

**MEETING REPORT:**

**Spatial approaches to the study of adaptation to climate: advances and challenges**

**Organisers:**

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## SUMMARY

In response to current climate change species may either change their distribution to follow their climatic niche, adjust to the new climatic conditions via phenotypic plasticity, adapt via genetic changes, or go extinct. When predicting species' responses to climate change it is essential to take into account spatial patterns of local adaptation and population dynamics at the landscape and geographical scale. To address these issues, an international workshop 'Adaptation to climate from spatial perspective' was organised at the Lammi Biological Station (University of Helsinki) in Finland from 11–14 September 2011. Sixty-four scientists from 18 countries attended the meeting, representing researchers with backgrounds ranging from ecology, evolutionary biology and genetics to theoretical modelling and conservation biology. The presentations included nine invited and 20 contributing talks, and 27 scientific posters. The meeting highlighted current theoretical and empirical understanding of the ability of species to adapt to climate change, and identified future research challenges and perspectives.

## SCIENTIFIC CONTENT

### *1. Introduction*

Advancing our understanding of the mechanisms underlying adaptation to environmental variation lies at the core of ecology and evolutionary biology and has become especially relevant in the light of current human-induced environmental change as the major threat to global biodiversity. Ecological consequences of recent climate change have been documented for a broad array of taxa on every continent and much attention has been given to predicting species' responses to future climate change. The majority of studies have reported on species range shifts (e.g. Chen et al. 2011), showing the predicted shift towards the poles and higher altitudes as a general trend. Recently, research has increasingly focused on the ability of species to cope with climate change by genetic adaptation (evolutionary rescue), and on the eco-evolutionary dynamics of range shifts. Taking into account spatial patterns of population dynamics and divergence is key in understanding the evolutionary processes that shape adaptation to environmental variation.

Studying phenotypic and genetic variation in populations along environmental gradients can reveal patterns of local adaptation. In particular populations along latitudinal and altitudinal clines are widely used as a tool in investigating thermal and climatic adaptation, since variation along these environmental axes generally indicates climate as the main selective agent. The spatial configuration of populations in the landscape affects the coupling between demographic and evolutionary dynamics and consequently has implications for how species respond to changing environment (presentation by Ilkka Hanski). Particularly important in this context is widespread human-caused habitat fragmentation, which impairs the ability of many species to track suitable climate conditions and can reduce the adaptive potential by decreasing genetic variation and gene flow between populations. Taking into account these spatial habitat patterns and population processes is also very relevant in making accurate predictions of species' range dynamics in response to climate change.

In this report we will first present some recent findings of research using populations with different selective histories in terms of climate (or other environmental conditions), and emphasize what these studies tell us about the ability of populations to adapt to future climate changes. Next we will discuss the advancement of theoretical and empirical studies that include spatial approaches to understand eco-evolutionary populations dynamics and to predict species responses to climate change. We will identify the current shortcomings of our knowledge on these topics, followed by the main challenges and ideas for future research in the next section.

### *2. What can we learn from population comparisons?*

There are many examples of studies demonstrating local adaptation when comparing populations from geographical areas that differ in environmental conditions. Genetic

differentiation and phenotypic plasticity can both lead to phenotypic differences among populations. Furthermore, populations can show local adaptation for their plasticity response as it is an evolvable trait. Phenotypic plasticity responses such as acclimation to temperature can be an important mechanism to cope with environmental variation but little is known about the energetic and ecological costs involved. Klaus Fischer showed that the acclimation response of stress resistance in the butterfly *Bicyclus anynana* comes at the cost of decreased immunity measured as the level of haemocytes. Volker Loeschcke's release-recapture field studies of *Drosophila melanogaster* indicated that acclimation may have large fitness benefits over a narrow set of thermal conditions, but may have strong negative side-effects when thermal conditions extend beyond the beneficial range. Hence, phenotypic plasticity may lead to mismatches of phenotype and environment due to climate change. This point is illustrated well by the widely observed changes in phenological events in response to climate warming, for example the timing of egg-laying in many birds. Thomas Reed showed how earlier breeding in great tits leads to a mistiming with the peak abundance of their prey, which could potentially have severe consequences for population dynamics and species persistence, whereas in Reed's study immigration from other populations prevented such effects. Heikki Hänninen showed that local adaptation along a latitudinal cline in phenology of trees is limited by climatic year-to-year variation, and that during most years even the locally optimal genotype is not doing especially well. Hence, as both temperature averages as climate variability are expected to increase under global warming, mismatches of plasticity responses to the environment are expected to occur more frequently. Moreover, the growing unpredictability of the climate may impair the ability of populations to adapt to changing conditions.

