Genomic divergence and differential gene expression in multiple pairs of Littorina saxatilis ecotype populations

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Adaptation to similar environments in independent populations may appear phenotypically parallel, but does the same genetic architecture underlie parallel phenotypic traits?

The rough periwinkle, Littorina saxatilis has evolved considerable morphological, ecological and behavioural diversity, and in western Sweden, crab and wave ecotypes appear to have arisen independently in parapatry multiple times as a result of divergent ecological selection. We used two different approaches to investigate the genetic mechanisms behind ecotype evolution. First, we analysed gene expression to search for the genes involved. Second, using RAD genotyping we identified >10 000 polymorphic SNP in three independent population pairs of L. saxatilis. FST based outlier analyses identified SNPs that show signatures of divergent selection between ecotypes. Here we present our initial findings on shared outliers among replicate pairs of ecotype populations.

Population genomics of Baltic cod (POSTER)

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Marine fishes generally show shallow population structures due to high dispersal and large population sizes. Genetic differentiation involved in local adaptation, on the other hand, is expected to be more pronounced in large populations.

Here, we investigated genomic signatures of local adaptation in Atlantic cod, a widely distributed marine fish with high fecundity and pelagic larvae, and thus high potential for gene flow. Using 8800 SNP loci located in both coding and non-coding genomic regions, as well as a set of candidate genes, we simultaneously investigated neutral and adaptive divergence in four cod populations along the environmental gradient from the fully marine North Sea to the low saline Baltic Sea.

Genome scan analysis identified 113 statistical outlier loci with high levels of divergence. Most of these outlier loci were also identified with a landscape genomic approach, and were associated with habitat differences in salinity, oxygen and temperature. Outlier loci were annotated to genes and regulatory networks involved in osmoregulation, indicating local adaptation to low salinity. The outliers were clustered to few single linkage groups suggesting genetic hitchhiking and the presence of genomic islands of divergence.

Baltic Sea cod was strongly differentiated from North Sea cod and fish collected in the salinity transition zone in Kattegat and Öresund, both for putatively neutral loci, and when using outlier loci only. The strong barrier to gene flow between Baltic cod and adjacent populations most likely result from effective reproductive isolation. Adaptation to the ecological conditions in the Baltic, such as egg buoyancy, sperm motility and spawning time constitutes a strong and effective reproductive barrier. Baltic cod may thus be viewed as an example of ongoing ecological speciation.

Tracking genetics of migration in willow warblers

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Impact of the rate of change on adaptation: response of Mnemiopsis leidyi to low salinity through multiple generations

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The rate of change to an environmental stressor (rapid abrupt vs gradual changes) modulates selection pressure and result in various strategies for adaptation. This project aimed at testing the impact of abrupt vs. gradual changes of salinity (high vs low) on acclimation and selection processes (hard and soft selection). We compared abrupt vs gradual changes in salinity on the ctenophore Mnemiopsis leidyi responses over 5 generations and how these changes alter phenotypic (growth, survival, egg production) and genetic variability.
Selection on enzyme genes over microenvironmental gradients

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North Atlantic periwinkles (Littorina spp.) are renowned for their adaptability and ecotype formation in response to varying littoral microenvironments. Here we approach the topic of local adaptation by a candidate gene approach, sequencing two different genes (AK and Aat) that show non-neutral dispersion over different microenvironmental gradients. Coding sequences from several Littorinid species show different phylogeographic patterns and histories, granting insights into potential paths of local adaptation, as well as complications with this approach.

