Factors influencing progress toward ecological speciation

Andrew Hendry
Redpath Museum & Dept. of Biology, McGill University, 859 Sherbrooke St. W., Montreal, Quebec, H3A 2K6 Canada

My lab has tested for elements of ecological speciation in salmon, guppies, stickleback, and Darwin’s finches. We have found straightforward evidence for ecological speciation in only two of these systems. This has led us to more carefully consider factors that promote or constrain “progress” toward ecological speciation. We have done so through simulation models and through experiments and surveys of multiple population pairs that differ in their progress toward ecological speciation. In general, the greatest progress toward ecological speciation is associated with strong ecological gradients coupled with modest dispersal rates.

E-mail: andrew.hendry@mcgill.ca

Adaptive speciation: Linking pattern to process

Ulf Dieckmann

Unraveling how biological diversity originates through speciation is fundamental to understanding the past, present, and future of life on Earth. Promoting an ongoing paradigm shift, research on adaptive speciation elucidates how selection driven by frequency-dependent disruptive selection originates from dynamic biological interactions and can trigger the adaptive splitting of lineages. For sexually reproducing species, this process involves the adaptive evolution of reproductive isolation. This presentation will review recent progress in the field and provide an outlook on future challenges.

E-mail: dieckmann@iiasa.ac.at

Darwinian speciation on a regulated landscape

Géza Meszéna, András Szilágyi and Liz Pásztor
Department of Biological Physics, Eötvös University, Budapest, Hungary

Darwin essentially said that speciation is a gradual transformation from within-species diversity to between species one, driven by the fitness-advantage of reduced competition via niche-segregation. We identify three issues why Darwin’s suggestion has been considered problematic since the New Synthesis:
I: The notions of niche and reduced competition have no meaning in the context of a rigid adaptive landscape.
II: The observed often-allopatric nature of speciation seems to exclude a role for competition.
III: Biological species concept declared reproductive isolation as the defining issue of speciation.

Considering these issues together leads us to conclude that Darwin’s original idea is still the most parsimonious theory of speciation. Species diversity is necessarily based on competition-reducing niche segregation, i.e. segregation with respect to the way of being regulated. This structure translates to the concept of regulated adaptive landscape, providing selection pressure for competition-reducing branching evolution, which may, or may not be related to spatial segregation. As selection for ecological divergence is always caused by a fitness minimum, generically we expect selection also for reproductive isolation.

E-mail: geza.meszena@elte.hu

**Integrating population dynamics and evolutionary dynamics**

**Richard Svanbäck**
Department of Ecology and Evolution /Limnology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden

A high degree of trophic polymorphism has been associated with the absence of high variability in population density. An explanation for this pattern is that density fluctuations may influence the selective regime in populations. For example, it has been suggested that genetic variation is favored in stable environments, whereas phenotypic plasticity is favored in unstable and fluctuating environments. Indeed there is a lot of variation between species and populations in the degree of plasticity but this has rarely been investigated. Another facet of fluctuating population densities is that the level of competition will change over time. The effect of competition on morphological divergence and plasticity has however also rarely been investigated. Since low growth rates might constrain morphological modulation and individual growth rates usually are negatively related to the intensity of competition, there might be a connection between competition, growth rate and morphological divergence. In this talk I will show that there might be a connection between the degree of density fluctuations and the level of phenotypic plasticity in populations. I will further show that the level of competition will influence the degree of phenotypic plasticity in a population for example during different phases of a population cycle. These studies show that an explicit consideration of population dynamics may be essential to explain the long term...
evolutionary dynamics in populations. In particular, fluctuating population dynamics may be one explanation for why not all polymorphic populations lead to speciation. Instead fluctuating population dynamics may favor the evolution of phenotypic plasticity.

E-mail: Richard.Svanback@ebc.uu.se

Phenotypic divergence in perch (Perca fluviatilis) – visibility as a driving force?

Pia Bartels
Department of Ecology and Evolution, Limnology, Uppsala University, Norbyvägen 18 D, SE-75 236 Uppsala, Sweden

Fish are well known as integrators of spatially separated food webs within lake ecosystems. However, differences in habitat structure and resource abundance associated with spatially separated food webs can lead to phenotypic divergence due to individual specialization. Strong phenotypic divergence might decouple cross-habitat linkages, thus attenuating overall food web connectivity. In this study, we evaluated differences in cross-habitat coupling by the European perch (Perca fluviatilis) in four lakes in central Sweden that varied in their visibility. Perch are visual predators and thereby, likely affected by changes in visibility. In high visibility lakes, we found that intra-population niche partitioning led to subpopulations in littoral and pelagic habitats with distinct habitat-specific morphologies. Resource utilization of littoral and pelagic subpopulations was consistent with habitat-specific resource availability. Furthermore, pelagic fish showed lower individual specialization than littoral fish in high visibility lakes. In contrast, in lakes with decreased visibility, cross-habitat linkage was high and morphological discrepancy between littoral and pelagic perch was low. Resource utilization of littoral and pelagic fish was less distinct, and generally consisted of high proportions of pelagic resources. Individual specialization tended to be higher in pelagic than littoral fish. Hence, these results suggest that the degree of food web connectivity is likely related to differences in phenotypic divergence which in turn are likely affected by visual conditions in the lake.

E-mail: pia.bartels@ebc.uu.se
Indirect interactions across two trophic levels trigger increased phenotypic divergence in a top consumer

Philipp E. Hirsch
Department of Ecology and Evolution, Limnology, Uppsala University, Norbyvägen 18 D, SE-75 236 Uppsala, Sweden

While there has been extensive research on the evolutionary effects of predation and competition, little is known about how indirect species interactions can affect phenotypic divergence and ultimately speciation. In this study, we used lakes with and without an invasive species (the zebra mussel) to investigate phenotypic divergence between littoral and pelagic subpopulations of perch. We found a greater phenotypic difference between littoral and pelagic perch populations in lakes with zebra mussels compared to lakes without zebra mussels. Perch populations in the pelagic zone of lakes containing zebra mussels had a higher growth, larger body size and a more pelagic adapted morphology while perch in the littoral zone of either lake type showed no response to the mussels. Our results suggest that species at lower food web levels can indirectly trigger phenotypic divergence in species on the top of the food chain.

