, 2007).

Studies of ancient DNA from the fossils of extant mammals during the late Pleistocene shows that animal species that lived in non-analogue communities in the past were often made up of extinct genetic clades (with no living descendents) (Dalén et al., 2007). This may in part explain the fact that they lived in non-analogue associations in the past. It has also been shown that at times these extinct populations were subsequently replaced by allopatric conspecific populations (Leonard et al., 2007).
The latter implies that population turnover is a process that can take place due to climate change and that widespread genetic populations can become extinct and be replaced by less widespread populations. This may not always, or even generally, be the case as it depends on the availability of a suitably adapted population to replace the extinct one.

Finally, many cold adapted species are likely to have evolved from more temperate ones during the Quaternary as the cold environments are relatively new (Stewart et al., 2010). The most obvious example is the polar bear which nests within the brown bear phylogenetic tree. This is in addition to the speciation scenario that has been invoked by the differentiation within temperate species while in different southern refugia (Hewitt 1996; Lister 2004).

What we need to know now is more about the genetic make-up of the populations of animals living in different ecological community combinations. The hypothesis is that organisms living in non-analogue combinations are made up of extinct populations. The results would give us a better understanding of the relationship between ecology and evolution driven by climate change.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Martin Sharman, European Commission, Belgium

N.B. The following views are purely those of the writer and may not be regarded as stating an official position of the European Commission.

The contribution by John Stewart, which I find particularly interesting, gives rise to the following reflection. Humans are currently wildly and heedlessly stripping the assets of their own planet. This has brought on a poly-crisis, of whose various elements increasingly afflict the most disadvantaged nations and peoples, and one of whose manifestations is a ruinous assault on the rest of the living world. Many of the elements of the poly-crisis seem to be approaching a cusp at which we can expect transitions from a regime that we recognise to one that will not be familiar.

Whatever the next quarter-century will bring, we can be sure that it will be nothing like the last 25 years. If you find this hard to believe, work out the doubling time of a 3% growth in the economy of the world, and observe that $8 = 4+2+1+1/2+\ldots$ The meaning of this is that in the next 23 years, a 3% growth would mean that we will consume as much resources, and generate as much waste, as all humans in the history of the world. That's the rock. The hard place is this: we have no idea how to survive as a society without that growth.

We can no longer avoid significant changes in the relationship between humans and the rest of the world. The change might be for the better. There is, after all, an outside chance that we can quickly establish a balanced and mutually beneficial relationship between "us" and "them," but unless you like betting on Black Swans, you might not want to wager your house on it. Except, of course that you already have. There is also an outside chance that – as one of my colleagues believes – God will deliver us from evil. Personally I'd put the chances of that happening in the femto or yocto realms of probability; as rumour has it, god is busy on a different M-brane.

Given the widespread lack of political understanding of, or attention to, the causes of this global malaise, what seems far more probable is that our institutions will be overwhelmed by the scale and speed of the change that will come upon us. What, then, will be the evolutionary consequences? I would surmise that after the crunch, humans will not be able to do nearly as much damage to the living world as we do now. The immediate pressure will be off, but the planet is already condemned to considerable change, if only from the inertia of the climate system. The extinction spasm will continue in the oceans and on the land. I do not think that the Quaternary is likely to give us much clue as to the future. I think we should be looking at what happened at and after the Triassic-Jurassic (or even the Cretaceous-Tertiary) boundary.

As for Pablo's comment, with which I completely agree, it seems to me that we should try as hard as we can to get the message across that any society or civilization that must decrease biodiversity for its survival or well-being is, by definition, not sustainable. Since the word "sustainable" has been so prostituted that it has lost all meaning, let us make it clear. If you must destroy biodiversity at a global scale to survive, your civilization is condemned. The

faster you get rid of biodiversity, the sooner the end will come. It doesn't matter a hoot whether the thing you are destroying is worth, by whatever imaginative reasoning, €1 or €1yotta. Losing biodiversity at a global scale is a symptom of a fatal disease.

What research should we be doing, then? Well, there are 2 kinds of research you could do. On the one hand, research on biodiversity itself. On the other, research into stopping the loss of biodiversity. In the first case, you will learn a lot about the living world, or about its history; interesting, certainly, but perhaps not, in the current conjuncture, terribly important, since such learning may have little worth in the strange years to come. In the second case, the focus is on the sustainability of the human endeavour. Accelerated biodiversity loss is not a thing in its own right. It is a symptom of a dysfunctional relationship between our species and its environment. That is where we must – urgently – focus our efforts. That is where research money should go. Where is the living world going? How might we establish and sustain a balance, even at this late date? What can we do to prepare for a world unlike any we have ever known?

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Gernot Gloeckner, IGB, Berlin

Indeed economic growth condemns the planet to doom. But who will tell, say, 50 % of the people that they have to die for ecological reasons? Of course in the long run, this will be inevitable, but it is even more discouraging that no society ever survived exploiting their immediate surroundings. If we centre our efforts round the well being of humankind then in the very best scenario we would end up with an agrarian planet with mere crop diversity. In this case we must act like librarians who store away their books for future use. Thus, it is better to spend every single Euro on the inventory of what we will certainly loose. This has to be done down to the nucleic acid level of every species and up to the interconnections of the so far existing ecological communities. If we are lucky a time will come that we can use our knowledge to restore an environment which resembles what we have lost. In the worst case, amoebae will survive and start a new evolutionary round.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

John Stewart, Natural History Museum, UK

In response to Martin Sharman's comments: we are still in the Quaternary so I think that to dismiss what this time period has to offer out of hand is not wise. I concede that other time frames can also be looked at but necessarily the resolution will be much poorer. The last 30 thousand years include a dramatic cooling with ice coming down as far as southern England and then warming events leading to today's climate. This is pretty dramatic and we can date them to within as little as 200 years. Earlier time frames would involve dating to an accuracy of millions of years. The other advantage of the Quaternary is that it mostly involves extant species, the very ones we are worried about which also helps understand what is happening ecologically despite the problems I discussed.

The reason I believe that we should look at the Quaternary is simply because we have to make decisions about what we spend money on in any efforts to conserve etc. This signifies that priorities will have to be drawn up. In that case and from an evolutionary perspective we should be thinking about what are the most important evolutionary units or maybe more importantly the populations that will need to survive to cope with future natural oscillations of climate. Additionally, beyond the time frame of current policy thinking, a very challenging perspective is that we may need to consider conserving for the next Milankovitch cycle (glacial event) because in our present Quaternary mode we are due for a glacial next (likely in a hand full of millennia). If we are serious in conserving for our broad time frame then this is a consideration that we need to make. It has of course been argued that global warming negates any future glacial stage however this is not something that can be assumed.

So I would say that if we are to pursue "evidence-based" conservation as suggested by Bill Sutherland then our past is one good source of evidence, especially if we are talking about evolutionary processes that are not visible on short time scales.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Joachim Mergeay, e-conference chair, INBO, Belgium

As I wrote earlier, is this wake-up call really a message to be brought by biologists? The answer is two-fold:

Biologists and other scientists have been crying hey ho for attention for the biodiversity crisis for the past fifty years, starting in 1962 with Rachel Carson's Silent Spring, followed by the Club of Rome, etc. In 1798, Thomas Maltus (an economist, by the way) was already warning for the consequences of overpopulation. Being also a vicar, he suggested sexual restraint. The club of Rome was mocked later on, as the earth is not (yet) destroyed, as our oil reserves have not (yet) been depleted, acid rain has not destroyed all our forests, economies worldwide are still growing, and so on. Predicting the future, as mentioned earlier in this e-conference, is a tricky business.

Nevertheless, we know perfectly well that we are slowly compromising our future; we don't really need additional research for this (but see below). So why don't we act? It comes down to the tragedy of the commons: Benefits of using and depleting common goods (ecosystem services, fish stocks, pollution, CO_2 production etc) are personal; the costs associated with restoring them are for the entire planet. Almost everybody agrees with the fact that this should stop. But almost everybody is not enough, because a single cheater is enough to destabilize the system (cf game theory). Hence, short term economic benefits always take the upper hand (but see below).

A second problem is the shifting baselines paradigm: we have a short memory when it comes down to remembering what a good situation looked like. Every generation sets its standard according to those of the previous generation, and therefore biodiversity decline, ecosystem service decline etc. are perceived as only declining moderately, apparently remaining within acceptable levels. But we are fooling ourselves, unless we are capable of clearly and scientifically documenting this loss of biodiversity, of ecosystem services, of evolutionary potential, of global nutrient cycles and so on. So yes, we need to study this, more than ever.

Especially in Europe the biodiversity crisis has a very long history. When is the last time you saw a pack of wolves in Western Europe? Currently we are focusing on protecting "exotic" steppe species, such as corn buntings and hamsters that colonized the extensive agriculture landscape in the wake of mankind since agriculture started, because that's about all we have left. Deforestation (and habitat fragmentation of forests) started 5000 years ago, and peaked at the onset of the first industrial revolution. We now have more forested area in W-Europe than 400 years ago. But we need to document the changes in biodiversity, within and among species.

With regards to the answer to the crisis: should this come from the UN or some other global commission? Look at the European Commission and its fisheries policy, a relatively simple problem with a simple solution. Around half of the fish sold in Europe are caught illegally. The EC is not even capable of temporarily halting its own Bluefin tuna fisheries, despite catastrophic declines in stocks, and despite the fact that according to its own definition, the Bluefin tuna is a critically endangered species. All commercially exploited fish species in European waters is not overexploited. When it comes down to listening to scientists bringing bad news (suggesting drastic reduction of quota), politicians turn their back and try to please (in the short term) their voters (fisheries lobby). So how should we expect that vastly more important and complex problems are tackled at a global scale?

Part of the solution is gradually coming from economic industries themselves, which are starting to realize that ecological/sustainable and economical are not antonyms. A

multinational company like Coca Cola heavily relies on clean water for its production process, also in Africa. To ensure clean water in their African factories, Coca Cola is investing heavily in clean water and sanitation, to its own long-term benefit, but as a corollary also for that of local people and the environment.

Should we stop warning politicians? Certainly not, but we should come up with sound arguments, real data on ecosystem services and the role of biodiversity, good hypothesis testing, etc. instead of constantly warning for apocalyptic scenarios without a sound foundation.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Rasmus Ejrnæs, Aarhus University, Denmark

Joachim Mergeay notes that decision makers fail to control over-exploitation of common goods motivated by short term economic profit. This is definitely true, but not always, as history also presents examples of the opposite, namely that overexploitation was halted for the sake of common goods. This issue of insufficient decision-making cannot however be solved by biologists.

Joachim stresses that the role of biologists should rather be to come up with scientific evidence for the role of biodiversity in ecosystem services. I certainly agree that more sound scientific evidence is needed if the ecosystem service argument is ever going to convince politicians. But I also think we leave an important question only partly solved by focussing entirely on ecosystem services, and I suggest that this lack of understanding will severely obstruct attempts to convince the public and decision makers about the value of biodiversity.

Let us take the forests as an example. As Joachim notices the forest area has been steadily increasing in W-Europe. In Denmark the forests were severely over-exploited around the year 1800, where a new legislation effectively protected the forests from overgrazing and premature logging. In 1939 one of the founders of Danish Nature conservation Professor Carl Wesenberg Lund complained in an essay about the silviculture practices implying drainage, forest planting in woodland glades, meadows and grasslands, eradication of insect-pollinated shrubs and logging of trees. Lund complained about the loss of beetles, butterflies and dragonflies. He also, with clear address to decision makers and stakeholders, argued that some of these declining species might play important roles in the forest ecosystem, e.g. by pest control. Few listened and no action was taken, and Danish forests have been converted largely to plantations without old-growth habitats (ancient trees, forest glades, forest swamps) and with major declines and regional extinctions of species of butterflies, beetles, fungi etc.