Modelling local adaptation under gene flow

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The periwinkle Littorina saxatalis forms ecotypes as a consequence of adaption to specific shore microhabitats. Since mutations are a source of genetic variation driving local adaptation, it needs to be understood how mutant alleles spread in sub-populations connected by migration. In [1] it was analysed how a migration-selection balance in a one-locus model affects the probability that a mutation introduced during the initial phase of adaptation spreads in the population. In order to gain an insight into the genetic architecture during adaptation, multilocus models were studied in [2,3]. However, it has not been explicitly analysed how the system preference for a given mutation effect size changes as the degree of divergence between the sub-populations increases, and how this preference depends on the joint effect of the processes of selection, migration and recombination. In order to investigate this, we trace the adaptation of two sub-populations using analytical tools and individual-based stochastic simulations. We show how the probability that a given mutation spreads in the population depends on the degree of divergence between the subpopulations. Initially, the system favours large over small mutations, but as the adaptation proceeds this effect decreases. We define a critical migration rate above which an adaptive mutant allele is not able to invade the subpopulations. Our results show that this rate decreases the more diverged the sub-populations are.


Dynamics of sex ratio and genetics in populations with mixed sexual and asexual reproduction

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The brown algae Fucus radicans is endemic to the Baltic Sea and reproduces both sexually and asexually. Intriguing patterns of sex ratio and genetic diversity are observed for this species [1]. To assess the possible explanations for these patterns, two models for a population with mixed sexual and asexual reproduction are developed and explored. One model describes a well-mixed population, and the other a spatially structured one. Based on the results obtained for these models, I argue that populations with both sexual and asexual reproduction have a tendency to adopt a certain sex ratio that sensitively depends upon the amount of sexual and asexual reproduction. Spatial structure can cause colonization of empty habitat to go in the form of a clonal wave that enables one genotype without selective advantages to gain dominance. Under specific conditions, this domination is replaced by a pattern of mixed genotypes as a second sexual wave establishes sexual reproduction. Through demographic fluctuations, a sexually active population can consist partly of clonal islands with a low genetic diversity. I explore the question whether the mechanisms provided in the models can explain the patterns observed in F. radicans populations.


Aerodynamic performance of a gliding Jackdaw

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The separated primary feathers of birds are often interpreted as an adaptation aimed at improving flight
efficiency, usually in relation to the vertical extensions at the ends of the wings of man-made aircraft. However, the separated primaries differ from the aeroplane winglets in several ways. Most obviously, where aeroplanes commonly have one surface bending upwards, birds have several, which are separated in streamwise direction and bend up to various degrees.

A juvenile Jackdaw (*Corvus monedula*) was trained to glide in a tilted wind tunnel. The airflow in the wake was measured using a quantitative flow visualization technique (PIV). Flight speed was varied between 6.5 m/s and 12.5 m/s and the glide angle between 4.5 and 6 degrees. Across this range, the bird changes its wing shape, including the degree of separation of the primary feathers.

The measured flow fields contain information about the gliding performance of the bird, where two different types of cost (drag) can be distinguished. One type shows as regions of air being slowed down, corresponding to the air sticking to the surface of the wing (profile drag) and the body (body drag). The second type shows as kinetic energy perpendicular to the flight direction, which is due to the production of lift (lift induced drag). The latter component is related to the expected beneficial effect of the separated primaries.

From the measured induced drag, the efficiency of the wing can be derived, which then can be compared to the degree of feather separation, at each combination of glide angle and flight speed. The analysis of the data is still in progress, but preliminary computations suggest a very high efficiency.

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**Developing genomic resources in non model species**

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Questions of ecological and evolutionary import are increasingly benefitting from an understanding of the genomic landscape of the species involved in the interactions and adaptations being studied. Driven by the requirements of clinical bioinformatics, sequencing technology is becoming widely available and affordable to scientists in all of the fields of biology. Our group is striving to apply this sudden availability of technology to fundamental questions of butterfly biology by constructing a high quality genome for a species that is already the subject of extensive ecological and evolutionary evaluation. Diapause behavior, host plant preference, and immunity are all phenotypes that will be more fully understood with a complete genome of *Pieris napi*. To this end we have used a hybrid scaffolding approach in which second generation sequencing data from Illumina libraries was combined with third generation long read PACBIO data to make good progress towards this goal. The current state of the assembly, lessons learned, and next steps will be discussed.