E-mail: philipp.hirsch@ebc.uu.se

The importance of ecology for phenotypic diversity — Diversification of Lake Mývatn stickleback: spatial and temporal variation in patterns and processes

Katja Räsänen¹, Antoine Millet¹,²,³, Árni Einarsson², Mike Senn¹, Skúli Skúlason³, Mat Seymour¹,³ and Bjarni K. Kristjánsson³
¹Department of Aquatic Ecology, Eawag/ETH-Zurich, Ueberlandstrasse 133 P. O. Box 611, 8600 Duebendorf, Switzerland
²Lake Mývatn Research Station, Skútustöðum, Iceland
³Hólar University College, Department of Aquaculture and Fish biology, IS-550 Saudarkrokur, Iceland

Spatial and temporal variation in environmental conditions have strong effects on natural populations both through ecological and evolutionary processes, as well as feed-backs between them. We investigate how phenotypic diversification is influenced by such dynamic interactions in an ecologically well-studied model system, threespine stickleback (Gasterosteus aculeatus) of Lake Mývatn. Long term monitoring of the lake has revealed strong spatial and temporal variation in several important biotic (e.g. chironomid densities and vegetation gradients) and abiotic (e.g. temperature) environmental conditions - as well as in stickleback population dynamics. We study spatial and temporal phenotypic (e.g. body size, feeding structures and parental investment) and genetic (e.g. extent of gene flow) variation with the aim to understand

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the dynamic nature of eco-evolutionary processes. In this talk we will explore current evidence for diversification in this model system, and discuss two “forgotten” factors in evolutionary diversification: temporal variation and interactions between male and female reproductive traits.

E-mail: bjakk@holar.is

**Intra-species population divergence in Belgjaskógur threespine sticklebacks (Gasterosteus aculeatus)**

Mat Seymour¹,², Bjarni K. Kristjánsson¹ and Katja Räsänen²

¹Hólar University College, Department of Aquaculture and Fish biology, IS-550 Saudarkrokur, Iceland
²Department of Aquatic Ecology, Eawag/ETH-Zurich, Ueberlandstrasse 133 P. O. Box 611, 8600 Dübendorf, Switzerland

Rapid adaptive radiations are rapid divergences in related lineages, often in response to different ecological habitats, and rely greatly on standing genetic variation and phenotypic plasticity. The most readily mechanism for populations to adapt to changing or new environments is through phenotypic plasticity. However, recent studies also suggest, standing genetic variation plays an important role in species adaption and divergence. Whereas mutation relies on new alleles arising and fixating within a population, standing genetic variation utilizes existing allelic variation. This allelic reserve allows for rapid adaptive radiation in response to ecological changes. Using a known adaptive radiated species, coupled with ecological recordings we can assess relationship between ecological variation, adaptation and other evolutionary processes. Threespine sticklebacks are a model species for studying adaptive radiation based on their ability to rapidly acclimate and adapt to new environments over a wide geographical range. The Belgjaskógur woodlands northwest of Lake Mývatn, Iceland includes over a hundred lakes and ponds of various sizes from a few square meters to over 520 m² within 7.5km². The main objective of this study is to assess the effects of environmental factors on intraspecific diversity. This study addresses three main questions 1) To what extent does phenotypic diversity of sticklebacks vary over a small spatial scale in Belgjaskógur woodland? 2) What is the neutral genetic pattern of divergence across geographically close, and presumably, allopatric populations of Belgjaskógur threespine sticklebacks? 3) Is there a strong correlation between environmental, phenotypic or genetic variation across populations of Belgjaskógur threespine sticklebacks?

E-mail: mats@mail.holar.is
Determinants of spatial and temporal phenotypic variation in threespine stickleback from Mývatn

Antoine Millet1,2, Árni Einarsson3 and Bjarni K. Kristjánsson1 and and Katja Räsänen2
1Hólar University College, Department of Aquaculture and Fish biology, IS-550 Saudarkrokur, Iceland
2Department of Aquatic Ecology, Eawag/ETH-Zurich, Ueberlandstrasse 133 P. O. Box 611, 8600 Duebendorf, Switzerland
3Lake Mývatn Research Station, Skútustöðum, Iceland

Understanding the processes and factors that determine phenotypic variation, and how these feed back to population level processes in natural populations is of fundamental importance for understanding how biological diversity emerges, is maintained and changed. We explore how spatial and temporal variation in agents of natural selection (e.g. prey availability and habitat quality) and potential for dispersal/gene flow influence phenotypic variation (e.g. body size and feeding morphology) of the threespine stickleback (Gasterosteus aculeatus) in Mývatn (NE Iceland). To address this question, we use spatial (multiple sampling sites across the lake) and long-term data on ecological variables (e.g. chironomids densities and major habitat types) and stickleback populations (population density and phenotypic variation), as well as molecular genetic methods (microsatellite markers).

Our first results indicate that the extent of gene flow is overall relatively high, however it varies among sites. Our results also indicate that the number of long gill rakers slightly differs among sites, however not between years of high vs. low chironomids densities. These morphological differences found are possibly due to variation in habitat and/or type of food available. This is a first step towards a more complete insight in the ecological and evolutionary process involved in Mývatn stickleback population dynamics.