With genetic tools becoming increasingly available, our understanding of the molecular underpinnings of adaptation to climate is rapidly growing. Most progress has been made on model systems such as *Drosophila*, for example the studies on widely observed clinal variation in chromosomal inversions presented by Bryant McAllister and Marta Pascual.

Advances are also being made in studies using non-model organisms, which often have the benefit of a clear ecological context. Several speakers presented work on associations of single genes with adaptation to climate (latitudinal/altitudinal clines) or other environmental variation. Examples included butterflies (Ilkka Hanski, Klaus Fischer), beetles (Elizabeth Dahlhoff), and frogs (Anssi Laurila). Although these studies present important examples of the effects single genes can have on morphology, life history traits and physiology, most fitness traits have a complex genetic architecture involving many genes. Moreover, fitness traits are often genetically correlated with other traits, which may decrease their adaptive potential due to antagonistic selection on linked traits. A method to study these evolutionary constraints is to use experimental evolution. Volker Loeschcke showed that selection for heat and cold resistance in the lab affected recapture rates in the wild in *Drosophila*, and that these lines differed in their genetic background associated with thermal resistance. Patricia Schulte's study on freshwater and marine populations of threespine stickleback, which are genetically differentiated in cold tolerance, indicated that marine stickleback populations that were transplanted to the freshwater environment evolved a lower cold tolerance than their marine ancestors within three generations, which was no longer different from that of freshwater fish.

In short, there is evidence for adaptive potential resulting from studies using geographical variation between populations. However, as Juha Merilä pointed out in his presentation, studies showing conclusively adaptation to ongoing climate change are still very rare.

### ***3. Understanding adaptive dynamics and predicting future change***

Much can be learned about the adaptive potential (or lack of it) by studying the range margins of populations and by taking into account the spatial configuration of populations in the landscape. Changes in climate are often accompanied with drastic alterations in habitat structure and connectivity, and disentangling these possible sources of selection is therefore

important. Different environmental factors may cause opposing selection pressures, for example, climate change may increase selection for increased dispersal where as severe habitat fragmentation at the range margin may select for decreased dispersal. A high level of dispersal may prevent adaptation (migration load; Bell & Gonzales 2011), but non-random gene flow can facilitate genetic and phenotypic divergence even at a very fine spatial scale, as shown by Anssi Laurila. The habitat configuration and habitat quality can also influence plasticity of life history trajectories such as dispersal, highlighting again the importance of phenotypic plasticity, as was demonstrated by Hans Van Dyck's talk (Gibbs et al. 2011).

The amount of genetic variance for traits under selection is crucial in determining to what extent species may adapt to environmental change. At the range margins, factors such as founder effects, small population size and genetic drift may each affect the amount of additive genetic variance. In addition, Mats Björklund discussed how genetic variances and covariances (G-matrices) are not stable over time and how the selective past matters with regard to changes in G-matrix. New environmental conditions experienced by organisms will hence influence the adaptive potential, making even short-term evolutionary predictions for natural populations very challenging. In addition, ecological constraints, such as biotic interactions (e.g. host-parasitoid interactions as presented by Patricia Gibert) and evolutionary time lags were identified as possible factors preventing microevolutionary changes due to climate change as was discussed by Juha Merilä.

In any case, there is abundant evidence for recent species' distribution responses to climate change (Chen et al. 2011). These range shifts may show micro-evolution at the margins, but it remains difficult to obtain empirical data to demonstrate this. As mentioned by Chris Thomas, range shifts may change selection pressures at the advancing margins as organisms are experiencing new climatic conditions, new community composition etc., which may result in evolutionary responses. Recent work by Thomas and Jon Bridle on the Brown Argus butterfly suggests evolutionary changes in host plant use associated with micro-climate in the new parts of the range (Thomas et al. 2001, Bridle et al. in press).

From a conservation point of view, predicting where the suitable niche for an organism will be in the future and where species ranges are likely to shift is essential. Several presentations in the meeting highlighted the importance of extending the traditional species distribution models that are commonly used to make these predictions by including factors such as habitat structure and variance in fitness related traits. Work by Robert O'Hara showed how the best models explaining species occurrence include habitat type. Frederico Mestre presented a conceptual framework that aims to link bioclimatic suitability models with spatially explicit (meta)population models in voles. In the future, these models may be coupled with genetic data to assess more completely present phylogeographic structure and main barriers to species dispersal, as these factors may constraint future range shifts. In general, niche models assume that trait values are fixed across the range. Work presented by Rebecca Swab combined a niche model with a demographic matrix model to test whether incorporating variability in life history traits change model predictions and whether this will mitigate or exacerbate the impacts of shifting habitat? Changes in habitat at the margins of a species range may generate source-sink dynamics between core and margin. Robin Aguilée showed how the effects of pollen and seed dispersal on adaptation in sink populations differ due to the latter having both genetic and demographic consequences, whereas pollen dispersal has only genetic consequences. He concluded that niche expansion can occur when the critical level of genetic variance is reached. Ophélie Ronce highlighted how selection imposed by climate change is likely to affect multiple phenotypic traits and that the optimal trait combinations are likely to vary in space along climatic gradients. She presented ongoing work on a theoretical model that includes these joint adaptations of multiple traits in a species under a climate change scenario, tracking favourable conditions through space. Jon Bridle pointed out that theoretical models that try to couple population genetics with demography are highly dependent on biological parameters that are very difficult to measure in the wild in most organisms, and that these parameters are likely to change continuously. It thus remains a challenge to obtain appropriate ecological data to test such model predictions.