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**Genital divergence in sympatric sister snails (POSTER)**

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Speciation is the evolutionary process in which new species originate by the splitting of existing lineages. While it is recognised that reinforcement is one of the possible mechanisms of speciation, a major challenge remains to test the importance of this process in nature. However, few large-scale comparative analyses have addressed this prediction, especially for genital form. Here we present an exceptionally complete and robust phylogeny to underpin detailed analysis of the form of male genitalia in the marine gastropod family *Littorinidae* (periwinkles). Our study of sister-species pairs has found a strong pattern that could be a signature of the controversial process of reinforcement: the form of the elaborated male genitalia is more divergent between species pairs with overlapping geographical distributions than between allopatric pairs.

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**Migration confers survival benefits against avian predators for partially migratory freshwater fish (POSTER)**

*Kaj Hulthén* CANMove, Dept of Biology, Lund University

The role of predation risk in shaping patterns of animal migration is not well known, mainly because predation is extremely difficult to document in the wild. Here, we present data from an extensive field study that shows that winter migration from lakes to streams in a fish (roach, *Rutilus rutilus*) confers a significant survival benefit with respect to bird (cormorant, *Phalacrocorax carbo spp.*) predation. We assessed migratory behaviour using
electronic PIT tags and individually tracked over 2000 partially migratory fish over 4 years. Cormorants that prey upon tagged fish regurgitate fully functioning tags at communal roosts close to the lakes. What remain are explicit records of successful predation events on fish with a known migratory history. We analysed the relationship between migratory behaviour and individual predation risk, and show that the probability of being preyed upon by cormorants is positively related to the time individuals spend in the lake during winter.

**Genome-wide analysis of immune genes and their local adaptations in *Pieris napi* (POSTER)**

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Different environments pose different immunological threats, and therefore a population will adapt their immune system accordingly, making immunology an interesting study frame for local adaptations. The Green Veined White (*Pieris napi*) is highly suitable species for identifying local adaptation in immunity. They are common and widespread with limited gene flow between populations; have a well-defined ecology, a short generation time, and are easy to rear in the lab. Furthermore, they have previously been used in other immunological studies (Prasai & Karlsson, 2011, 2012).

The genes behind the immune system in *P. napi* have thus far not been identified. By using annotated genomes of other insects I am bioinformatically identifying orthologs of immune genes in the *P. napi* genome. Using population resequencing data, polymorphisms in these immune genes are being identified and characterized. Identification of these genes and the genetic variation within these genes are the first steps in clarifying local adaptations in immunology in *P. napi*.


**Evaluating the potential of ecological niche modelling as a component in invasive species risk assessments**

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Biological invasions have dramatically increased with the development of global trading, causing the homogenization of communities and the decline of biodiversity. Ballast water exchange from shipping and introductions from aquaculture are the two main vectors of invasive species in the marine environment, in which eradication is very difficult. Modelling approaches are invaluable to predict the impact of potentially invasive species before they establish themselves as breeding populations, allowing preventive measures to be put in place.

In this study, we developed a number of workflows for data mobilization, niche modelling and statistical analysis of raster layers. We analysed habitat suitability in the Baltic Sea and the Northeast Atlantic for a ‘black species list’ of 18 marine species invasive in Northern Europe, divided into four ecological groups: zoobenthos, phyto-benthos, zooplankton and phytoplankton. The data refinement workflow was used to mobilize more than 23,000 occurrence records from public databases and integrate them with observations from literature. Suitable habitats were modelled using Ecological niche modelling (ENM) and statistical analysis workflows.