E-mail: antm@mail.holar.is

Diversification along ecological gradients in the tropics

Thomas B. Smith
Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Charles E. Young Drive South, Room LS5120, Box 951606, Los Angeles, CA 90095-1606 USA

The mechanisms responsible for diversification in the tropics have long been a central question in evolutionary biology. Two competing hypotheses of speciation predominate: those that emphasize the role of geographic isolation during glacial periods and those that stress the role of ecology and diversifying selection across environmental gradients. We used genome scans of the African rainforest lizard
Trachylepis affinis from Cameroon to examine the spatial patterns and environmental associations of both neutrally evolving loci and those thought to be under selection. Neutral differentiation occurred along a cline from coastal lowland rainforest inland toward the ecotone, and was associated with both geographic distance and changing precipitation patterns. Outlier loci thought to be under divergent selection showed divergence predominantly along the forest-ecotone gradient in concordance with morphological divergence in traits related to fitness. Results suggest adaptive diversification in T. affinis is taking place along the forest-ecotone gradient during range expansions or contractions, with a smaller role relegated to refugial isolation augmented by divergent adaptation to different rainforest environments. Additionally, we examine conservation implications of human activities along gradients and show that recent deforestation in West Africa has homogenized the rainforest-ecotone gradient, causing a loss of adaptive phenotypic diversity. With as much as two-thirds of the world’s terrestrial land area impacted by human activities, gradient flattening is likely widespread, but its corresponding impacts on adaptive diversity and implications for conservation in a changing world are not fully recognized.

E-mail: tbsmith@ucla.edu

Phenotypic and genetic variation in a freshwater snail (Radix balthica) that’s been sampled along an extreme temperature gradient

Magnus Johansson
Department of Cell and Molecular Biology, Uppsala University Norbyvägen 18 D, SE-75 236 Uppsala, Sweden

The importance of divergent natural selection in creating and maintaining biological diversity is increasingly being realized in ecological and evolutionary studies. Thermal selection is expected to be ubiquitous in natural systems, but our understanding of thermal adaptation is in many ways incomplete. We will focus on the dynamics of thermal adaptation along thermal gradients in Icelandic lakes (mainly Mývatn in northern Iceland) subjected to geothermal activity, using a freshwater snail as a model system. These lakes have low and high temperature areas, providing a unique opportunity to study divergent thermal selection whilst allowing migration of individuals among the habitats. Population genetic structure along the thermal gradients will be determined using AFLP markers and thermal adaptation in phenotypic traits estimated in laboratory common garden experiments. We will study selection against immigrants, determine the potential for reproductive isolation and investigate the genetic basis of thermal adaptation using outlier estimation from genomic scans.

E-mail: joh.magnus@hotmail.com

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An empirically calibrated model of adaptive diversification along an environmental temperature-depth gradient

Jan Ohlberger¹,²,³, Åke Brännström³,⁴, Ulf Dieckmann³
¹Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, D-12587 Berlin, Germany
²Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, N-0316 Oslo, Norway
⁴Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187 Umeå, Sweden

Theoretical models suggest that sympatric speciation along environmental gradients might be common in nature. Here we present the first data-based model of evolutionary diversification along an environmental gradient. Based on genetic analyses, the sympatric speciation of two coregonid fishes (Coregonus spp.) in a postglacial German lake has been suggested. Within this lake, the two species segregate vertically and show metabolic adaptations to, as well as behavioral preferences for, correspondingly different temperatures. We test the hypothesis that this diversifying process has been driven by adaptations to different thermal microhabitats along the lake’s temperature-depth gradient. Using an adaptive dynamics model that is calibrated with empirical data and that allows the gradual evolution of a quantitative trait describing optimal foraging temperature, we show that under the specific environmental conditions in the lake, evolutionary branching of a hypothetical ancestral population into two distinct phenotypes may have occurred. We also show that the resultant evolutionary diversification yields two stably coexisting populations with trait values and depth distributions that are in agreement with those currently observed in the lake. We conclude that the ecological conditions in the lake are prone to speciation in these fishes, thus supporting the hypothesis that divergent thermal adaptations along the temperature-depth gradient might have brought about the two species observed today.

E-mail: jan.ohlberger@bio.uio.no

Processes of divergence in Icelandic sticklebacks

Guðbjörg Á. Ólafsdóttir
University of Iceland, Research Center of the Westfjords, Aðalstraeti 21, IS-415 Bolungarvík, Iceland

The threespine stickleback is a model organism in behavior and evolutionary biology. It has undergone rapid adaptive radiation since marine stickleback colonized northern freshwater habitats following the end of the Pleistocene period. Different stickleback morphs have been described in Icelandic neovolcanic lakes, most notable a lava morph
which inhabits a complex structured habitat made up of lava flows and a mud morph which is found in typical, vegetated soft mud habitats. Morphological and genetically divergent lava and mud morphs have been described in three Icelandic lakes, Lake Thingvallavatn, Lake Hredavatn and Lake Myvatn and assortative mating among the morphs has been confirmed in Lake Thingvallavatn. Recent studies on threespine stickleback have found that stickleback populations display various levels of ecological specialization exists with or without discreet variation and reduced gene flow. In a recent survey morphological and diet variation among spawning populations in several Icelandic lakes was examined. Parallels and generalities in divergence among lava/rock and mud habitats are examined and the role of various ecological and behavioral factors in potential divergence looked at.

E-mail: gaol@hi.is

Salmonid fishes: an ideal system for behavioural epigentics

David L. G. Noakes
Department of Fisheries & Wildlife and Oregon Hatchery Research Center, Oregon State University, Corvallis, Oregon 97331-3803 USA

Salmonid fishes present remarkable opportunities to study the interactions of behaviour and evolution. Salmonid (salmon, trout, charr) species show remarkable diversity in life history, alternative reproductive tactics, and trophic polymorphism. For example, steelhead, *Oncorhynchus mykiss*, can show more than 30 different life history types. These fishes are ideal experimental research subjects because they can be reared in large numbers under controlled experimental conditions. Several species are produced in large numbers for commercial aquaculture or stocking programs, and there is a wealth of basic information on their behaviour, physiology, genetics and embryology. Pacific salmon species have very high international priority for conservation and management. We study early development and behaviour of salmonids to understand the roles of environment and genetics in evolution. The Oregon Hatchery Research Center (OHRC) has a unique combination of productive capacity and research flexibility for studies of behaviour and evolution. I outline some examples of current research projects on behavioural epigenetics at the OHRC.