My point here is that the forest area and the ecosystem services have been maintained and even increased in the past 200 years in Danish forests. The forests produce timber, clean ground water and recreation for the public. Unfortunately biodiversity crashed, but who cares?

Optimal resource exploitation may satisfy our concerns for ecosystem services to human society, but at the same time it may lead to continuing loss of biodiversity. I could add to the forest example the example of organic farming. This is definitely an environmentally friendly way of farming, but, it is still farming, driven by production logics and mechanical weeding and has become so effective today that you can hardly tell the difference in Denmark between organic and conventional cereal fields.

The unsolved part of the question is thus: can we, as scientists or humans, explain and motivate values of biodiversity that transcend the usual utility-argument? Why accept and protect a pack of wolves if they hunt our sheep and game and make us nervous? Perhaps the answer to this question is linked to a proper understanding of evolution. How come evolution produced so many subordinate, rare and apparently useless species?

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Arturo Arino, University of Navarra, Spain

Martin's recent, sharp comments on Evolutionary response prompted a sinister thought linked to a similar rationale I used recently on a talk on J. Diamond's hypothesis: Given that only fourteen mainstream animal species were ever able to be domesticated (and only one originally in the Americas), what if this is actually a fixed ratio of extant biodiversity? The smaller its numbers, the fewer possibilities of us being able to "use" nature's services that we depend on. That alone should lead to mandatory, global protection of biodiversity.

I would just partially agree with the views in the last paragraph, though. "Research into stopping the loss of biodiversity" must certainly be promoted, no doubt. That's the whole point. However shouldn't we assess what biodiversity is being lost and how? We feel, fear and experience it—however we should be able to *know* it too. If we are to assess "Where is the living world going? How might we establish and sustain a balance, even at this late date?", knowing how biodiversity fares, and especially how it responds to human actions on the environment, seems to me material in devising "what can we do to prepare for a world unlike any we have ever known".

Therefore, even if that "applied" research is to be promoted, I fear that the more basic research cannot be left out without significant risks of taking blind steps. The one (referring back to Martin Sharman's contribution) is very urgently needed. But the other is urgently needed by that one.

Earmarking limited funds for one or the other type of research seems to me, thus, a terribly tricky and agonizing business. In a sense, it may suffer from exactly the same issue we're discussing: By addressing immediate, paramount concerns (biodiversity loss), we might risk hampering the long term knowledge (basic research) that might perhaps help us better understand (and therefore, address) the complexities of such loss. That said, paralysis is the last thing we can afford.

Of course, the key word to combat here is "limited".

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Balint Czucz, Institute of Ecology and Botany of the Hungarian Academy of Sciences, Hungary

I absolutely agree with Martin Sharman. We are living in exceptional times of a (the?) great transition, where most people are simply not aware of the magnitude of the changes ahead of us. The twin constraints of climate change and peak oil will unquestionably (well, at least in authoritative academic circles) reshape our world in no more than a couple of decades (but probably even sooner). And ecologists should definitely know better than anyone what the key for the survival of systems during times of heavy external changes is: it is resilience.

Just as under relatively stable circumstances evolution selects for increasing complexity (specialization), chaotic environmental changes favour simple, resilient solutions. (Several examples could be mentioned, including the one in the subject...)

I think ecologists, as scholars of an inherently "systems-aware" discipline, have much more to teach to society (if they are ready to listen), than just about species conservation itself. Socio-economic systems are no less complex systems than natural ones, governed by the same universal laws/rules. During the last century society has almost completely lost all of its capability for resilience through emphasizing efficiency, economies of scale, just-in-time solutions, globalization, etc. Now the entire global economy comprises of a single, highly interconnected system, with several critical (but still vulnerable) components, the failure of which could bring down the entire system in a very short time.

In this context, ecologists - I think - have a lot to say, teach and preach (?!) to the whole of society. Studying resilience, resource constraints, the internal dynamics of systems, etc from this perspective would be again an example of "learning from Nature", a strategy that proved successful several times in the past. Is this basic science or applied science? I don't

know. I don't even care. But since my own and my children's future depends directly on this, there is no other science that could be more justified for me.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Ferdinando Boero, University of Salento, Italy

I study the phase shift from fish to jellyfish, a dramatic change that is happening at a global scale. There are very few scientists who study gelatinous plankton, so it is not being studied due to lack of funded projects. Or, even worse, the usual lobbyists are drawing money to study something that they have never worked on, suddenly changing topic, and being totally ignorant about it. They would do anything for some more research money. Decisions of what to study are proposed by influential scientists (sometimes influential just at the bureaucratic level) who give advice to finance their topics of research. It is a catch 22. If there are lots of jellyfish out here and no jellyfish lobbyists, nobody will push for proposals about jellyfish. If the lobbyists see that it is imperative to study jellyfish, they will say that they study jellyfish. As it happened with molecular biologists and information technologists who suddenly became experts in biodiversity condemning taxonomy to extinction while lots of money was dedicated to biodiversity exploration.

Part of the blame on how science is managed and directed also falls upon us, members of the scientific community. Nobody will ever say that the topics of other scientists are more relevant that own topics, and I am no exception.

RE: Understanding evolutionary processes during past Quaternary climatic cycles

Jan   Jansen,   Experimental   Plant   Ecology,   Radboud   University,   Netherlands

Biodiversity in Europe is in most places the outcome of both natural conditions and human interference. After the Last Glacial, climate was still the major environmental agent of change to biodiversity, changing formations from grasslands to shrublands to forests, while later on the evolution process became more and more affected as a result of human interference when forests turned into shrublands and grasslands, finally developing partly towards planted forests in the past century. In these events species had to find their niches.

After the Neolithic revolution farming would become progressively important, triggering a sedentary way of life and the development of larger communities in which political-administrative and socio-economic functions would become considerable driving forces of landscape change as well. Except by collecting, fishing, hunting and early domestication, food security was achieved rather by increasing the productivity of single crops than depending on the diversity of species. Biodiversity became an unintended by-product of human intervention. Within this course of events the presence of well-nigh inexhaustible albeit low productive commons still reflected a situation in which multifunctional land use still prevailed and reflected an economic reality, which until the end of the 19th century depended on natural diversity, at least in many places in Europe.

Since the 19th century society became ever more involved in the idea that preservation may be necessary to prevent further loss of biological diversity. At first the accent lay on preservation of wilderness, targeting biodiversity as only being the product of natural processes. Forest conservation and nature conservation were -at least in Europe- almost synonyms not in the least because virgin forests largely disappeared as a result of farming. However, later on it was recognized that traditional land use contributed considerably to biodiversity, or in economic terms: that biodiversity became an external benefit of traditional land use. Many plant species in Europe are associated with semi-natural habitats and traditional farming contributed to an optimal distribution of species.

While the CAP has been successful in post-war agriculture securing food supply, it has among others been unintentionally also a major driving force behind the decline of

biodiversity and the decrease of other positive externalities such as cultural heritage and water resources in many parts of Europe.

To counteract these developments, the Bird and Habitat Directive were implemented and Natura 2000 was designed, transforming biodiversity from being a by-product of traditional farming activities into at least one of the objectives of multifunctional land use. This transformation poses the question to what extent the present socio-economic and climatic circumstances enable the achievement of the rather fixed biodiversity objectives of the Natura 2000 network, taking into account that present biodiversity and habitats are the result of natural and human-induced dynamics that prevailed in the past. In this respect we need to understand the evolution processes that took place both during the Quaternary climatic cycles and later when landscape changes became increasingly triggered by historic land use practices in socio-economic and political-administrative settings. How can there be a balance between socio-economic and biodiversity objectives and which evolutionary processes can be optimized?

The next question might be to what extent the Natura 2000 criteria should be based on fixed biodiversity and habitat indicators, whereas it is inevitable that -taking into account the changing environment- indicators may also change. These questions should have attention in research programs in the coming years.

Resurrection ecology, zombie biology, paleogenetics and genomics: reconstructing evolutionary responses of natural populations to past selection pressures

Luisa Orsini, Laboratory of Aquatic Ecology and Evolutionary Biology, Belgium
Joachim Mergeay, Research Institute for Nature and Forest, Belgium

Monitoring populations in time is a straightforward way to document evolutionary dynamics in response to environmental change, but requires long-term studies and usually cannot be done in retrospect. As a result, many studies instead study evolutionary dynamics over a spatially varying environmental gradient. One major drawback of this approach is the difficulty to disentangle the effect of population history (genetic drift, effective gene flow, population bottlenecks) from the one played by selective processes. The understanding of neutral and selective variation in natural populations along extended time axes is a promising approach to unravel patterns of adaptation to a complex and ever changing environment.

Aquatic organisms that produce dormant propagules build up an archive of past evolutionary changes in sediment layers, representing an extremely valuable resource to reconstruct past evolutionary changes. Dormant propagules can remain viable for decades to centuries (Hairston et al., 1996), giving us the possibility to reconstruct evolution over long time spans through 'resurrection ecology' (Kerfoot et al., 1999) and paleogenetics. By studying propagule banks extracted from dated sediment cores, we can reconstruct changes at the population level without the complicating patterns superimposed by spatial genetic variation. By complementing the study of neutral and adaptive variation in individual populations with the one at the landscape (metapopulation) level we can infer how immigration, genetic drift and other neutral genetic processes (Mergeay et al., 2006, 2007), contribute to shaping the adaptive responses at the metapopulation level. The integrated analysis of neutral and adaptive variation in environments with known evolutionary history with regards to climate change, will allow the reconstruction of local adaptation in response to global warming. Aquatic ecosystems, such as lakes and ponds are a valuable source for these kinds of studies as they represent discrete well-defined ecosystems with known changes in temperature over time. We have a relatively detailed measured climatic, environmental and industrial history for Western Europe spanning the past 110 years, which can be used to study populations in situ. By hatching dormant stages we can contrast performances of hatched organisms exposing them to controlled selection pressures, represented by temperature, as well as other environmental stressors (land use, cyanobacterial tolerance, pollution, predation, etc.).

Dormant propagules don't remain viable for extended time periods, therefore limiting our ability to reconstruct evolution in experimental trials to ca. 100 years. However, we can reconstruct the evolutionary responses over longer time axes by using the genome signature of natural selection dating back to the era of the Industrial Revolution or to the Little Ice Age (c. 1600 AD) (Mergeay et al., 2007), to even thousands of years (Bisset et al., 2005).

The water flea Daphnia represents an ideal model organism for the reconstruction of evolutionary responses over long time periods. Few organisms have been so intensively studied ecologically and evolutionarily. With the advent of genomic tools, it has become a major model organism in ecological genomics (Colbourne et al. 2005). Dormant egg banks of Daphnia in layered sediments have been successfully used to reconstruct evolutionary responses to predation (Cousyn et al. 2001), cyanobacteria (Hairston et al., 1999), red-queen parasite-host dynamics (Decaestecker et al., 2007) and interspecific competition (Michels et al., submitted). An increasing number of candidate genes with respect to responses to specific stressors are being identified. Therefore we have more and more knowledge and tools to link genomic variation to trait variation and fitness in an extremely well-known species, ecologically and genetically.

This combination of paleolimnology, ecology, evolutionary biology and genomics is thus facilitating the reconstruction of long-term (hundreds of generations) and short-term evolutionary adaptations in real populations that underwent real environmental changes.

Will all these new technologies and recent findings allow us to anticipate future evolutionary changes? Let's be careful and realistic in our ambitions, and say that we'd be happy to first accurately reconstruct past evolutionary changes. It will help us, however, to better understand the role of evolution in ecology and ecosystem functioning.

RE: Resurrection ecology, zombie biology, paleogenetics and genomics
Conserving the genetic basis of evolution in a seed bank

Katalin Török, Gabriella Kutta, and Geza Kósa, Hungarian Academy of Sciences, Institute of Ecology and Botany (IEB), Hungary.

The establishment of the Pannonian seed bank for the conservation of vascular plants is under way by taking evolutionary issues into account.