We found several potential risk zones (hotspots) for invasive species in the Skagerrak and the Kattegat, a transitional area for invasive species entering the Baltic Sea. Cold spots showing a low risk of invasive species spread were found in the Bothnian Bay. Our niche modelling results are compared to traditional risk assessment methods based on salinity matching to assess risk of spread along an example shipping route (Gothenburg - St. Petersburg). We discuss the potential of ecological niche modelling methods based on several environmental parameters in providing useful predictive information to policy makers in relation to ballast water management. The study shows the utility of e-science approaches in providing scalable tools for rapid integration of biodiversity data and for producing predictive models that improve the prevention and management of marine invasions.

**Metapopulation dynamics: local and global extinctions**

Bernhard Mehlig  
Dept of Physics, University of Gothenburg

**Scaffolding poor genome assemblies with protein sequences**
Ramprasad Neethiraj, Dept of Zoology, Stockholm University

2nd and 3rd generation sequencing techniques make it possible to sequence whole genomes within days. However, this data is not useful as such since it needs to be assembled into long contiguous sequences called contigs. Ideally, these contigs should equate to complete chromosomes but owing to limitations in the data generation, assembly methods, and genomic complexity, it is currently not possible to recreate whole chromosomes but only fragments of them. Therefore assessing the quality of genome assemblies is a critical step, as it informs the user as to when improvements are necessary. Several metrics are available to assess the quality of an assembly such as the N50, average contig size etc., but their reliability is debatable. We have developed a method called MESPA (Mining Exons for Scaffolding Poor Assemblies) that make use of sets of protein sequences, from a related species to enumerate gene fragmentation in the assembly. This is a biologically informative metric since it contains data from orthologs. This method not only informs us about the fragmentation in the assembly but also can be used generate models for genes when using data from a highly fragmented (i.e low quality) genome assembly by making use of exon-intron splice site information to align the proteins to contigs.

Colour change in fish - regulation and function
Helen Nilsson-Sköld, Dept of Biological and Environmental Sciences, University of Gothenburg

Colour change of the skin of lower vertebrates such as fish has been a subject of great scientific and public interest. However, colour change also takes place in other places such as eyes of fish, but this appears to be a highly neglected phenomenon and very little is known about its regulation. By testing effects of a range of hormones and factors on sand goby eyes, we now provide a fist set of regulatory factors involved in colour change of fish eyes. By comparative analyses we further show that the regulation pattern of chromatohores in eyes is relatively similar as for skin and peritoneum. Further studies aim to reveal effects of contrasting eyes in relation to body coloration on predation and mate choice, using sandgoby. In addition, regulation of skin and eye color change is also analysed in tropical species where color change can occur swiftly and there involved in additional behavioral contexts such as mimicry.

Insect life cycle genomics and adaptation in the wild
Sören Nylin, Dept of Zoology, Stockholm University

The cross-disciplinary project "Insect life cycle genomics and adaptation in the wild" is briefly presented and an overview is given of the progress during the project's first year. A major goal for biology is to reveal the genetic, developmental and evolutionary basis of the adaptations that permit organisms to survive and reproduce by fitting their life cycles to local conditions. Only by understanding the genetic architecture and developmental pathways of such adaptations can we fully understand natural selection in the wild. The genomics revolution now provides ecologists and evolutionary biologists the tools to find and study the relevant genes. However, in order to make significant, meaningful connections between genes, phenotypes, and the environment a synthetic, integrative, and functional approach is required. Insect biologists at Stockholm University have therefore teamed up to create a dynamic and reciprocal process of functional genomic study of the butterfly Pieris napi, an ecological model species, and functional studies of candidate genes in both this butterfly and the genomic model species, Drosophila melanogaster. We target genetic and plastic variation in three linked phenotypes – diapause, wing pattern and immunity – but our ultimate aim is to determine how the independent genes regulating these phenotypes are functionally integrated to create a life cycle adapted to local environmental conditions.