E-mail: David.Noakes@oregonstate.edu
Towards a general theory of plant trait diversity

Daniel Stein Falster\textsuperscript{1,2}, Åke Brännström\textsuperscript{2,3}, Mark Westoby\textsuperscript{1}, Ulf Dieckmann\textsuperscript{2}
\textsuperscript{1}ARC-NZ Research Network for Vegetation Function, Macquarie University, Australia
\textsuperscript{2}Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
\textsuperscript{3}Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187, Umeå, Sweden

Many thousands of species of plants currently exist on earth and securing understanding of how this magnificent variety arose is of both theoretical and applied interest. We investigate how frequency-dependent resource competition for light leads to emergence and coexistence of a range of growth strategies in environments with repeated disturbance. Vegetation is structured according to trait, patch, and size, with competition between individuals giving a fitness advantage to strategies able to pre-empt light availability through height growth. The phenotypic evolution of height growth rate is modeled under a tradeoff between the speed and efficiency of growth, with fast growth leading to higher mortality and shade-intolerance. The model predicts evolution of fast-growing strategies for a range of ecological scenarios, despite the inherent disadvantages of the fast-growth phenotype. It also indicates that evolutionary diversification of growth strategies is likely in productive sites and under intermediate disturbance intervals. These results offer an explanation for the evolution of rapid growth rates and the emergence of successional diversity, and provide some explicit predictions on how trait compositions may vary across the landscape.

E-mail: ake.brannstrom@math.umu.se

Ecological variability in Icelandic Arctic charr: an arena for studies of adaptive dynamics and ecological speciation

Pamela J. Woods\textsuperscript{1,5}, Åke Brännström\textsuperscript{2,3}, Skúli Skúlason\textsuperscript{1}, Ulf Dieckmann\textsuperscript{4} and Sigurður S. Snorrason\textsuperscript{5}

\textsuperscript{1}Hólar University College, Department of Aquaculture and Fish biology, IS-550 Saudarkrokur, Iceland
\textsuperscript{2}Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
\textsuperscript{3}Department of Mathematics and Mathematical Statistics, Umeå University, SE-90187, Umeå, Sweden
\textsuperscript{4}Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
\textsuperscript{5}University of Iceland, Department of Biology, IS-101 Reykjavík, Iceland

Intraspecific ecological variation, such as resource polymorphism, is rarely considered in ecosystem studies. However, in relatively species depauperate regions, intraspecific ecological variation may be functionally more important than species diversity, indicating that species that exhibit resource polymorphism may have disproportionate
effects on ecosystem processes when viewed from a larger geographicscale. This study is a first step toward understanding how a polymorphic species interacts with its landscape. The first objective is to form a general relationship that describes how morphology and size predict diet within the species across 50 lakes in Iceland. Generalized linear models (GLMs) are fit to morphological and diet data collected through the Ecological Survey of Icelandic Lakes Project. Because Iceland is a hotspot of geological activity, creating a wide variety of physical habitat within freshwater systems, the second objective is to use this relationship to determine how ecological effects are further related to diet after accounting for the effect of morphology on diet. Residuals of GLMs are then used in multivariate analyses to determine 1) what environmental characteristics are good indicators of the presence of polymorphism, and 2) how average diets within a lake vary with abiotic and biotic lake characteristics. Results indicate that polymorphism is closely related to biotic characteristics of lakes, and that the type of polymorphism that develops depends on food availability, low interspecific competition, and physical diversity. The third objective is to analyze the potential for morph divergence based on biotic components only (i.e., population dynamics of Arctic char and three resources) and the evolution of two traits, morphology and size, within an adaptive dynamics model. Some results do not follow expectations based on smaller spatial or temporal scales, indicating the importance of large-scale comparative studies.

E-mail: pamelajwoods@gmail.com

Genetics of adaptive divergence in resource polymorphic Arctic charr from Iceland

Moira M. Ferguson
Department of Integrative Biology, University of Guelph, Ontario, Canada N1G 2W1

Resource-based or trophic polymorphisms, in which sympatric morphs (or species pairs) show differential resource use and often various degrees of reproductive isolation, are ideal for studying the genetic architecture of adaptive divergence and the role of selection. These systems make it possible to examine the evolutionary genetic mechanisms responsible for the initial stages of adaptive divergence all the way to those promoting speciation itself. Adaptive divergence is the product of natural selection, which interacts and changes the underlying genetic basis of phenotypes. Thus, the genetic architecture (number, type and magnitude of gene effects) of phenotypic variation is central to predicting the rate and direction of evolution. We used a gradient of phenotypic divergence in Icelandic Arctic charr from two populations (lakes) to first test the hypothesis that the relative roles of genetic divergence and phenotypic plasticity vary during different phases of population divergence. We then determined
the genetic architecture (quantitative trait loci, QTL) of a set of position traits that describe the morphological variation among ecomorphs from the two lakes. The charr were reared under two diets that mimicked those found in either benthic or limnetic habitats. We tested for a parallel genetic basis for morphological divergence among morphs in different lakes versus differential effects of QTL across environments/diets (phenotypic plasticity).