With a long background in international seed exchange as a botanical garden, the Pannonian seed bank is being developed with the help of a consortium. The aim is to gather enough diversity without jeopardizing the conservation goals of rare species. Therefore, the sampling methodology has to be designed accordingly.

Based on literature, figures demonstrate that the great majority of total genetic content of most plant species is present in a single 'typical' population (Centre for Plant Conservation, 1991). However, to minimize the risk of genetic loss, other research results should be used, like the correlation between species traits and gene diversity (Brown and Marshall, 1995). Life form, breeding systems, seed dispersal and successional status can be used as surrogates for genetic diversity estimates. This way, for example, annual, gravity-dispersed, early, or mid-successional species probably have higher genetic diversity among populations; therefore sampling of more than one population is required. For such species, seed collection of five populations will be targeted. In other trait types with low probability of high genetic diversity among populations, two populations will be sampled, as supported by the studies of Ceska et al. (1996) where 99% of recorded isoenzyme diversity was found within two populations. Seeds originating from different populations will be stored as different samples.

A crucial question for conserving the genetic basis of evolution is the handling of rare and endangered species. If there is a significant risk of damaging the population or the habitat, the collecting plan should be modified or the collection attempted elsewhere, if possible. The collector must judge in the field how to best meet the objective to collect seeds without threatening the given population. As a general rule, collected seed amount should never reach 10% of seeds of the population yearly seed output. Monitoring methods for the effect of seed collection on the wild population will be realised by revisiting the sites in the coming year. As information on the populations (area, estimated specimen number, etc.) will be gathered during sampling, this can be used as a reference in the coming year to test the effect of seed collection. Suggestions provided by Menges et al. (2004) will be taken into consideration.

By the end of the project (by 2015) approximately 50 percent – at least 800 species – of the native flora will be collected and stored. A strategy will be developed for seed collection of wild vascular plants, by assessing existing seed collection and ex situ storage methodology, adapted to the Pannonian biogeographical region. Field collection experts will be trained to undertake the project activities in a standard way. The project will develop a computer-based comprehensive information system for data management of the Pannon Seed Bank. It will establish storage and laboratory capacity by expanding the current functions of the existing crop gene bank. Seed samples of wild vascular plants native to Hungary will be collected, processed, tested and stored. Duplicates will be stored at two separate locations in different geographical areas. Selected seed bank samples will be used for model reintroduction.

RE: Resurrection ecology, zombie biology, paleogenetics and genomics
The evolution of phylogenetic systems and ecology

Nina Katrich, Moscow State University, Russia.

Systematization of plants has a long history. From the first attempts at classification based on a few external attributes up to modern systems, which are based on a huge number of facts and take into account true-related groups. As a whole for phylogenesis the attributes that are important are ones that do not depend or only partly depend on environmental conditions. From a macro-evolutionary perspective attributes need to be steady, i.e. attributes that are not directly connected with survival (and are therefore weaker than others) by current natural selection are useful, for example, the number of parts of a flower, or fruit type. These attributes are much more resilient against environmental an influence, which is why they are more important for classification, depending on varying environmental conditions. Determinants and so-called 'Florae' editions are where the expanded description (in comparison with determinants) of plants in certain regions is given ('Florae of Voronezh', 'Flora of Moscow and the Moscow area' etc), such as morphological attributes, species distribution, vegetative cover, i.e. landscape features and environmental conditions.

Deciding on determinants of plants for the given climatic regions, geographical and phytocenological data are described:

The creation of determinants is not casual. The issue is that factors influencing the environment are very stressful. The question needs to be asked: "are there preconditions of revision of phylogenetic systems of higher plants in the conditions resulting from varying environments?" Thus the problem with the mutual relationship of taxonomy and ecology in its technogenic execution is explained. We need to focus on these new taxonomic scales.

Evolutionary systematization of plants has a synthetic character, which is built-up using data of comparative and evolutionary morphology, embryology and phytochemistry etc. The use of taxonomy enables parameters to be set and provides a structure whereby revision of regional flora can occur, especially in areas with considerable external influence.

Plants possess certain sets of changing morphological attributes. One type of change (for example, spots on leaves) can result from various factors (mushroom illnesses, shortage of microcells, chemical poisoning).

Our task is to allocate the most dynamic attributes of plural character to the individual attributes that change in response to concrete influences and the set of changes of morphological attributes in reply to concrete influence. And to define a set of conditions at which the display answer of one or more morphological attributes (vital forms) on concrete environmental influences is possible.

Keeping up with a warming world; the importance of the rate of adaptation to climate change

Marcel Visser, Netherlands Institute of Ecology (NIOO-KNAW), The Netherlands

The author highlights the importance of assessing adaptation potential of species to two major climate change induced shifts: changes in phenology and range shifts.

The world's climate is changing at an unprecedented rate and this change will continue over the next decades. There is ample evidence that climate change has ecological consequences (Parmesan, 2006). The two best recorded climate change induced shifts are changes in phenology, i.e. in timing of vegetation development, return date of migrant birds, egg hatching date in insects, laying dates in birds, etc., and in range shifts, in the distribution butterflies, breeding range or overwintering range of birds, etc. Less widespread documented consequences of climate change are shifts in body size and in changes in the strength of competition between species.

The pivotal question in the debate on the ecological effects of climate change is whether these observed shifts are sufficiently large, i.e. whether species will be able to adapt fast enough to their changing world. Establishing the maximal rate of adaptation is therefore of crucial importance in the general debate on climate change (Visser, 2008). The rate of temperature increase up to 2100 is not determined yet as it strongly depends on socio-economic developments world-wide. The Intergovernmental Panel on Climate Change (IPCC) predicts climate change for six of such socio-economic scenarios. It is up to biologists to predict the ecological consequences for these different IPCC scenarios, for instance in terms of reduced population viability or loss of biodiversity, which should then in turn be taken into account in the discussion on which IPCC scenario the world should aim for. As the magnitude of the ecological consequences will strongly depend on the rate of adaptation of species to their changing environment, assessing this rate of adaptation will set an upper limit to the rate at which temperatures can increase without loss of population viability or biodiversity.

Species can adapt to climate change using various mechanisms but the rate of adaptation will be primarily set by the rate of micro-evolution, a rate which is estimated to be alarmingly low in vertebrates (Gienapp et al., 2007). Long term studies on wild populations with individually known animals play an essential role in detecting and understanding temporal trends in life history traits, and to estimate the heritability of, and selection pressures on, life history traits. However, additional measurements on other trophic levels and on the mechanisms underlying phenotypic plasticity are needed to predict the rate of micro-evolution, especially under changing conditions.

Future research needs to assess the rate of adaptation for the different IPCC climate scenarios and include this adaptation into eco-evolutionary dynamic models that can forecast population viability and from there biodiversity loss. We need to do this for a number of ecological model species, as only then will we have enough long term data to do so. By choosing species which differ in their general life-history, we will get insight in how under different climate change scenarios biodiversity will be affected.

Re: Keeping up with a warming world; the importance of the rate of adaptation to climate change

Pablo Goicoechea, NEIKER-Tecnalia, Spain

I liked very much this contribution from Mark Visser. It shows us an elegant way to link climate change and biodiversity loss.

However, I should disagree at one point: "but the rate of adaptation will be primarily set by the rate of micro-evolution".

On the one hand, climate change is so strong (under any IPCC scenario) that micro-evolution will not have time to act. However, already existing micro-evolutionary mutations will provide the basis for adaptation; i.e., the most diverse species/populations will have the greatest chances to adapt. On the other hand, epigenetic changes will probably play a larger role on adaptation than existing variation (but this will be discussed next week, I guess).

Evolutionary processes under global change

Sabine Hille, Andreas Tribsch, Steven Weiss, Matthias Kropf, Günter Gollmann, Elisabeth Haring, Dominique Zimmermann and Stefan Schindler, Austrian Platform for Biodiversity Research (BDFA), Austria

Outcome of the 2nd annual meeting of the Austrian Platform for Biodiversity Research (BDFA):

Past and recent adaptation of organisms to cultural landscapes:

Future research is required to investigate the plasticity and evolutionary potential of plant and animal species to cope with changes in land use (GMO's, intensified production, choice and sequence of agricultural products, agricultural abandonment). One focus may be on the origin of, and ongoing (cryptic) evolutionary processes in species of meadows and pastures in cultural landscapes.

Plasticity and adaptation of selected mountain species along elevational gradients:

Differences along temperature gradients offer best possibilities to study adaptability of species to different climate regimes in a given study area. It also allows for modelling of population dynamics under different climate scenarios. A multidisciplinary approach is needed to assess relevant, directly selective parameters that are influenced by temperature (food, parasites, etc.). The challenge will be to distinguish the evolutionary responses from other confounding factors and to identify the traits that force selection.

Evolutionary consequences of anthropogenic habitat fragmentation:

There is a need to study the consequences of changes in population fragmentation on gene flow and genetic drift and on the evolutionary potential of populations for adaptation to present and future environmental changes. Studies should include animal species with large home ranges and with migrating and seasonal moving patterns.

Evolutionary potential and change in alien versus native species:

Periods and rates of change may differ between aliens and native species. Adaptation speed to changing environments and changes in competition between natives and aliens might result in increased loss of native biodiversity. Research is needed in both, isolated and non-fragmented habitats.

Hybridisation:

Hybridisation of aliens and natives, the introgression of natives and the invading of GVO's and/or taxonomically related aliens into gene pools of native populations and the consequence of the evolutionary potential of the "species" are important questions to study. Also the discussion on the value of the genetic admixture in respect to the gain or loss of genetic biodiversity needs to be done for the different cases.

Endocrine disruption:

Pollutants that act in organisms like hormones are a major threat since they act on gonad function and therefore on reproduction in populations. Studies on trait selection in populations under depressed reproduction are needed (e.g. in freshwater species). Different target species and groups need to be identified.

We recommend the implementation of the above evolutionary knowledge to define nature conservation units, strategies, and priorities at all levels of conservation planning and action (i.e. international to local).

Regarding the methodological aspects, we strongly recommend:
- Use of museum collections to study phenotypic and genetic variation and its change over time (time series analyses) and advancement in molecular study methods
- Monitoring to find target species for less adaptable and probably more endangered species
- Long term studies

Evolutionary potential of animal taxa to adapt and survive climate change

Sabine Hille, University of Applied Sciences (BOKU), Vienna, Austria

The author outlines the importance of gaining a better understanding of species life history traits and their ability to respond to phenology shifts in food abundance as a result of climate change.

Climate change has led to shifts in phenology in many species distributed widely across taxonomic groups (Hughes, 2000; Parmesan & Yohe, 2003; Dunn, 2004). It is, however, unclear how we should interpret these shifts without some sort of a yardstick: a measure that will reflect how much a species should be shifting to match the change in its environment caused by climate change. In fact, many species are becoming mistimed due to climate change and the shift in the phenology of a species' food abundance is, by a first approximation, an appropriate yardstick. The review on phenology change across the animal kingdom by Visser & Both (2005) suggests that an insufficient response to climate change is the rule rather than the exception, and that only in a few cases has the consumer shifted its phenology to the same extent as its food. A trophic decoupling of food web phenology may have severe consequences, including biodiversity loss (Visser et al., 2004).

There is a great need to gain long-term datasets on phenology of species to link their data with those that may serve as a yardstick, because documentation of the incidence of climate change induced mistiming is crucial in assessing the impact of global climate change on the natural world. We need to know the potential adaptability of the species and their life histories to the change of environment due to climate change. Crucial data will be on the plasticity of the species in the observed traits and their heritability. Mountain systems provide an excellent field laboratory with the necessary conditions, namely a range of temperature regimes close to each other to assess the effect of climate differences on species life histories; this provides novel avenues towards testing evolutionary and ecological theory. Finding the genes of the respective traits observed will be a challenge and assessing the genetic structure of the taxa and populations observed in order to assess evolutionary potential will be an important task.