## MAIN RESULTS AND FUTURE DIRECTIONS

A general discussion was held at the end of the meeting to sum up the highlights of the meeting and to discuss important questions and directions for future research. Here, we list the main results of the meeting and the most important issues and ideas for follow-up research that were identified during the general discussion.

There are many examples of studies using populations along climate gradients (altitudinal and latitudinal clines) showing past adaptive differentiation for morphological, physiological, and life history traits, either by genetic adaptation or phenotypic plasticity. Especially in model systems like *Drosophila*, rapid advances are being made in unravelling the genetic and genomic basis of these adaptations. However, examples of adaptation to ongoing climate change are still very rare, and this may be caused by biological reasons such as genetic constraints, lack of genetic variance and complex ecological interactions, as well as technical reasons including the problem of proving causality in research efforts and the difficulty of obtaining genetic evidence (reviewed by Juha Merilä). When substituting time for space, as in clinal studies, there are confounding factors that complicate the interpretation of population divergence, such as covarying variables, evolutionary time-lags and historic neutral population processes. These issues seem to be less problematic in altitudinal clines compared to latitudinal clines, because altitudinal gradients are generally much steeper, and confounding ecological factors or neutral population genetic processes (such as isolation-by-distance) are expected to play a smaller role.

A major challenge in predicting the adaptive potential of populations to climate change is the estimation of (additive) genetic variance and correlations of traits. In fragmented landscapes or at range margins, population processes such as founder effects, genetic drift and (other) effects of small population size often play an important role, and may each affect the additive genetic variance of traits. In addition, genetic variances and covariances (G-matrices) are not stable over time and depend on the selective past. Hence, the past and current environmental conditions experienced by organisms will influence their adaptive potential to a changing environment. Despite the importance to the adaptive potential, predictive models that take into account variances of or correlations between fitness-related traits are very rare. Moreover, the development of appropriate models is hindered by the lack of ecological data to test model predictions.

These points emphasize the importance of gathering appropriate data under ecological conditions, even though may be very difficult to do for most organisms. Increasing our knowledge on the genetic and ecological processes that influence population dynamics and adaptation in the wild is not only crucial to make predictions about the adaptive potential of populations. It is also important in the light of conservation efforts to ensure population viability in a changing environment, such as determining the level of connectivity of protected areas, the distance of assisted dispersal or the creation of climate change refugia.

On the positive side, there is a definite recent movement towards conducting ecological studies in model organisms such as *Drosophila*. In addition, research on non-model organisms, which often involves wild populations, benefits from the current rapid development of genetic tools, resulting in an increasing knowledge on the genetic basis of adaptation to climate in wild populations. However, so far genetic studies in non-model organisms mainly take single-gene approaches to adaptation to climate. Although these studies have generated important insights, most fitness traits are likely underpinned by a much more complex genetic architecture, involving many genes and correlations between them (e.g. due to pleiotropy). The current rapid developments in genomics give an exciting prospect of whole-genome approaches to unravelling the genetic basis of fitness. In the near future it will for example be possible to make genomic population comparisons along ecological gradients, or between the core and margins of species ranges.

## References

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## **ANNEX 1: MEETING PROGRAMME**

**Monday 12.9.2011**

**08:00 – Breakfast**

### ***SESSION 1: CLINAL VARIATION IN THERMAL ADAPTATION***

**08:45 Opening words**

**08:50 A systems biology approach to the study of thermal adaptation**  
Volker Loeschcke, Aarhus University (keynote)

**09:30 Genome Structure and Local Adaptation**  
Bryant McAllister, University of Iowa

**09:50 Going deep into latitudinal clinal variation in inversion polymorphism**  
Marta Pascual, University of Barcelona

**10:10 - Coffee break**

**10:40 Altitudinal variation in life history and stress resistance in Copper butterflies**  
Klaus Fischer, Greifswald University (keynote)

**11:20 Adaptive response of *Drosophila* parasitoid populations to climate change**  
Patricia Gibert, University of Lyon

**11:40 Altitudinal and other clinal patterns of life history variation Among *Drosophila melanogaster* populations from sub-Saharan Africa**  
Daniel Fabian, University of Vienna