E-mail: mmfergus@uoguelph.ca

Modularity in the cichlid mandible: Its inheritance and genetic basis

K.J. Parsons¹, E. Marquez², R.C. Albertson¹
¹Dept. of Biology, Syracuse University, Syracuse, NY
²Dept. of Biological Sciences, Florida State University, Tallahassee, FL

Most organisms are comprised of anatomical units recognizable from their developmental origins, or function. An emerging area of interest to biologists involves understanding how organisms are partitioned into units or modules. Modularity suggests clusters of connectivity, whereby a module represents a unit that is tightly integrated but relatively independent from other such modules. The structure of this connectivity could have major evolutionary implications but until recently methods of quantitatively determining modularity have been elusive. Here we use recent advances in morphometrics to investigate modularity in the mandible of African cichlids from lake Malawi. The cichlid mandible exhibits an extraordinary level of diversity that is associated with a variety of ecological niches. Currently little is known about patterns of modularity that may exist in this adaptively important trait. Patterns of modularity could be especially important for determining the rate and direction of adaptive divergence in cichlids. We tested for patterns of modularity in members of the genus Labeotropheus, which consist of algae-scraping specialists, and Metriaclima, who are relative ecological generalists. We also assayed modularity in a genetic mapping panel of their F2 hybrids. We then extended our methods to produce an individual-based metric of modularity by selectively removing individuals from our analysis and recalculating a goodness of fit. This metric was used in a quantitative trait loci approach to map the genomic regions associated with modularity. This approached identified genomic regions specific to patterns of modularity in each group. This powerful set of techniques will be valuable for uncovering the genetic architecture of modularity, which may ultimately lead us to a greater understanding of its role in evolution.

E-mail: kjpars01@syr.edu
Does egg size affect behaviour and morphology of Arctic charr (*Salvelinus alpinus*)?

Camille Leblanc\(^1\)\(^2\)\(^3\), Bjarni K. Kristjánsson\(^3\), Sigurður Snorrason\(^1\), Skúli Skúlason\(^3\) and David L. G. Noakes\(^2\)

\(^1\)University of Iceland, Department of Biology, IS-101 Reykjavik, Iceland.
\(^2\)Oregon State University, Department of Fisheries and Wildlife, Corvallis, OR, 97331, USA.
\(^3\)Hólar University College, Department of Aquaculture and Fish biology, IS-550 Saudarkrokur, Iceland

Northern freshwater fish show an unusual intraspecific phenotypic diversity, with two or more sympatric morphs, or even species, within the same area (often a lake). This polymorphism can commonly be seen in structure or behaviour for exploiting certain resources. Resource polymorphism can give rise to discrete morphs or even new species. One of the most polymorphic species is Arctic charr (*Salvelinus alpinus*) where body size, diet, and morphology differ significantly between morphs. Furthermore, different morphs show clear differences in behaviour especially in foraging behaviour. Behaviour and morphology at early stages of development could affect individuals life-history. Variability in these traits may be important for the first steps in the evolution of resource polymorphism and speciation. It is likely that these factors can be influenced by maternal effects, such as egg size.

We examined differences in foraging behaviour and morphology of progeny of nine females. We split the progeny of each female into two groups based on egg size, and reared them at standard aquaculture conditions. At 300 days post fertilization we observed total number of foraging at surface and at the bottom. The morphology of the fish was examined using geometric morphometric.

We found differences in both foraging behaviour and morphology between the fish coming from small and large eggs. The observed differences in behaviour and morphology might be important for habitat diversification within a species which could jump start morph formation. We discuss how maternal effects could affect or reinforce divergence of phenotypes in fishes.

E-mail: camille@holar.is

What European minnows (*Phoxinus phoxinus*) tell us about local adaptation?

Hélène Collin
Department of Ecology and Evolution, University of Lausanne, Le Biophore, CH-1015 Lausanne, Switzerland

Natural selection is an important evolutionary process shaping variation in nature. At small temporal and spatial scales, geographically localized natural selection can drive local adaptation, especially in heterogeneous and fragmented habitats. Although
natural selection is of major concern in evolutionary biology, we still need to understand how this process is acting on populations in changing environments, and what is the mechanistic of local adaptation due to selection in natural populations living in heterogenous habitats.

To investigate this issue we chose the European minnow (*Phoxinus phoxinus*), an endemic fish in the Alps and the Pyrenees. This species lives along a wide range of altitude and occupies different habitats such as lakes versus streams. To infer the evolutionary potential of this species to adapt in different environments, we used a multifaceted approach based on the quantification of genetic and morphological variation within and among populations. We first explored body shape divergence due to different selection pressures with a geometric morphometrics approach. Then, adaptive and neutral genotypic divergence were investigated with AFLP markers using respectively a genome scan approach and phylogenetic trees. This methodology will allow us to better understand (1) Wich proportion of the genome is implicated in local adaptation and (2) what is the role of neutral patterns (i.e. genetic drift and gene flow) in population divergence.

We detected morphological divergence in minnows associated to different habitat. We also found evidences supporting the hypothesis of *Phoxinus phoxinus* local adaptation to fragmented and ecologically different environments. Even though most of the genome conform to genetic neutral expectations and therefore explain geographical patterns, a low proportion of genes display genetic divergence to different selective pressures.

E-mail: helene.collin@unil.ch

*Phenotypic changes in a recent adaptive invasion event of Swiss sticklebacks*

**Kay Lucek**
Fish Ecology & Evolution, EAWAG, Seestrasse 79, 6047 Kastanienbaum, Switzerland
and
Aquatic Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

The study of species invasion is of great interest as it allows investigating evolutionary changes occurring over a short period of time. Especially species that invade different niches provide the possibility to study ecological speciation events at a very early stage. In Switzerland, the threespine stickleback has been introduced into the lake Geneva basin in 1870. Since then, sticklebacks underwent a range expansion occupying now both the pelagic zone of the lake as well as benthic type environments in creeks as far as 100 kilometers upstream. We used available specimens from museum collections to investigate the phenotypic changes across time and habitats by studying the underlying phenotypic covariance matrices and compared historical with contemporary
populations. All in all we were able to retrieve 500 historical and 350 contemporary individuals, providing a unique possibility to investigate phenotypic adaptation over 100 generations. In addition, we compared the recent occurrence of different lateral plate phenotypes with their historical distribution, which may represent an adaptive phenotypic trait. We found that indeed the contemporary distribution of the number of lateral plates differs tremendously across habitats and phenotypes differ over time and habitats.