Most studies on climate change effects on biodiversity concentrate on correlations of species' occurrence with temperature or certain habitat variables that lead to models on future distributions of species. Sadly they may well be misleading and not be satisfactory, because firstly temperature and habitat parameters may not be the key variable determining actual survival rates and distribution patterns. Secondly, an area experiencing environmental change may well lack behind the present carrying capacity of this area, particularly when species numbers are higher than expected since they well reflect former but not any more existent habitat conditions and species can already be at the brink of extinction (see also Kuussaari et al., 2009). A rapid decline and loss in individual numbers and biodiversity may easily happen soon in these areas.

Therefore, only if the evolutionary potential, the phenotypic plasticity and the adaptability of a taxon including its yardsticks are known may we come up with better models and get a better view on future potential biodiversity loss and distribution patterns of taxa.

The tendency in the teaching programmes of Life Sciences at European universities is to support microbiological and molecular genetics approaches on the cost of organism biology. It is more than crucial that universities are able to provide teaching in the basics of "organism biology" namely identifying species, monitoring, biology of species, animal behaviour etc.. Universities need extra personnel to insure future generations of students will not lose the ability to know, measure and conserve biodiversity.

RE: Evolutionary potential of animal taxa to adapt and survive climate change

Viktor Kotolupov, Centre of Systematic Medicine, Slovenia

I would like to mention that despite diversity, all biological systems have common characteristics (Kotolupov and Levchenko, 2009a), in the framework of which they evolve during evolution. These characteristics are written in their DNA. Common characteristics of living systems (biological principles) allow us to elaborate the definitions of various illnesses and with this to establish their causes, for instance the definition of psyche (Kotolupov and Levchenko, 2009b). Therefore I suggest the evolutionary process should be investigated and elaborated inside the framework of biological principles.

RE: Evolutionary potential of animal taxa to adapt and survive climate change
Role of genetic diversity on fish evolution and conservation in the Mediterranean

Adriana Vella and Noel Vella, University of Malta, Malta

Being a semi-enclosed sea composed of several different habitat types, the Mediterranean offers a great potential for genetically distinct stocks and the important evolutionary process of speciation. This diversity found both between the Mediterranean and other seas and also within the Mediterranean basin itself, adds value to the Mediterranean Sea's uniqueness, while highlighting the importance of sustainably safeguarding its natural resources and biodiversity at various levels.

It is a known fact that in the Mediterranean there is a good number of endemic marine organisms, including some large species such as, the Giant devil ray (*Mobula mobular*). Other species, which may not be exclusive to the Mediterranean Sea, enter the Mediterranean at specific stages of their life-history, thus exhibiting specific migratory patterns and home range sizes. The complexity of some of these conditions require intensive research to elucidate facts that may allow for best conservation practice or sustainable exploitation of specific stocks, such as, the Atlantic bluefin tuna (*Thunnus thynnus*) which is being over-exploited in the Mediterranean. In addition to these, one can add the possibility of separate stocks due to geographical boundaries and physical/biological conditions, that limit the exchange of genes in a species and the possibility of having cryptic species that cannot be identified yet except with the use of genetic markers. Anthropogenic activities and requirements place pressures on small populations especially those with certain life-history parameters, the Mediterranean stocks are being faced with a higher risk of extinction compared to similar stocks in other regions (Cavanagh and Gibson 2007; Vella - CP/RAC 2009).

Within this scenario, conservation genetics plays an essential role in the identification and conservation of cryptic species, sexual dimorphism and ontogenetic forms of the same species, thus aiding in more rigorous fisheries statistics data collection down to the species level. Moreover genetic identification of body parts from markets would aid in law enforcement and monitoring for legally protected species. Conservation genetics, which aims at maintaining evolutionary processes intact, also aids in the identification of population structures, stocks, migratory patterns and population sizes, all leading to better understanding of populations and their health. This knowledge proves to be essential to improving and updating policy making, and management plans for Mediterranean species/stocks. Furthermore genetic markers can also be applied to check on alien genotypes to the Mediterranean region, either due to the introduction of individuals from areas outside the Mediterranean or from aquaculture. Such genetic 'contamination' could lead to the loss of the unique genetic characteristics and acquired adaptations, thus genetic monitoring could ensure that native stocks are preserved.

Back in 1993, the Convention on Biodiversity identified the importance of genetic diversity and recognized the resources required to seriously support maintenance of such an

important condition in our natural environment. However currently the lack of financial input linked to the research required in this field, together with political and commercial agendas, pushing the rate of change toward faster and shorter term gains, are not considering the importance of knowledge on genetic diversity, possibly missing important leads and baseline information on the conservation methodologies that need to be adopted in order to preserve the natural heritage and essential evolutionary processes.

Measuring evolutionary responses to global climate warming

Francisco Rodríguez-Trellez, Department of Genetics and Microbiology, University of Barcelona, Spain

The author looks at our current understanding of genetic responses to recent climate change, focussing on the studies carried out on Drosophila. It highlights the need for a causal link to be established linking climate and inversion frequencies and for a better understanding of the genetic architecture underpinning the 'climate-sensing' character set.

Populations can respond to directional selection imposed by ongoing climate warming by: 1) evasion through dispersal to suitable habitats, 2) in situ by adjustment through phenotypic plasticity without altering their genetic constitution, and 3) changing genetically through evolution.

Evolutionary responses are thought to be a requisite for coping with environmental changes in the long term. In practice, any given population's response to climate warming is likely to be an idiosyncratic blend of the three above-mentioned mechanisms. Inference of evolutionary responses from purely phenotypic data faces the difficulty of disentangling genetic and plasticity factors. Ideally, the par excellence means to quantify evolutionary responses should be by direct measurement of genetic change. Yet the quality of evidence of genetic responses to recent climate change is far from satisfactory. The number of studies is scarce. The ones that picked out the clearest signatures of a climate-driven evolutionary response have focused on Drosophila chromosomal inversion polymorphisms.

Drosophila species have long been recognized as potential useful candidates for assessing evolutionary responses to climate change. As ectotherms, their basic physiology is strongly influenced by environmental temperature. Their fast generation time makes it possible to follow evolutionary processes over many generations in relatively short time periods. Drosophila chromosomal inversions were found to cycle with the seasons at the early stages of experimental population genetics. Their seasonal and latitudinal cline patterns were shown to be consistent with what would be expected from temperature. There is a great deal of historical data to investigate effects of global environmental changes by comparison with present configurations. In spite of these and other advantages derived from Drosophila's privileged condition as a model organism in the 'omics' era, the use of chromosomal inversion polymorphisms to investigate evolutionary responses to climate warming has uncovered important limitations.

First, a causal link between climate and inversion frequencies has yet to be established, since all the gathered evidence for adaptive responses is correlational in nature. Second, there is an urge to fill the gap in the understanding of both the genetic architecture –e.g. how many and specifically which genes/transcription units, and their connections— underpinning the 'climate-sensing' character set, and the relevant ecology of the best known genetically Drosophila species. Because of this gap, allocating efforts to long-term tracking of genetic markers other than inversions has to be necessarily perceived as hardly cost-effective. And third, the premise implied by some recent long-term monitoring surveys, according to which the rate of temperature increase is homogeneous between spatiotemporal coordinates is not valid. Neglect of the ongoing lengthening of the growing season in scheduling updates of historical records can lead to overestimate the magnitude of long-term responses to global warming. Standardizing old and new collections by climatic dates instead of by calendar dates can, however, conflict with other relevant parameters, such as photoperiod or the responses of other species on which the focal species depends. Provided the two temporal patterns have a common causal ground, the seasonal cycling of inversions would afford an embraceable experimental setting towards understanding why inversion frequencies change directionally in the long-term.

Evolution and Biodiversity
The evolutionary basis of biodiversity and its potential for adaptation to global change

Mallorca, 13-15 April 2010

Session III: Evolution in complex systems and coevolutionry networks

Eco-evolutionary dynamics: interactions between ecology and evolution in contemporary time.

Andrew Hendry, Redpath Museum and Department of Biology, McGill University

The author highlights the need to further understand how contemporary phenotypic changes influence ecological variables on similar time frames; it outlines three examples at the population, community and ecosystem levels.

Evolution is obviously driven by ecological differences: think of the adaptive radiation of Darwin's finches. Just as obviously, ecological processes are influenced by evolution: ecosystems depend on the oxygen produced following the evolution of photosynthesis. Less obvious is how these interactions play out on the short time scales most relevant to conservation and management. Do ecological changes (e.g., invasive species, climate change) drive appreciably evolutionary change over years or decades (i.e., "contemporary evolution")? Does any such evolution influence ecological variables (population dynamics, community composition, ecosystem function) on a similar time scale? These interactions between ecology and evolution represent the growing field of eco-evolutionary dynamics (figure 1).

Many studies (Stockwell et al., 2003; Reznick and Ghalambor, 2001; Hendry et al., 2008) have shown that ecological changes cause phenotypic changes in natural populations (eco-to-evo). Examples include species introduced to new environments, native species responding to introduced species, populations exposed to harvesting or pollution, and populations facing climate change. Existing work has shown that the phenotypic changes can be substantial, particularly when humans are involved (Hendry et al., 2008; Drimont et al., 2009). What isn't known generally is just how much of this phenotypic change is the result of evolutionary change versus phenotypic plasticity (Hendry et al., 2008; Gienapp et al., 2008). Even less is known about how these contemporary phenotypic changes then influence ecological variables on similar time frames (evo-to-eco) (Pelletier et al., 2009) – but some nice examples can be provided.

Populations: Phenotypic changes from one year to the next clearly influence population size in ungulates (Pelletier et al., 2007, Ezard et al., 2009). The genetic contribution to this phenotypic change is not known, whereas a study of butterflies has documented effects of genetic change on population sizes (Hanski and Saccheri, 2006). What remains to be determined is just how common these effects are, and how important they are relative to traditional "ecological" effects (e.g., rainfall or temperature). In addition, it isn't clear under which conditions these population dynamical effects of evolution can actually save natural populations from extinction (i.e., evolutionary rescue) (Kinnison and Hairston, 2007).

Communities: Genetic and phenotypic differences between individual plants have been shown to have noteworthy effects on arthropod communities (Johnson et al., 2009). Similarly, genetically-based phenotypic differences between fish populations have strong influences on aquatic macro-invertebrate communities (Palkovacs et al., 2009; Palkovacs and Post, 2008). What remains to be determined is, again, how common these effects are and, also, how year-to-year changes in these genes and traits (as opposed to the currently studied static differences) influence those communities.

Ecosystems: In the same plants and fish studied for community effects (above), genetic and phenotypic differences have been shown to influence ecosystem variables such as decomposition rates, dissolved organic material, light attenuation, and primary productivity (Palkovacs et al., 2009; Palkovacs and Post, 2008; Harmon et al., 2009; Whitham et al., 2006). Since the study systems are the same as above, what remains to be discovered is also the same. It will also be interesting to know how often these ecosystem effects of evolution fall into the category of "ecosystem services" that have become so integral to conservation efforts.

The above listing highlights a few specific examples of how evolutionary change might influence ecological variables on short time scales. In addition to the specific uncertainties listed above, some additional general ones come to mind. How often do evolutionary effects on communities and ecosystems flow through the effects of evolution on population dynamics (indirect effects – red to black arrows in figure 1, see appendix 1) versus changes in the traits themselves (direct effects – red arrows only, see appendix 1)? Do the effects of evolutionary change on ecological processes decrease from population to community to ecosystem variables (Bailey et al., 2009)? How often do true feedbacks occur – that is

Figure 1. A conceptual framework for eco-evolutionary dynamics. The blue arrows represent the inheritance of phenotypes through genes. The black arrows represent interactions between various levels of ecological dynamics. The green arrows represent the effects (through selection and plasticity) of ecology on evolution (eco-to-evo). The red arrows represent the effects of evolution (and plasticity) on ecological dynamics (evo-to-eco).

an ecological process drives evolution (green arrows) that then alters that same ecological process (red arrows) and so on (Post and Palkovacs, 2009)? Eco-evolutionary dynamics is an area ripe for future work.