RAD-sequencing reveals parallel and non-parallel genomic divergence in multiple Swedish Littorina saxatilis populations (POSTER)
Mark Ravinet, Marina Panova, Roger Butlin, Kerstin Johannesson and Carl André.
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How parallel is adaptation within a species? Adaptation to similar environments by independent populations may appear phenotypically parallel but does the same genetic architecture underlie these traits? Widely available genome reduction and genotyping-by-sequencing methods mean that it is now possible to ask these questions in non-model organisms. The rough periwinkle, Littorina saxatilis has evolved considerable morphological, ecological and behavioural diversity within its European distribution. In Western Sweden, crab and wave ecotypes appear to have arisen independently in parapatry multiple times as a result of divergent ecological
selection. Wave ecotypes inhabit exposed rocks and are small with a larger relative foot area in order to withstand wave action. Crab individuals experience considerable crab predation and are typically larger with a thicker shell. We have identified 30 000 polymorphic SNPs in three independent populations of *Littorina saxatilis* through restriction-site associated sequencing (RAD-seq). Using FST based outlier analyses we further identified SNPs that show signatures of divergent selection between ecotypes within localities. Here we present our initial findings on shared outliers among the three localities, suggesting a parallel genomic basis for adaptation in this system.

Genetic variation in diapause-related genes in *Pararge aegeri*

**Peter Prüsscher** Dept of Zoology, Stockholm University

Environmental variation is a significant cause of stress for organisms, which can vary spatially across habitats or temporally across seasons. In insects, one widespread adaptation for mitigating stressful periods is to enter a state of arrested development called diapause (Denlinger, 1986; Tauber & Tauber, 1976). The decision of whether to go into diapause is generally triggered by photoperiod (Beck, 1980; Lankinen, Tyukmaeva, & Hoikkala, 2013; A. D. Lees, 1955; Nylin, 2013). A strong genetic component is present in diapause (Emerson et al., 2009), which becomes apparent in the butterfly *Pararge aegeria* where there is such a difference between populations that at 18 hours of light 100% of individuals of populations from northern Sweden will go into diapause while 100% of populations in southern Sweden will develop directly, when held under identical lab conditions (I. Aalberg Haugen & K. Gotthard, submitted). At the moment we are searching for genetic differences in candidate genes that might explain this pattern. For this we are comparing population resequencing data from both a northern and a southern population of Speckled Wood.


Modelling geographically structured populations with mixed sexual and asexual reproduction

**Marina Rafajlovic** Dept of Physics, University of Gothenburg

Mixed sexual and asexual reproduction is observed in many species (see [1] and references therein). Empirically observed distributions of genotypes sampled from such species often suggest that in marginal, young and unstable areas clones are more common than sexual recruits (“geographic parthenogenesis”). In order to explain this observation, a number of studies invoked the process of selection favouring asexual over sexual reproduction in marginal environments. However, in order to test whether empirical genetic data reveal signatures of selection, it first needs to be understood how neutral local competition between clones and sexual recruits shapes the patterns of genetic variation. In this study we present a neutral spatially-explicit model of a population with mixed sexual and asexual reproduction expanding into a new habitat. Using simulations we show that, starting from equal number of males and females, the population exhibits a local abundance of one sex over longer or shorter time periods depending on the parameters of the model. This effect arises mainly because dispersal capabilities of gametes and the spatial sex structure may disallow local sexual reproduction. We find that an uneven distribution of sexes along the habitat is promoted by: 1) longer lifetimes of individuals, 2) long-range dispersals during invasion, 3) stochastic fluctuations governed by random sequences of births, and deaths. We show that our selection-free model supports a number of empirical observations concerning species with mixed sexual and asexual reproduction. We therefore propose it as a null-model for studying the joint effect of the two reproduction mechanisms on the patterns of genetic variation.

[1] D. Kleinhans et al. (in preparation). A neutral model suggests that geographic parthenogenesis can be explained by Alee effects during invasions.