E-mail: Kay.Lucek@eawag.ch

**Does character displacement initiate speciation? Competition and divergence in populations of polyphenic toads**

**Amber Rice**
Dept. of Animal Ecology, Evolutionary Biology Centre (EBC), Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden

Ecological character displacement — trait evolution stemming from selection to lessen resource competition — has long been regarded as important for finalizing speciation. In contrast, its potential for initiating speciation has received less attention. Because selection for character displacement occurs only where competing species co-occur, individuals in allopatric populations will experience different selective pressures than their conspecifics in sympatric populations. If this divergent selection results in reproductive isolation and reduced gene flow, then character displacement may trigger speciation. A potential example of this can be found in a species of spadefoot toad, *Spea multiplicata*. Spadefoot toad tadpoles are polyphenic; they can develop as either omnivores, which specialize on detritus, or carnivores, which specialize on fairy shrimp. In allopatric populations, intermediate frequencies of both morphs are found. However, where *S. multiplicata* co-occurs with a closely related competitor, *S. bombifrons*, selection to reduce resource competition has favored ecological character displacement in tadpole morph production: *S. bombifrons* produces only carnivores while *S. multiplicata* produces only omnivores. The different patterns of selection experienced by allopatric and sympatric populations of *S. multiplicata* appear to be responsible for extrinsic postmating reproductive isolation. “Hybrid” type tadpoles (tadpoles with one parent from allopatry and one from sympatry) are not well adapted for competing in either sympatric or allopatric environments, and perform worse than parental type tadpoles (with both parents from either sympatry or allopatry). Moreover, this extrinsic postmating isolation may be responsible for a reduction in gene flow between *S. multiplicata* populations in sympathy and allopatry. Nuclear microsatellite data indicate that gene flow between populations in different competitive environments

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is slightly reduced relative to gene flow between populations within sympatry or allopatry. Thus, evidence from spadefoot toads suggests that speciation may be initiated as a by-product of character displacement.

E-mail: amber.rice@ebc.uu.se

Isolation by time and environment and strong selection against recombinants explain fine-grained local adaptation in a pond-breeding amphibian

Alex Richter-Boix¹, María Quintela¹², and Anssi Laurila¹

¹Population Biology and Conservation Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen18D, SE-752 36 Uppsala, Sweden
²Dept of Animal Biology, Plant Biology and Ecology, Faculty of Sciences, University of A Coruña, Alejandro de la Sota, E-15008 A Coruña, Spain

Patchy contrasting habitats can generate strong divergent selection and should provide opportunities for genetic and phenotypic divergence. Divergence in mosaic sympatric populations implies a gradual reduction of gene flow that should reflect increasing reproductive isolation of populations. Without extrinsic barriers to gene flow among populations, gene flow among local populations is usually expected to impede local adaptation by homogenizing populations. However, when gene flow among populations is asymmetric because of non-random dispersal some adaptive divergence between populations can arise. Two non-random dispersion mechanisms can influence the divergence between populations and the maintenance of local adaption processes: (i) isolation by time (IBT), i.e. non-random dispersal attributable to differences in the timing of reproduction, which may create temporal barriers to gene flow, and (ii) isolation by environmental distance (IBED) i.e. habitat preference induction, which increases disperser’s preference for those habitats that are similar to their natal one or previous environment. Additionally strong selection against recombinants for traits affecting adaptive divergence (QTL recombinants) facilitates ecological differentiation among populations. The three aforementioned mechanisms cause a reduction in gene flow that leads to an increase of adaptive divergence. As a result, a pattern of isolation by adaptation (IBA) arises. We explored these mechanisms in the moor frog, *Rana arvalis*, across a system of 17 breeding ponds by combining field and common garden data with molecular data from neutral markers and a candidate gene. We found strong life-history differences among populations correlated with differences in the environment, and significant relationships between the phenotype and the candidate gene genotype. We found that genetic distances for neutral markers were correlated with differences in the timing of reproduction and local environment among sites, but not with geographical distances (no isolation by distance [IBD]), suggesting that both...
IBT and IBED are operating in this system. The patterns of IBT and IBED shape population structure facilitating adaptive divergence among adjacent populations with different environmental selection pressures. In addition a higher, almost ten-fold, differentiation between $F_{ST}$ estimated with the candidate locus than with the neutral markers suggested a “genetic mosaic of speciation” given strong selection against recombinants in this genome region. The combination of these mechanisms provides an explanation for the strong fine-scale local adaptation often found in amphibian systems.

E-mail: alex.richter@ebc.uu.se

**From resource polymorphism to the evolution of reproductive isolation: some required conditions**

Pierre Magnan, R. Proulx, J. Adams, F. Marchand, M. Pepino, and A. Bertolo
Université du Québec à Trois-Rivières, Québec, C.P. 500 Trois-Rivières (Québec) Canada G9A 5H7

Brook charr (*Salvelinus fontinalis*, Mitchell) display a subtle resource polymorphism in some Canadian Shield lakes. The littoral ecotype has longer pectoral fins, is found in shallow water (0–2 m), and feeds mainly on zoobenthos, whereas the pelagic ecotype has shorter pectoral fins, is found in deeper waters (3–6 m), and feeds mostly on zooplankton. Four-month-old littoral offspring raised in the laboratory (progeny of parents captured in the field) inherited some of the morphological characteristics of their parents (pectoral fins, dorsal fins, and body width or depth) and were more efficient at feeding on benthic prey than were pelagic offspring. A common garden experiment confirmed that differences between ecotypes seem to be determined by both genetic and environmental factors. A seven-year survey on the timing of arrival of littoral and pelagic individuals on a spawning ground showed that littoral individuals arrived during the first two weeks of the spawning season and pelagic individuals during the last two weeks. Although there is some overlap in the occurrence of littoral and pelagic individuals on spawning sites in the middle of the spawning periods, these results suggest the evolution of reproductive isolation between the two ecotypes. Different scenarios could explain the differences in timing of littoral and pelagic spawning. In this presentation, I will use the brook charr model (subtle polymorphism in a recent system) to show that (i) the differences in timing of littoral and pelagic spawning could be maintained simply by environmental mechanisms and that some traits may be inherited in the first generation (e.g. through epigenetic mechanisms) without reproductive isolation, and (ii) to have resource polymorphism evolving toward reproductive isolation, we need some specific conditions that are sometimes just assumed or not observed.