RE: Eco-evolutionary dynamics

Simona Mihailescu, Institute of Biology Bucharest, Romanian Academy, Romania

Hierarchical organization:

Botnariuc (2003) noted: It is accepted that natural selection acts on individuals and on its genes. Natural selection is driven by the ecosystem and results in an interaction between three levels: individual-population-ecosystem. Ecological progression and the evolution of ecosystems and the existence and generality of these two processes and the difference between them and the mechanisms that take place, were not well clarified issues until now.

Philosophical foundations of conserving biological diversity are based on several assertions (Primack, 2000) generally agreed by most experts:
1. The diversity of species and biological communities should be preserved
2. Premature extinction of species should be prevented
3. The complexity of ecosystems needs to be maintained
4. Evolution must continue
5. Biological diversity has intrinsic value

Progress in DNA Technology:

Recently, Popescu (2009) indicated that natural selection is involved in any "group of elements" possessing the following three properties: reproduction, variability and gene-copying. In the context of molecular biology, it is necessary to further understand in detail the molecular level of biological organization, i.e. do genes allow deduction of what is happening at the level of cell and body? Genome sequencing of numerous prokaryotic and eukaryotic organisms has allowed the characterization of very many genes. Gene sequences from databases are very useful, but are not an ultimate goal. The most important contribution of molecular biology to evolutionary theory is to evaluate genetic distance between species based on molecular data. The main problem is that currently we do not have all the tools necessary to understand the language of genes.

Case study: Maintenance of biodiversity in complex systems represented by the Romanian Natura 2000 network:

Is there a chance that evolutionary processes will be able to run at the desired individual-population-ecosystem levels, so that diversity of life continues to exist?

Since 2007 Romania has designated its Natura 2000 network. The Romanian Natura 2000 network covers all five bio-geographical regions: Continental (53.6% of national surface area), Alpine (22.8%), Steppe (16.8%), Pannonian (6.0%), and Black Sea (0.7%). Romania is the only Member State with the Steppe bio-geographical region and only one other state (Bulgaria) has the Black Sea region. To establish a coherent Natura 2000 network, Romania has proposed 273 Sites of Community Interest (pSCIs) and 108 Special Protection Areas (SPAs). In these protected sites we should not forget a very important aspect: "the values, driving forces and human influences, as well as the measures for the conservation and sustainable use of biodiversity vary greatly within and between different cultures. This aspect of biodiversity is, therefore, sometimes referred to as cultural diversity, recognizing the important role of sociological, ethical, religious and ethno-biological values in human activities." (Heywood and Watson, 1995). Is this network of sites suitable to be used as a model to achieve the cultural diversity and all five philosophical foundations of biological diversity conservation above?

For Natura 2000 a number of human activities were identified that had a strong negative influence on natural sites, e.g.: quarries (desires for fast profits lead to the creation of many quarries for sand, limestone, loess and basalt), forest felling, hydro power plants, extraction of gold by cyanide, wind power plants, ski resorts, overbuilding on the Black Sea coast, golf courses, etc.

In the context of evolutionary processes in complex systems and to lower the pressure on "oases of biodiversity conservation", the following actions are essential:

- Appropriately evaluate the impact of human activity on species, habitats, landscapes and whole ecosystems;
- Properly implement the management plans of Romanian Natura 2000 sites;
- Accurately evaluate the impact of molecular biotechnology on global biodiversity.

RE: Eco-evolutionary dynamics

Martin Sharman, European Commission, Belgium

N.B: The views expressed are purely those of the writer and may not be regarded as a position of the European Commission.

Each ecosystem differs in detail from every other, and changes over time. We identify and classify the ecosystem by reference to a set of defining characteristics, which themselves emerge from a set of mutually reinforcing processes and structures. As emergent properties, these defining characteristics more or less robustly accommodate the continuous change in the ecosystem processes and structures. The resilience of an ecosystem is a measure of its capacity to retain the characteristics by which we define it, as its elements, processes and structures are submitted to pressure. How much disturbance can the ecosystem absorb before the processes that give rise to its behaviour are themselves changed sufficiently for the

character of the ecosystem to change? This question underlies the persistent request from policy makers to define thresholds. The mental model that admits the concept of a threshold is similar to a table; you can push the ecosystem this far and no further, or it will drop off the edge. So up to that point we are safe – the world has organised itself to absorb the punishment, provided it doesn't hurt too much. This concept underlies a notorious paper published in a prestigious journal last year.

It is not easy – and sometimes simply impossible – to predict the behaviour of complex systems under stress, especially if that stress includes random shocks big enough to disturb that set of mutually reinforcing processes and structures. Although ideal understanding of the underlying system might allow you to make excellent predictions in quiet periods, your prediction would only be interesting up to the point at which the next shock occurs. If big random shocks occur relatively frequently, prediction is essentially impossible. For complex self-organising systems "ideal understanding" is also impossible. All natural systems, including social ones, are subject to frequent small disturbances even if big shocks are rare. Such small disturbances may unexpectedly trigger positive feedback within the system, driving it in unexpected directions, making predictions inevitably imprecise.

If something stresses a complex self-organising system enough to alter the intensity of the feedback loops on which it depends, runaway feedback may cause it to reach a tipping point or catastrophic bifurcation, pass through a critical transition, and end up in a new state of dynamic stability. In a variety of complex systems the approach to the critical transition seems frequently to be characterised by a squeal – increasingly major oscillations in the feedback loops. A plot of the variance in its behaviour would show a smooth line that becomes jagged (squeals) and then goes wild (transition) and finally settles down again (new regime).

Ecosystems are not subject to selection pressure in the same way as organisms. Why, then, do we not see runaway positive feedback more frequently than we do? Experiment and observations that have shown tipping points in ecosystems are as rare as hen's teeth. Do ecosystems have some sort of magical get-out-of-jail-free card? Or does this lack of example come about because ecosystems with a high probability of runaway feedback quickly experience that feedback and transit to a state where the probability of runaway feedback is low? If so, then in evolutionary timescales, ecosystems quickly find local minima, where they robustly resist change. It seems to me likely that the propensity of an ecosystem to change is governed, like everything else, by the availability of surplus energy. Systems with a high probability of transition are those with little or no access to surplus energy. Biological systems are well-adapted to ensuring access to surplus energy, so it is hardly surprising that left to themselves ecosystems are highly unlikely to suffer catastrophic transitions. Unless, that is, they suffer a big shock. A plague of technologically-equipped humans is a big, big shock.

A threshold is a sharp edge to a simple, essentially two-dimensional, system. A tipping point, by contrast, is a poorly-defined and unpredictable volume in a multi-dimensional phase space. A threshold, we are informed, can be predicted – at least, policy-makers want us to predict them. A tipping point can only be identified once you have begun the transition; and even once the system has begun its transition, we may be psychologically unable to accept it. Both thresholds and tipping points are characteristics of a non-sustainable relationship between the system and its environment. The two-dimensional threshold implies a low-dimension set of drivers, and holds out the hope of reversing course as you approach the edge of the table. The concept of a fundamentally unpredictable tipping point is much less reassuring. It suggests a highly-dimensioned set of drivers and since there is no single reverse gear it therefore requires a far more complex response, which cannot be implemented piecemeal.

So where does this lead in terms of research recommendations?

1. We need to know a lot more about how our current understanding concerning complex self-organising systems applies to ecosystems, and if it doesn't apply, then why not.
2. We need to get a much better handle on the evidence for and against critical transitions in ecosystems, and characterise, where possible, the tipping points.

3. Where we have evidence of critical transitions, we need to find out whether the approach to the tipping point was characterised by a squeal. If so, can we hope that by detecting the squeal we can perhaps forewarn ourselves of a change?
4. We need to understand better the psychology surrounding our attitudes to tipping points.

RE: Eco-evolutionary dynamics

Peter Bridgewater, Global Garden Consulting, Isle of Man

These three weeks have had really interesting contributions, showing the importance of evolutionary issues in ecosystems. And there have been many interesting suggestions on research topics just now from Stefan Schindler for example.

Last week Pablo Goicoechea, also raised some interesting questions on fragmentation and 'sufficiency' - how much gene flow is sufficient. This relates to a question which has been worrying me for some years: how much of biodiversity (ecosystems, species, genes) in one place do we need? And does redundancy in species in an ecosystem have important evolutionary insurance values, or is this mere wishful thinking?

I ask these questions because in the reductio ad absurdum life of policy generation policy-makers will start asking these questions - I'm surprised they haven't already. In climate change we have many metrics being used to drive the policy debates, yet in biodiversity we don't. This current week's topic on complexity gives some reasons, but I wonder what research we need to understand what use our protected area systems will be in 100 years? The contribution of Simona Mihailescu is relevant here and she raises, as do others, the role of cultural pressures, and cultural diversity on future evolutionary possibilities.

So are protected areas likely to be useful as places for evolutionary potential, or in fact will they just become areas for the decay of complex systems while evolution will be more likely to happen in the wider landscape and even urban systems? I hope the former, yet I don't see the evidence that the blunt policy instrument of protected area establishment, regarded as highly successful of course, is actually the best thing we should be doing with our land and seascapes. I would like to see how research can help advance policy on biodiversity generally, but perhaps especially the role and value of protected areas. If research can't, or doesn't, help policy development and implementation, then we do face the sort of bleak future that Martin Sharman described last week…However today the sun is shining, so I feel more positive!

RE: Eco-evolutionary dynamics

Martin Sharman, European Commission, Belgium

N.B. The views expressed are purely those of the writer and may not be regarded as a position of the European Commission.

Peter worries how much of biodiversity (ecosystems, species, genes) we need in one place. I suggest that the answer is in the name of his consultancy: global garden. Our galaxy might contain a planet on which all that is not barren is gardened by the dominant species, whose population is kept in check by reproductive restraints, whose rate of consumption of energy never exceeds the amount delivered daily by the sun, and whose recycling is so efficient that it produces no waste. Some of the garden would be marine, some terrestrial, and some would be there to help to maintain rainfall regimes or other public goods, but it would all be there solely to keep the dominant species alive.

Research cannot tell us how much biodiversity loss is too much. It's a societal choice. Our biological future is in our hands; we took responsibility for it when we invented fire and agriculture.

Multi-species interactions

Pedro Jordano, Integrative Ecology Group, CSIC, Spain

The structure of multi-species interactions resembles other complex networks and is central to understand its evolution and the consequences of species losses for the persistence of the whole ecosystem network.

Complexity is a basic property of the biological world, often limiting our understanding of the basic principles that drive and generate their diversity. Interactions among species in mega-diverse assemblages, such as the mutualistic interactions among vertebrate frugivores that disperse seeds and plants that produce fleshy fruits in a tropical forest can take a formidable diversity, generating complex patterns of mutual dependence among animals and plants that are more than the sum of the pairwise interactions. These ecological interactions among species are the backbone of biodiversity. Interactions take a tremendous variety of forms in nature and have pervasive consequences for the population dynamics and evolution of species. Thus, recent analyses indicate that mutualistic networks have specific signatures in their topology and structure (i.e., the way species are interconnected through mutual dependences) that confer more robustness and stability than expected for randomly assembled interactions. A persistent challenge in evolutionary biology has been to understand how coevolution has produced complex webs of interacting species, where a large number of species interact through mutual dependences (e.g., mutualisms) or influences (e.g., predator-prey interactions in food webs).

Recent studies on mega-diverse species assemblages in ecological communities have uncovered interesting repeated patterns that emerge in these complex networks of multi-species interactions. They include the presence of a core of supergeneralists, proper patterns of interaction (that resemble nested Chinese boxes), and multiple modules that act as the basic blocks of the complex network. All these main properties of the ecological networks appear to be omnipresent in nature, independent of the type of interaction or the specific ecosystem or community we study. The challenge remains to understand how these mega-diverse assemblages co-evolve, i.e., how pairwise interactions add up to modules of tightly-interacting species to whole communities as diversified as those in tropical forests. These patterns suggest both precise ways on how coevolution goes on beyond simple pairwise interactions and scales up to whole communities.