**12:00 - Lunch**

**13:30 The genetic basis of adaptations in seasonal phenology across a latitudinal gradient in European aspen (*Populus tremula*)**  
Pär Ingvarsson, Umeå University (keynote)

**14:10 Ecophysiology of phenological timing in perennial plants: local adaptation is limited by climatic year-to-year variation**  
Heikki Hänninen, University of Helsinki

**14:30 Tree growth across a 1700 meter altitudinal gradient in the humid tropics**  
Joshua Rapp, Harvard University

**14:50 – Coffee break**

**15:20 Intraspecific variation in the thermal biology of estuarine fishes at differing spatial and temporal scales**  
Patricia Schulte, University of British Columbia (keynote)

**16:00 Adaptations in the thermal physiology of a latitudinally widespread species of watersnake, *Nerodia sipedon***  
Lacy Danikas Chick, University of Tennessee

**16:20 Aquatic consumer growth rates are higher at higher latitudes – but at what cost?**  
Antonia Liess, Umeå University

**16:40 Utilizing over 50 years of Sea Eagle research for global climate change monitoring and assessment**

William Bowerman, University of Maryland

**17:00 – Dinner**

**19:00 – 20:30 Sauna for women**

**20:30 – 22:00 Sauna for men**

**21:00 onwards - Evening snack and socializing**

**Tuesday 13.9.2011**

**8:00 – Breakfast**

*SESSION 2: LANDSCAPE AND METAPOPOPULATION DYNAMICS*

**08:50 Detecting climate change responses in the wild: problems and prospects**

Juha Merilä, Helsinki University (keynote)

**09:30 Interpreting empirical landscape studies in the light of metapopulation processes**

Heidi Paltto, Swedish University of Agricultural Sciences

**09:50 Consequences of mistimed reproduction for population dynamics and viability: a case study of Dutch great tits**

Thomas Reed, Netherlands Institute of Ecology

**10:10 – Coffee break**

**10:40 Eco-evolutionary metapopulation responses to environmental changes**

Ilkka Hanski, University of Helsinki (keynote)

**11:20 Selection and non-random gene flow explain fine-grained adaptive divergence in an amphibian**

Anssi Laurila, Uppsala University

**11:40 The role of climate change refugia in population stability and adaptation strategies**

Toni Lyn Morelli, U.C. Berkeley

**12:00 – Lunch**

**13:30 Butterfly development and climate change: on the significance of developmental pathways and of development on drought stressed host plants for life history and flight morphological traits**

Hans van Dyck, UCL, Louvain-la-Neuve

**13:50 How well can we predict evolutionary change in a variable environment?**

Mats Björklund, Uppsala University

**14:10 Predicting the effects of temperature changes on population fitness and species interactions**

Samraat Pawar, University of California Los Angeles

**14:30 – Coffee break**



*SESSION 3: RANGE SHIFT DYNAMICS*

- 15:00 Ecological and evolutionary dynamics at expanding range boundaries**  
Chris Thomas, University of York (keynote)
- 15:40 Estimating the effects on distributions of interactions between climate and habitat**  
Bob O'Hara, Biodiversity and Climate Research Centre
- 16:00 How do genetic correlations affect species range shifts in a changing climate? A theoretical model.**  
Ophelie Ronce, University of Montpellier (keynote)
- 16:40 If niche models tell half the story: does demographic plasticity influence species responses to climate change?**  
Rebecca Swab, University of Riverside, CA and University of Copenhagen
- 17:00 – 18:30 Poster session**
- 19:00 – Conference Dinner**

**Wednesday 14.9.2011**

**08:00 – Breakfast**

*SESSION 3: RANGE SHIFT DYNAMICS (continued)*

- 09:00 Evolutionary change along smooth and fragmented ecological gradients**  
Jon Bridle, Bristol University (keynote)
- 09:40 How does pollen versus seed dispersal affect niche evolution?**  
Robin Aguilee, University of Montpellier
- 10:00 Combining biogeographic, ecological and genetic tools to predict metapopulation responses to climate change across spatial scales: an ongoing case-study with Cabrera and water voles**  
Federico Mestre, University of Évora

**10:20 – Coffee break**

**10:50 General discussion and perspectives**

**12:00 – Lunch**

**13:30 Departure to Helsinki-Vantaa airport**  
**15:30-16:00 Arrival at the airport**

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### **ANNEX 3: TRAVEL REIMBURSEMENT**

Participants from ESF-member countries received full travel reimbursement when requested. Participants from other countries could apply for partial travel reimbursement (300€ for PhD students and 200 € for others) as agreed with the ThermAdapt chair (Prof. Wolf Blanckenhorn) and senior administrator (Ms Ellen Degott-Rekowski).