E-mail: Pierre.Magnan@uqtr.ca
Genomic architecture of speciation: theory and data from two insects systems

Patrik Nosil
EBIO, Ramaley N122, Campus Box 334, University of Colorado, Boulder, CO 80309-0334, USA

It is now well-established both theoretically and empirically that adaptive divergence via natural selection can promote the process of ‘ecological speciation’. However, the extent to which this occurs varies dramatically both within and among study systems. This variability in the degree of speciation could be due to variation in the genetic and genomic basis of adaptive divergence, for example the number, location, and distribution of genes subject to divergent selection. Under one hypothesis of ‘divergence hitchhiking’, decreased inter-population gene flow surrounding one or a few loci under strong divergent selection generates a few regions of genetic differentiation within the genome. These few ‘genomic islands of divergence’ can then act as seeds for driving speciation. Alternatively, speciation may be driven by ‘multifarious’ selection acting on many loci dispersed across the genome. I will present formal mathematical models of divergence hitchhiking which show that for a single locus under selection, regions of neutral genetic differentiation do not extend far along a chromosome away from a selected site except under specific conditions. However, with many loci under selection, genome-wide divergence occurs. Thus, theory predicts that speciation may often require multifarious selection acting on many, isolated and physically-unlinked genes. I will conclude by reviewing empirical population genomic and experimental data on speciation from two insect systems: host ecotypes of Timema cristinae walking-stick insects and apple and hawthorn host races of Rhagoletis pomonella flies. These data illustrate how speciation can involve a combination of strong selection on a few loci and selection on many loci distributed across the genome, highlighting how the individual genes driving speciation can be embedded within an actively diverging genome.

E-mail: patrik.nosil@colorado.edu

Repeated evolution of reproductive isolation in a marine snail — unveiling mechanisms of speciation

Kerstin Johannesson1, Marina Panova1, Petri Kemppainen1, Carl André1, Emilio Rolán-Alvarez2, and Roger K. Butlin3

1Department of Marine Ecology – Tjärnö, University of Gothenburg, SE 452 96 Strömstad, Sweden
2Departamento de Bioquímica, Genética e Immunología, Facultad de Biología, Universidad de Vigo, Campus As Lagoas-Marcosende, 36310 Vigo, Spain
3Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK
Distinct ecotypes of the snail *Littorina saxatilis*, each linked to a specific shore microhabitat, form a mosaic-like pattern with narrow hybrid zones, in between, over which gene flow is 10-30% of within-ecotype gene flow. Multi-locus comparisons cluster populations by geographic affinity independent of ecotype, while loci under selection group populations by ecotype. The repeated occurrence of partially reproductively isolated ecotypes and the conflicting patterns in neutral and selected genes can either be explain by separation in allopatry followed by secondary overlap and extensive introgression that homogenizes neutral differences evolved under allopatry, or by repeated evolution in parapatry, or in sympathy, with the same ecotypes appearing in each local site. Data from Spain, UK and Sweden give stronger support for a non-allopatric model of ecotype formation than for an allopatric model. Several different non-allopatric mechanisms can, however, explain the repeated evolution of the ecotypes: (i) parallel evolution by new mutations in different populations, (ii) evolution from standing genetic variation, and (iii) evolution in concert by rapid spread of new positive mutations among populations inhabiting similar environments. These models make different predictions that can be tested using comprehensive phylogenetic information combined with candidate loci sequencing.

E-mail: Kerstin.Johannesson@marecol.gu.se

**Origin of local ecotypes in *Littorina saxatilis***

*Marina Panova*

Department of Marine Ecology – Tjärnö, University of Gothenburg, SE 452 96 Strömstad, Sweden

“Crab”- and “wave” – ecotypes of the intertidal snail *Littorina saxatilis* live in sympathy in UK, Galician coast in Spain and the west coast of Sweden. Possibly, ecotype pairs evolved independently in each country by local ecological adaptation to different environments. Alternatively, “crab”- and “wave”-ecotypes of the snail evolved only once and spread to different regions, coming into secondary contact. Recently, we started a project to resolve phylogenetic relationships between the ecotypes and test the hypothesis of independent origin of ecotypes in the three countries using a number of molecular markers (mtDNA, nuclear genes, AFLP). In addition, we use oligoarrays to search for genes, differentially expressed in different ecotypes and environments and/or genes with high sequence divergence between ecotypes. Since the project is still in progress, I will mostly present molecular tools we developed for the species and discuss how they can be used to study the origin of local adaptations, with some very preliminary results.

E-mail: marina.panova@marecol.gu.se
Asexual reproduction following a rapid and recent speciation event

Daniel Johansson
Department of Marine Ecology – Tjärnö, University of Gothenburg, SE 452 96 Strömstad, Sweden

The endemic alga *Fucus radicans* speciated from *F. vesiculosus* in the Baltic Sea as recent as after the latest ice age. It is a foundation species and the dominating macro alga in its northernmost range. We saw that it reproduces mainly asexually, with one female clone being present throughout much of the distribution and dominating some populations. The number of genotypes varies greatly between neighbouring sites though, with some populations being nearly exclusively sexual. Also *F. vesiculosus* reproduces asexually, and like *F. radicans* increasingly so along the salinity gradient inwards the Baltic Sea. We sampled the female clone at three localities and kept her in three salinities. Growth did not differ between salinities, while more receptacles developed in the high salinity, in algae from one locality. We now aim at resolving the fine scale pylogeography of the Baltic Sea fucoids, and the consequences of clonality, facing changing marine environments. The sympatric fucoids of the Baltic Sea enable the study of a rapid and recent speciation event in a young and ecologically marginal habitat.