The recent use of network-based tools to study complex patterns of ecological interactions underscores the relevance of multidisciplinary approaches: from statistical mechanics in physics, biocomplexity, ecological modelling, and basic natural history. It is probably the only approach that can successfully decipher the simple, general, patterns that lie behind the extreme complexity of interaction webs in ecosystems. A fascinating aspect of these webs is their similarity and analogy to other complex networks, spanning biotic (e.g., gene regulation, cell metabolic reactions) and abiotic (e.g., the internet) scenarios. The multidisciplinary, integrative, approach to the study of complex networks can be a key to develop early warning diagnostic criteria to identify critical situations of disturbance in natural areas well before the functional aspects of key ecosystem services, like animal-mediated pollination or seed dispersal, reach a no-return point for their successful restoration. On top of these applied objectives, research on complex ecological networks has set the first steps to a fuller understanding of how coevolution drives mega-diverse assemblages of interacting species which are the backbone of biodiversity.

RE: Multi-species interactions
The importance of functional diversity

Edit Kovács-Láng, Institute of Ecology and Botany of the Hungarian Academy of Sciences, Hungary.

The scientific concept of biological diversity involves the compositional, structural and functional variability present at all levels of organization of the living world.

We rarely refer to the scientific concept of biological diversity anymore, instead using the political term 'biodiversity' which narrows the content and dimensions of the concept and emphasizes the compositional component. I would like to argue for the importance of functional diversity, because I think in times of global change it is a key factor of survival.

Biotic communities implement so called "biological cycles", the circulation of nutrients essential for life. This process ensures the recycling and reuse of elements on Earth where we have them in a limited supply. Therefore this process ensures the maintenance and continuity of life on Earth. This function of biotic communities/ecosystems is based on the functional diversity of the component organisms and on the presence and functioning of the three main functional groups: the primary producers, consumers and decomposers. This basic ecosystem function is, at the same time, a major ecosystem service. I agree with Martin Sharman, who called for future research on the loss of biodiversity, but I would emphasize the functional aspect of it, and agreeing with Pablo Goicoechea I suggest to make politicians understand that economic value of biodiversity is not the only (and main!) reason to preserve it.

I would like to quote the words of Ferdinando Boero who stated that "Evolution is genetics and ecology". I can find the same idea from Dawkins, who stated that evolution is governed by the non random survival of small, random heritable changes in an adaptively non random direction. I think that the functional aspect is the most important, both on the genetic and ecological sides.

In terms of genetics, the evolutionary genetic potential is based on the functional diversity of genes and is a major precondition of mutations. On the side of ecology, non random adaptive survival is realized by natural selection, which preserves and accumulates the fittest from the genetic changes. In my mind to become the fittest, the best adapted (under given conditions), is a matter of proper function. The essence of natural selection is that organisms come to match their environment in both the abiotic and biotic sense. Co-evolution in communities is a permanent matching process, and it is based on functional traits.

We have to focus research on the role of structural and mainly functional diversity in the functioning of complex biological systems/ecosystems. And we have to study and understand the mechanisms of natural selection (with a secret hope that sometimes we can help it in a proactive way, when necessary).

RE: Multi-species interactions

Tiiu Kull and Kalevi Kull, Tartu, Estonia

This contribution adds some aspects in the development of contemporary research on coevolution, using the concept of consortium.

An important aspect that the study of coevolution (different from a study of evolution as described for a separate population) can add is the emphasis on the role of the relationships between evolutionary and ecological dynamics. This concerns both the establishment of new relationships, and the heritance of existing relationships.

In the case of relationships, it is evident (however not always clearly formulated) that it cannot be inherited without the partners of the relationship - in the case of a binary relationship, without both species of the co-functioning pair.

A general term that can be proposed for a wider use in the description of co-functioning species is consortium. In this sense, it was introduced by Johannes Reinke in 1872 (see also Sapp et al., 2002; for a more contemporary use, see, Masing, 1981). Consortium can be thus

defined as a group of organisms of different species connected via relationships of recognition. i.e., the consortial relationship (including symbiotic, parasitic, commensalists, etc.) persists because the organisms inherit the ability to recognise the partner species.

When new relationships are established the organisms' learning capacities may certainly play a role. In terms of evolutionary mechanisms, the Baldwin effect and organic selection can be applied (Weber and Depew, 2003; Kull, 2000).

The mechanisms of organic selection can work together with the system of inheritance as described in the works of Jablonka and her colleagues. Namely, she distinguishes between four major types (and mechanisms) of inheritance: genetic, epigenetic, social (or behavioural), and cultural (or lingual) (Jablonka, 2001; see also Laland et al., 2001).

Thus, epigenetic inheritance (together with social inheritance mechanisms), together with the Baldwinian understanding of evolution (which is particularly relevant in the understanding of the role of plasticity), seems to provide a fruitful approach to the evolution of consortia, i.e., the complex ecological relations.

RE: Multi-species interactions

Andreas Tribsch, Hans-Peter Comes, Hannes Paulus, Sabine Hille and Stefan Schindler, Austrian Platform for Biodiversity Research (BDFA), Austria

Although ecosystems do not evolve themselves, they are significantly influenced by multiple evolutionary responses to environmental change that act on species' relationships with other species. These multi-species interactions range from different symbiotic interactions like mutualism to true co-evolution, which is difficult to distinguish. In Europe, the relevance of co-evolutionary networks is poorly understood in several ecosystems that might be vulnerable to global change, like alpine and arctic tundras, but also anthropogenic habitats like pastures and meadows. Important co-evolutionary networks also include pollinator plant interactions that are also an economically relevant ecosystem service.

Further research is required to:
- Test hypotheses on co-evolutionary relationships and networks in presumptive cases of plant/mycorrhizal relationships in subalpine/alpine heathland, temperate deciduous, subarctic tundras, and meadows and pastures, i.e. in habitats where mycorrhizal symbiosis is supposed to be exceptionally relevant.
- Test hypotheses on co-evolutionary and systemic interactions between pollinator communities and flower communities within habitats. It may be that adding or removing single members of a given community might cause a stronger change of the host-pollinator system.
- Further understand cryptic co-evolutionary networks, especially interactions of important vascular plants (ecological key species like trees, meadow species…) in order to distinguish loose mutualism from symbiosis and true co-evolution.
- Develop models of the distribution of co-evolutionary networks and its comparison with single species responses.
- Test hypotheses of co-evolutionary networks with phylogenetic/phylogeographic methods on multiple species groups that are supposed to be co-evolved. This will allow for the estimation of the degree of co-evolution and for discriminating co-evolution from looser interactions.

Environmental change causes changes in the distribution of single species including the potential increase of the immigration of neobiota. Such migrations might result in new species-species interactions like pollinator shifts, new host-parasite systems, and hybridisation after new contact.

Further research is required to:
- Assess the potential impact of environmental changes on economically important pollinators.
- Predict the influence of hybridisation among species in new contact and the consequential impact on co-evolutionary networks.

- Evaluate distribution changes (with phylogeographical and phylogenetic methods) in relation to future hybridisation and potentially resulting host shifts, e.g. parasites and resulting ecological/environmental impact.

Managing co-evolutionary relationships under environmental change would help to preserve not only these networks, but also ecosystem services provided by them.

Further research is required to:
- Compare predicted changes in biodiversity with predictions of the impact on multi-species interaction networks.
- Identify the ecosystems that will suffer above-average impact from global change, especially those with high binding capacity of CO_2. These ecosystems might include mires and bogs, tundras, subalpine heathlands, or boreal forests as they have humus rich soils.

RE: Multi-species interactions
Coexistence verses competence

Eva Barreno, University of Valencia, Spain

The hologenome theory of evolution emphasises the role of microorganisms in the evolution of animals and plants. The theory posits that the holobiont (host plus all of its symbiont microbiota in the sense of Margulis, 1993) is a unit of selection in evolution (Zilber-Rosenberg and Rosenberg, 2008). Genetic variation in the holobiont that can occur either in the host and/or in the microbial symbiont genomes (together termed hologenome) can then be transmitted to offspring. In addition to the known modes of variation, i.e. sexual recombination, chromosomal rearrangement and mutation, variation in the holobiont can occur also via two mechanisms that are specific to the hologenome theory:
1. Amplification of existing microorganisms, (the increase of one group of symbionts relative to others which can occur when conditions change)
2. Acquisition of novel strains from the environment (under the appropriate conditions, the novel symbionts may become more abundant and affect the phenotype of the holobiont).

Microbial amplification can be a powerful mechanism for adapting to changing conditions. Acquisition of new symbionts can introduce new genes into the holobiont. Animal and plants harbour abundant and diverse microorganisms and these symbionts affect the environmental fitness of the holobiont and /or mechanisms of co-evolution.

Lichens are complex organisms with a specific biological organization. Their thalli are the result of cyclical symbiotic associations (Chapman and Margulis, 1998) between at least two very different organisms, a heterotrophic fungus (mycobiont) and a photosynthetic partner or photobiont (cyanobacteria or unicellular green algae). The symbiotic interaction between the mycobiont and the photobiont(s) occurs through a process of symbiogenesis and results in the lichen thallus, which is a unique entity, or holobiont (Margulis and Barreno, 2003). It is plausible to propose the symbiogenetic thalli of some lichens as a possible scenario for the horizontal transfer of genetic material among distantly related organisms such as bacteria, fungi, and green algae, making lichens a useful tool for studying the evolutionary history of genetic elements, especially in the case of potentially mobile elements like introns. Del Campo et al. (2009) studied in the lichenized algae *Trebouxia spp.* several group of introns which showed a significant similarity to those of distantly related organisms such as prokaryotes and fungi.

Ramalina farinacea is an epiphytic fruticose lichen that is relatively abundant in the Mediterranean, subtropical or temperate climates. Little is known about photobiont diversity in different lichen populations. Herein, we studied the phycobiont composition in several populations collected from the Iberian Peninsula, Canary Islands and California. Anatomical observations and molecular markers [plastid 23SrDNA and nrITS] allowed us to determine the coexistence of two different taxa of *Trebouxia* (working names, TR1 and TR9) within each thallus of *R. farinacea* in all the analysed populations. Phylogenetic analyses based on

nrITS revealed genetic variability due to the presence of seven genotypes forming two clades, defined by both TR1-like and TR9-like genotypes. The effects of temperature and light on growth and photosynthesis indicate that TR9 displays superior performance under relatively high temperatures and irradiances while TR1 seems to prefer more temperate and shaded conditions. *R. farinacea* thalli seem to represent a highly specific pattern of symbiotic association involving the same two *Trebouxia* phycobionts. The strict preservation of this pattern of algal coexistence may be favoured by the different and probably complementary ecophysiological responses of each photobiont facilitating the proliferation of this lichen in very different habitats and areas. Coexistence verses competence: there are multiple theoretical models and practical examples in nature demonstrating that positive interactions among potential competitors can sustain stable multispecies coexistence (Gross, 2008).

Nitric oxide (NO) is a ubiquitous and multifaceted molecule involved in cell signalling and abiotic stress. NO has an important role in the regulation of oxidative stress and in the photo-oxidative protection of photobionts in lichen thalli. The results point to the importance of NO in the early stages of lichen rehydration, in the sensitivity of these organisms to air-pollutant gases, and to the evolutionary role of NO in the establishment of lichen symbiosis due to its dual function as an antioxidant and a mediator of cell communication.

Introducing space and time in multi-species networks

Luis Santamaria, IMEDEA (CSIC-UIB) and **Miguel Rodriguez- Girones,** CSIC, Spain

It has been argued that multi-species interaction networks represent the backbone of biodiversity. The challenge is now to understand the labile nature of their (internal) interactions and predict its dynamics. Because pollination and dispersal networks have direct bearings on the movement of genes and species, they should represent a cornerstone of models aimed at predicting eco-evolutionary responses to landscape and climate change.

Recent work on mutualistic networks has spurred interest on the ecological and (co)evolutionary processes that determine the complex patterns of interactions observed within species assemblages. The identification of topological and structural features that confer robustness and stability has been used to further explore the consequences of species loss for community stability, aimed, for example, at informing future conservation policies.

Owing to the enormous complexity of the task at hand, the analysis of mutualistic networks has mainly relied on short-term observations. Evidence that observed interaction networks may greatly change over time and space is generally disregarded as "experimental noise" and smoothed out by averaging over the complete observation period. However, we will argue that this kind of variation represents the signature of processes with important ecological and evolutionary consequences. Understanding the labile nature of multi-species interactions and the processes that govern them is a pre-requisite to be able to predict changes caused by environmental changes or disturbances, and explain the existence of (local) co-evolutionary processes in the midst of species-rich communities dominated by ecological generalists.

In particular, subtle changes in interaction dynamics (such as the foraging behaviour of pollinators) may result in strong consequences for network structure and evolutionary dynamics, and may explain the co-evolution of morphological traits (Rodríguez-Gironés and Santamaría, 2010). The coupling of ecological models incorporating foraging behaviour, which predict differences in floral and pollinator traits that will lead to resource partitioning, and evolutionary models based on game theory, used to predict changes in traits of flowers and pollinators, shows that pollinators can drive the evolution of floral divergence in the presence of behavioural noise and temporal variability in the composition of pollinator ensembles. Because resource partitioning processes are contingent on the composition of plant-pollinator assemblages, they are likely to vary following any perturbation (e.g. species introductions or extinctions), therefore affecting predictions on network resilience or its robustness to extinctions.

A second aspect of mutualistic networks deserving attention is their spatial component. Pollination and seed-dispersal networks represent a one-shot description of the simultaneous operation on multiple processes of redistribution of plant genes/individuals over space, caused by patterns of animal movement which, in turn, respond to the existing distribution of plant resources (nectar, pollen, fruits). In this context, predicting how changes in species distributions will affect both the future distribution (e.g. through changes in resource availability for pollinators), migration capacity (e.g. though changes in plant dispersal) or evolutionary potential (e.g. through changes in pollen-mediated gene-flow) of inter-dependent species will require detailed knowledge on the factors driving the assembly and structuring of mutualistic interaction networks. While the "static" analysis of existing networks may provide a rough guidance, we should be urged to explore the ecological and evolutionary mechanisms that drive their dynamics.

RE: Introducing space and time in multi-species networks

Ferdinando Boero, University of Salento, Italy

The knowledge of species interactions is still in its infancy, especially in marine environments. The example of zooxanthellae and coral bleaching is a very popular one, but there are many cases of symbioses that are waiting to be described. Besides mutualism, trophic cascades are also important. Darwin, for instance, was probably the first to describe one (much earlier than Hairston, Smith and Slobotkin): Bumble bees pollinate British clovers, mice feed on bumble bee nests and, in doing so, they harm clover by harming their pollinators; cats feed on mice, so cats favour clover. These intricacies in positive and negative interactions require detailed knowledge of natural history, a discipline that is considered as naive and obsolete since Elton's times (1926) (Darwin was a naturalist, by the way).

As for pollinators, I expect that, with the use of pesticides, wind-pollinated plants tend to win over insect-pollinated plants. It would be interesting to test this prediction. If so, the high frequency of allergies to pollen might be linked, in a trophic cascade fashion, to the widespread use of pesticides that favour wind-pollinated plants: Fewer insects mean fewer insect-pollinated plant species, therefore creating more space for wind-pollinated species, leading to more pollen in the air, and therefore an increase in pollen allergies.

The great success of alien species, however, shows that life invariably finds its way. If a species is favoured by local conditions, it starts to develop relationships with the natives, and eventually the system starts to work in a different way. The original system is radically altered, but a new one starts to function anyway. This does not mean that all changes are positive and that there is nothing to worry about, but I want to stress once more how little we know about species roles and species interactions.

The greatest majority of species are unnamed. This means that we end up describing the few known cases, pretending that they cover our needs of knowledge. Great efforts are still needed in describing biodiversity and to understand their life cycles, and their interactions. For instance, in spite of the enforcement of the ecosystem approach to fisheries, fisheries science does not care about gelatinous plankton. Fish eggs and larvae are eaten by jellyfish, but fisheries science concentrates mainly on adults. The phase shift from a fish to a jellyfish ocean is changing the interactions through the food chains.

Evolution in metacommunities: eco-evolutionary dynamics in space

Mark Urban, University of Connecticut, USA

Complex interactions between ecological and evolutionary dynamics across multiple spatial and temporal scales determine the diversity of life on Earth. Most past research on eco-evolutionary dynamics has focused on a single local population and one or two species. However, in real natural systems, we can expect complex multi-species food webs and that dispersal will integrate ecological and evolutionary dynamics across multiple populations.

What is an evolving metacommunity?
The evolving metacommunity framework assumes that the evolution of species interactions will affect the ecological dynamics of sets of multi-species communities connected by dispersal (Urban and Skelly, 2006; Urban et al., 2008). Dispersal is a key organizing principle because it alters the interplay between ecological and evolutionary dynamics, often in unexpected and non-linear ways. Local natural selection and regional gene flow affect local evolutionary dynamics in spatially structured populations (Hanski and Gaggiotti, 2004) at the same time as local species interactions and regional gene flow determine ecological dynamics in metacommunities (Leibold et al., 2004). Combining theories on evolutionary dynamics in structured populations and on metacommunity dynamics is expected to generate more accurate predictions than either approach alone.

Three important findings from evolving metacommunity theory:
First, evolutionary dynamics in a metacommunity can alter species richness by introducing additional evolutionary tradeoffs among competing species (Urban, 2006). Second, a community monopolization effect can occur when an early colonist to a patch evolves higher local fitness and excludes future colonizers by monopolizing local resources (Urban and De Meester, 2009; Loeuille and Leibold, 2008). Third, the spatial evolutionary processes that generate ecologically relevant trait variation between populations can feed back to influence local community and ecosystem dynamics (De Meester et al., 2007; Harmon et al., 2009). These findings are relevant for applied questions because eco-evolutionary interactions across landscapes likely characterize all natural communities.

What does the evolving metacommunity concept predict about responses to climate change?
Species can respond to climate change through dispersal or adaptation. However, dispersal and adaptation bracket a continuum of spatial evolutionary processes that include some level of gene flow and adaptation. We know little about how these interactive effects play out across shifting geographic clines in temperature. Also, species will disperse at variable rates, such that some species will track climates through dispersal alone, adaptation alone, or through some combination of these responses.

Species interactions have been generally ignored in climate change predictions. We can expect that the individualistic responses of species to climate change will break apart obligate species combinations and create novel non-analogue communities. The role of rapid evolution will be critical in understanding the resulting persistence of members of these novel communities.

Where are the gaps in our knowledge?
1. We need to develop a suite of theoretical models that incorporate multi-species interactions, regional dispersal and evolutionary dynamics.
2. We need to understand the evolution of quantitative traits across natural landscapes by performing large-scale, collaborative experiments that estimate genetic variation in traits and the potential for future adaptation among dozens or even hundreds of natural populations arranged along climatic gradients.
3. We need to study how individualistic responses to climate change will alter species distributions and food web structure.
4. We should begin conducting "common garden experiments in time" where climate-related traits are measured repeatedly in the same populations over long timescales.

Evolution in metacommunities and global change

Luc De Meester, Laboratory of Aquatic Ecology & Evolutionary Biology, Belgium.

The concept of evolution in metacommunities (see also keynote of Mark Urban) integrates evolution, community ecology and space. It explores how eco-evolutionary dynamics may impact species composition and trait change across environmental gradients in space and time. It is a challenging – because of its complexity – but unifying and rewarding framework to view biological responses to global change.

Anthropogenic change implies selection pressures that may act at both the level of the community (inducing changes in relative abundance of species, i.e. species sorting) as well as at the level of the individual (inducing genetic changes - micro-evolution - in the different species that make up local communities). Anthropogenic change will thus induce both trait changes at the species and community level, and these two levels of response may influence each other. Applied to climate change, there are four processes that may interact with each other: species sorting in the local community, micro-evolution in local populations, immigration of new species from other habitats, and immigration of new genotypes from other habitats. As mentioned, the responses at the community and species level may interact with each other. In addition, however, local and regional processes also interact with each other: if immigration rates are high (i.e. high rates of dispersal), then local populations and communities can be swamped by immigrant genotypes and species. If, however, local responses are fast and effective, either through micro-evolution or through species sorting, then this may effectively reduce immigration rates. It is only by quantifying these four processes and quantifying their interactions (see Van Doorslaer et al., 2009 for the quantification of the interaction between local micro-evolution and immigration of new genotypes) that one can understand the proximate causes of biological responses to climate change or other anthropogenic disturbances such as the introduction of invasive species.

Effective micro-evolution or species sorting within local communities potentially have the power to "localize" responses to climate change, i.e. reduce the impact of migration to levels lower than one would predict from climate envelope models that do not take evolution into account. In addition, climate envelope models also need to be modified so as to explicitly take dispersal limitation into account. To this end, quantifying metacommunity structure of organisms across landscapes is an important research theme.

The evolving metacommunity concept provides a strong but challenging framework to study responses to global change. Local rates of trait change versus immigration rates are crucial. Genetic studies using neutral and genomic markers in the near future may provide important tools to better quantify immigration and adaptation rates in local populations. Once genomic studies have identified markers linked to specific traits, studies can contrast patterns for neutral markers (reflecting population structure and history, thus allowing reconstruction of migration events) and selected loci (quantifying trait adaptation). This is a promising avenue for research, as the identification of such markers would allow large-scale surveys across space and time. The latter may involve long-term monitoring studies, but in model systems that have layered dormant egg banks or for which archived material is available, this approach can also involve paleogenomic analysis (De Meester et al., 2007).

Evolution takes place in communities

Rasmus Ejrnæs, National Environmental Research Institute, Aarhus University
Hans Henrik Bruun, Center for Macroecology, University of Copenhagen

Species richness in plant communities may be explained by ecological processes or by species pool sizes building up over time spans of centuries and millennia by migration and speciation. While these explanations are often presented as competing, this contribution suggests that the same basic mechanisms may be working at all temporal and spatial scales.

Communities are products of immigration and environmental sorting (Warming, 1909; Gleason, 1926). Hence, formation of a viable population at a site requires successful dispersal, followed by establishment, survival and reproduction. Two competing paradigms in community ecology put very different emphasis on either dispersal and species pools or ecological interactions and even tend to neglect the alternative. Explanations for species richness in biotic communities have often been sought amongst properties and processes in the community, e.g. resource availability, disturbance (including grazing) and competition (Grace, 1999). Although lottery models have suggested that coexistence is possible even with strong competitive hierarchies, at least for organisms with a sessile habit, the effect of competition has been demonstrated repeatedly.

During the last decade, the idea that local richness is largely determined by species availability, i.e. by the regional species pool, has gained wide support. Evidence for the species pool theory comes mainly from correlative studies (e.g. vascular plants: Pärtel et al., 1996; freshwater fishes: Kelso and Minns, 1996; zooplankton: Shurin et al., 2000; corals: Karlson and Cornell, 1998), which have reproduced positive and significant relationships between local and regional species richness, with different local communities as data points.

We propose that the rate at which new individuals recruit from sexually produced propagules and reach reproductive maturity is a key property of biological communities. That is what we call the community-level birth rate (new genets per established genet per unit time). If the community-level birth rate is low, no new species will establish. If it is high, the community is open to newcomers (Davis et al., 2000), and an increase in local species richness will depend on the per-birth immigration rate (the proportion of the recruits in one time-step belonging to species not present in the community) given a constant community size. We expect the community-level birth rate (CBR) to be highly dependent on the local environment.