E-mail: daniel.johansson@marecol.gu.se

An EST-based genome scan using 454 sequencing in the marine snail *Littorina saxatilis*

Juan Galindo, John W. Grahame and Roger K. Butlin
Department of Animal and Plant Sciences, University of Sheffield, UK

Genome scans have been used in studies of ecological speciation to find genomic regions (‘outlier loci’) showing reduced gene flow between divergent populations/species. High-throughput sequencing (‘454’) offers new opportunities in this field via transcriptome sequencing. Divergent ecotypes of the marine gastropod *Littorina saxatilis* represent a good example of incipient ecological speciation. We performed a 454-based genome scan between H and M ecotypes of *L. saxatilis* from the British Isles using cDNA of pooled individuals. Allele frequencies were calculated for 2454 single nucleotide polymorphisms (SNPs), within 572 contigs, and 7% of loci were detected as outliers. Functional annotation of the contigs containing outlier SNPs showed that they included shell matrix and muscle proteins (lithostathine, mucin, titin), proteins involved in energetic metabolism (arginine kinase, NADH dehydrogenase)
and reverse transcriptases. Follow-up investigations of these proteins and unannotated outliers will be a promising route in the study of ecological speciation in *L. saxatilis*.

E-mail: J.Galindo@sheffield.ac.uk

**What can postglacial fishes tell us about the speed of evolutionary processes?**

Colin E. Adams  
Scottish centre for Ecology & the Natural Environment, University of Glasgow, Loch Lomond G63 0AW, Scotland, UK

Estimates of the rate at which evolution may progress vary dramatically depending upon the traits examined and the study species.

Fishes living in post-glacial freshwater systems in particular, appear to be capable of rapid evolutionary change. There is now strong evidence that this is at least partly because fishes living in these habitats tend to exhibit high levels of phenotypic plasticity and partly because plasticity can play a major role in promoting evolutionary processes. Although there is a theoretical foundation for how plasticity may influence evolution, empirical studies have not fully tested theoretical predictions. In this talk I will describe a series of empirical studies that have sought to test the detail of the mechanisms through which phenotypic plasticity may have a role in driving evolutionary processes, using model species drawn from the freshwater fishes living in post-glacial lakes.

E-mail: c.adams@bio.gla.ac.uk

**Mechanisms driving population differentiation beneath the surface — analyzing the pan-European distribution of the small pelagic fish the sprat**

Morten T Limborg, Reinhold Hanel, Paul V Debes, Anna-Karin Ring, Carl André, Costas S Tsigenopoulos, Dorte Bekkevold  
Department of Marine Ecology – Tjärnö, University of Gothenburg, SE 452 96 Strömstad, Sweden

For the understanding of contemporary distributions of species and populations it is important to disentangle the different evolutionary processes shaping population structure.

It is now generally accepted that most marine organisms show population structure deviating from solely patterns of isolation by distance. Contemporary distributions of most temperate marine fish are affected by post glacial recolonisation from glacial refugia and likely also by genetic adaptation to local environments. By combining mtDNA and microsatellite marker data with environmental data and inference about a complex demographic history, we used landscape genetics methods.
to study the population structure in European sprat (*Sprattus sprattus* L.) through major parts of its distribution, including marginal populations.

The results show that population differentiation between Northeast Atlantic and Baltic populations are mainly driven by genetic drift, as opposed to mutation. In contrast, populations in the Mediterranean region display clear genetic breaks across three major transition zones with strong imprint from mutation.

E-mail: anna-karin.ring@marecol.gu.se

**Speciation within the subterranean amphipod *Crangonyx islandicus***

Etienne Kornobis and Snæbjörn Pálsson
Institute of Biology, University of Iceland, Sturlugata 7, 101 Reykjavik, Iceland

*Crangonyx islandicus*, an endemic subterranean amphipod found along the active volcanic zone in Iceland, shows genetical patterns which suggest subglacial survival during Ice Age [1]. Sequence variation in two mtDNA genes (COI and 16S RNA, covering in total 1072 bp), from 130 individuals sampled at 23 locations throughout the volcanic zone in Iceland confines six monophyletic lineages. Its phylogeny, based on nuclear genes suggests also that it defines a new genus within *Crangonyctidae*, a family of subterranean amphipods.

The abundance of cryptic diversity has been frequently documented in the last decade, particularly within subterranean fauna. The similar selective pressures observed in different subterranean habitats induce convergent evolution of morphological traits, hindering clear species delimitation. The bar-coding initiative using COI and 16S genes, as well as the development of molecular divergence threshold for putative species delimitation is therefore of particular interest for a better estimation of the biodiversity in subterranean environments. Under the prevailing model, the high local diversity of subterranean organisms is explained by the formation of stable populations with limited dispersal capacities which are prone to genetic isolation and allopatric speciation. The low number of ecological niches in such extreme environments supports also allopatric differentiation as the main speciation process.

Repeated glaciations and/or geological formations at the tectonic plate boundary in Iceland may have led to vicariance events, where populations have diverged in allopatry for up to four million years and may even represent two or more cryptic species within Iceland. Two different genetic thresholds, based on COI sequence variation, were applied and discrepancies between the two were observed for the delimitation of putative cryptic species. This indicates that speciation is ongoing, at least for the most divergent populations of *Crangonyx islandicus* in Iceland.


E-mail: snaebj@hi.is