While it is obvious that the CBR is important for the build-up of species over time during the assembly of a community, we also suggest that CBR is important for the build-up of the species pool by migration and speciation. We propose that the build-up rate of species pools, the metacommunity speciation rate (MSR), is dependent on three factors, the community-level birth rate (CBR; new genets per established genet per unit time) and the per-birth immigration (IR) and speciation (SR) rates, in the following way: $MSR = CBR \times (IR+SR)$

This means that the actual size of a regional species pool depends on CBR, the per-birth immigration/speciation rate, metacommunity size and time, or, in other words, on the total number of births in that metacommunity through time multiplied by the sum of the per-birth immigration and speciation rates. This rationale is similar to Hubbell's (2001) neutral theory of biodiversity, which has the per capita speciation rate, n, as a fundamental factor, and the constant metacommunity size, JM, as a precondition. However, the present model is based on deviations from neutrality at both the species level (unequal probability of death and speciation for different individuals in the community) and at the community level (unequal probability of death and speciation in different communities).

Implications for conservation and research

If our community-level birth rate hypothesis is valid, then conservation measures trying to protect evolution and genetic diversity should target not only extant diversity, but also the processes and environments promoting a high community-level birth rate. Although it may be

premature to produce a list of evolution-friendly environments, it is hard not to become pessimistic when considering the present European environment. For the following reasons:

1. Nitrogen deposition and fertilizer application is transforming open and infertile plant communities with high birth rates to dense communities with heavily asymmetric competition and low birth rates.
2. Over large parts of the territory extensive grazing by domestic herbivores have ceased leading to encroachment and declining birth rates.
3. The cultivation of plantations and fields combined with mechanical or chemical weeding, leaves birth rates in the silvicultural and agricultural landscape at very low levels.

The current mass extinction event may be discriminated from previous global mass extinctions not only by having a biotic cause, namely the human species. While the previous mass extinctions left vast vacant areas and resources, the current mass extinction leaves very little vacant space for new evolution. We therefore recommend research in the past and present impact of communities and environments on evolution and suggest that community-level birth rate could be a promising starting point.

Assessing conservation risks under uncertainty

Yiannis Matsinos, Department of Environment, University of Aegean, Greece

This contribution examines uncertainty as a factor affecting PVA predictions.

Population Viability Analysis (PVA) has enjoyed popularity within the last two decades as a tool in conservation biology to evaluate the risk of extinction and to evaluate possible management actions. In general, PVA develops a population dynamics model based on prior data availability and uses it to project population trends in the future. These models use ecological knowledge, parsimony, and statistical best-fit criteria and usually focus on single species on a prescribed spatial extent. The widespread use of the PVA approach in conservation biology is facilitated by the availability of several software programs and the ongoing improvement of computational capacity.

However, there is a main issue associated with PVAs: the role of uncertainty on extinction probability based in PVA case studies is not yet understood (Beissinger, 2002). Uncertainty can be an important issue regarding the biological parameters used in models. In some cases the parameters are not obtained from field data and are subject to sampling error; otherwise they are obtained from literature. Another source of uncertainty comes from a variety of independent studies that share no common rules for comparing results. A third case stems from the fact that environmental conditions are nevertheless changing and PVA predictions must adhere with future environmental conditions. From a statistical point of view it seems that Bayesian approaches perform better compared to frequentist statistics. But field data used for parameter estimation have been subject to past environmental conditions that introduce uncertainty about their validity for future use. A possible way to amend this is by developing solid sensitivity analysis in order to assess the degree that variability in parameter values affects model results. This feeds back in a useful way to the design of monitoring protocols since considerable lack and uncertainty in parameters may be corrected by providing relevant data in the future surveys. A final source of uncertainty deals with the spatial structure of most PVA studies. In a habitat study, Southwell et al. (2007) could not find examples in the literature in which the influence of habitat-model uncertainty on PVA-model predictions was measured. But habitat association is one source of uncertainty. I claim that the issue is more complicated; a scale-oriented approach could lead to a more integrated assessment of how uncertainty propagates in PVAs if the scale of operation is variable. A new ongoing FP7 IP "SCALES" (www.scales-project.net) is dealing with the issue of multi scale PVA models introducing genetic information, spatial autocorrelation and dispersal attributes with special emphasis on uncertainty modelling, in order to tackle the pressing conservation needs.

It is evident that the need for good (and continuous in time) monitoring data is more than urgent since all PVA modelling efforts are heavily dependent on them. It is anticipated that uncertainty will be restricted more on the structural complexity of the problem and less on the quantifiable information about ecological processes available.

Coevolution in complex environments

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The author examines co-evolutionary patterns and processes, in particular looking at the geographic mosaic theory of coevolution.

Complex ecological and ecosystem processes pose a difficult hurdle to detailed observations. Because communities and ecosystems typically include taxa with generation times ranging over more than four orders of magnitude, studying how such systems respond ecologically to environmental variation, almost inevitably means also studying evolutionary responses. Although cross-links are being formed between observation, theory, and experimentation in population biology, due to the complexity of natural systems we are still far from an integrative understanding of how biotic and abiotic environments influence population ecology and evolution.

Progress towards the above quest necessitates we understand inter-individual interactions. Interactions are identifiable in all natural communities, and they typically result in positive or negative effects for one or both individuals. When these are important enough to affect fitness in two or more interacting species, they provide conditions for coevolution. If we can understand coevolution, then we will have made a great leap in understanding how abiotic and biotic environments mould species biology.

Coevolution, even when resulting in a net mutual benefit, is open to conflict, and this plays an important role in the mode and tempo of reciprocal selection (e.g., Thompson, 2005). Given the multitude of positive and negative selective forces potentially underlying interactions, an important question in understanding both dynamics and long-term persistence of co-evolutionary associations is the extent to which selection is directional or fluctuating. Directional selection would be suggested by costly resistance and virulence genes, such that (ideally) monomorphic populations emerge. In contrast, in fluctuating selection, there is no overall winning strategy through time. These observations are largely based on simple two species interactions, in either homogeneous or simplified heterogeneous environments; it is unknown to what extent they emerge in nature.

An insightful approach to addressing questions of co-evolutionary pattern and process is the "Geographic Mosaic of Coevolution" (e.g., Thompson, 2005, 2009). The idea is that forces known to affect spatial evolution in single species are also at work in co-evolutionary associations, but these latter systems by the specific nature of reciprocal fitness feedbacks, exhibit characteristic behaviours (Nuismer et al., 2000). One of the many predictions is that local environmental conditions and gene flow potentially influence co-evolutionary progress, resulting in areas of intense reciprocal selection (tightly coupled interactions in so called "hot spots") and areas of weak selection in at least one of the two species (more loosely coupled interactions in "cold spots") (e.g., Gomulkiewicz et al., 2000). Much progress has been made in understanding the processes underlying geographical mosaics (Thompson, 2005), but as of present, actual controlled experimental demonstrations are few, as are detailed pictures of coevolution for any one system (e.g., examples in Thompson, 2005). Moreover, empirical observations that some antagonistic co-evolutionary systems produce more or less specialized host resistance and parasite virulence genotypes (Poullain et al., 2008), and exhibit variable phenotypic outcomes (Forde et al., 2008), have not been conclusively explained. Thus, a greater conceptual understanding of the forces at work in coevolution will require both new theory and experimentation, and must tease out the effects of the environment from those driven by traits.

A possible signature of the relative influences of environment and coevolving species' traits is the nature of specificity in adaptations and co-adaptations (Thrall et al., 2007), but it is unclear what it actually is about the environment that interfaces with phenotypic traits to create reciprocal selection, coevolution and adaptation. Environmental influences may be

subtle and protracted in time, interact in complex ways, and not translate in a simple, direct way into fitness changes.

Future research needs to provide answers to how complex environments—and in particular those associated with human activity—affect genetic and species biodiversity in tightly and loosely coupled interactions and networks. Both types of biodiversity are signatures of potential adaptability, through functional diversification and robustness. I argue that co-evolutionary interactions should be at the centre of such research, because they span a range of interaction strengths (hot spots and cold spots) and types (e.g., mutualism to parasitism), and influence the structure of populations, communities and ecosystems.

The Geographic Mosaic of Coevolution

John Thompson, University of California, USA

The author outlines the geographic mosaic theory and highlights the importance of developing a science of applied co-evolutionary biology.

If we begin with the view that species are often collections of genetically distinct populations and that selection often differs among populations in different environments, then interactions among species are bound to vary among environments. The geographic mosaic theory of coevolution was developed in an attempt to formalize analysis of this variation by evaluating interactions as genotype by genotype by environment interactions (i.e., G x G x E; or even G x G x G x…E). The goal has been to build a more ecologically realistic theory of the co-evolutionary process by incorporating the minimum additional complexity beyond panmictic models needed to capture the ecological and genetic structure and dynamics of real interactions. More broadly, geographic mosaic theory attempts to explain why evolving interactions can be highly dynamic yet sometimes persist for millions of years.

Geographic mosaic theory hypothesizes that the evolution of interactions among real species is shaped by three components of co-evolutionary variation (GxGxE): geographic variation in the structure of selection on an interaction (i.e., selection mosaics), geographic variation in the strength of reciprocal selection (i.e., co-evolutionary hotspots and coldspots), and additional geographic variation in the distribution of traits found within interacting species resulting from gene flow, random genetic drift, and meta-population dynamics, thereby creating an ongoing remixing of co-evolving traits across ecosystems.

At its most fundamental level, geographic mosaic theory argues that long-term coevolution in real species is an inherently geographic process. It argues that studies of local (co)adaptation and panmictic models of coevolution cannot fully capture the causes of the structure, evolutionary dynamics, and persistence of real interactions. It is not just the traits of species that shape coevolution; it is also the varying community and ecosystem contexts in which those species occur across their ranges.

Field studies, microcosm studies, and mathematical models have suggested over the past decade that selection mosaics, intermingling of co-evolutionary hotspots and coldspots, and trait remixing do indeed create dynamics that differ from the patterns found in earlier panmictic models of coevolution and local studies of coevolution. Some of those differences can be summarized in the following results:

1. Species interacting in a geographic mosaic may co-evolve faster and toward different equilibrial states than under panmictic conditions, at least under some conditions (Brockhurst et al., 2003; Forde et al., 2004; Forde et al., 2007; Lopez-Pascua and Buckling, 2008).
2. Species interacting in a geographic mosaic may maintain polymorphisms over a longer term than species interacting only locally (Burdon and Thrall, 2000; Kniskern and Rausher, 2007).
3. Differences in productivity among communities can create selection mosaics that lead to geographic differences in the levels or dynamics of host resistance, parasite infectivity, or ecological outcomes (Hochberg and van Baalen, 1998; Hochberg et al., 2000; Forde et al., 2004; Forde et al., 2007; Lopez-Pascua and Buckling, 2008).
4. Geographic differences in the web of interacting species can create selection mosaics (e.g., Benkman, 1999; Thompson and Cunningham, 2002; Zangerl and Berenbaum, 2003; Piculell et al., 2008). That is, the "environment" in genotype x genotype x environment interactions is often the "biotic environment" in which any pairwise interaction occurs.

We need to evaluate the generality of these and other results on the geographic mosaic of coevolution. A deep understanding of the ecological underpinnings of the co-evolutionary process is becoming increasingly important at a time when we are increasingly taking evolution into our own hands by altering webs of interacting species. We are continually

adding or eliminating species to ecosystems and manipulating interactions by imposing direct or indirect genetic changes on populations. These massive changes will continue. With better theory on the geographic mosaic of coevolution among webs of interacting species, we should be able at least to outline the range of realistic potential outcomes rather than just produce a long list of un-weighted possibilities. That process will lead us to a science of applied co-evolutionary biology.

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