Phenotypic plasticity and potential for adaptation of salinity tolerance in early life stages of a tunicate (Ciona

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Abstracts - CeMEB 11th Assembly, 9-11 April 2014, Strömstad
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**intestinalis)***

**Elin Renborg** Dept of Biological and Environmental Sciences, University of Gothenburg

It is widely considered that invasive species survive novel habitats through phenotypic responses such as plasticity or phenotypic buffering, but there is also evidence that local adaptation may be an important factor. The cosmopolitan and highly invasive tunicate *Ciona intestinalis* exists in a wide range of salinity conditions in Swedish coastal waters and previous studies have shown corresponding differences in larval salinity tolerance between populations from different salinity regimes. Despite the presence of pelagic eggs and larvae, we found populations at short distances to be genetically distinct, which should be favourable for local adaptation to take place. However, we found heritability of traits affecting larval development to be close to absent, eliminating a role for local adaptation. Instead, experimental studies showed clear transgenerational acclimation effects – that is, acclimation of parents directly affected larval development in different salinities. Hence, *C. intestinalis* may be an example of a species in which plasticity is a key feature in being tolerant to various salinity regimes.

**Population genomic analysis of central metabolism**

**Christopher Wheat** Dept of Zoology, Stockholm University

Central metabolic genes have long been the focus of molecular evolution study, starting with the allozyme era almost 50 years ago. Since then, great controversies have risen and fallen regarding the importance of the genetic variation uncovered. Here I try and revisit a bit of these issues by characterizing the genetic variation in central metabolism across a diverse range of species. The findings are interpreted in light of various theories of how natural selection may act upon the linear pathways of central metabolism.

**Insect Diapause - a life history perspective**

**Christer Wiklund** Dept of Zoology, Stockholm University

In tropical environments conditions are typically suitable for growth and reproduction throughout the year, but in temperate areas insect development is difficult during winter, which is spent in a state of arrested development (diapause). As insects are ectotherms the decision to diapause is made long before environmental conditions deteriorate. Characteristically, short daylength and low temperature signals the onset of autumn/winter and are used as cues for the pathway decision. Insects can spend winter diapause as an egg, larva, pupa or adult, but the diapause stage is typically species-specific, and phylogenetically conservative – closely related species generally diapause in the same stage. Insect diapause sets the stage for interesting life history adaptations in species that have more than one generation per year, because conditions typically change as the season progresses – hence selecting for phenotypic plasticity with the first generation having early season adaptations/constraints that differ from second generation. Hence, this is a situation where natural selection does not work – because the offspring from first generation adults will live their lives under second generation conditions and vice versa, and hence the genome is under selection to harbour alternative pathways with respect to many different traits.

**Evidence of countergradient variation and adaptive slow intrinsic growth rate in a marine Isopod (Idotea balthica) locally adapted to low salinity.**

**Hannah Wood** Dept of Biological and Environmental Sciences, University of Gothenburg

Local adaptation is crucial to the generation and maintenance of biodiversity, and is most likely to occur over strong environmental gradients in species with direct development. This study used a common garden approach to investigate the hypothesis that Baltic populations of the brooding marine isopod *Idotea balthica* (found in marine waters and in the low salinity Baltic Sea,) are locally adapted to low salinity. Countergradient variation (CnGV) on the Baltic population was found in metabolic rate analysis, while reduced growth rate in this Baltic population (independent of salinity treatment) reveals adaptive slow growth rate in comparison to fully marine counterparts. Increased oxidative stress in both populations with increased deviation from respective home salinity conditions, and differential mortality in the salinity treatments (32, 20 and 5 PSU) also validate the hypothesis of local adaptation within the Baltic. The suit of traits under selection in low salinity *Idotea balthica* have the common theme of metabolic budget management, a commonality with CnGV over temperature gradients but this is the first data with respect to salinity. Identifying and understanding the evolutionary significance of hidden genetic variation resulting from CnGV over environmental gradients is essential for conservation biology and predicting the effects of environmental change.
The genetic and metabolic basis for the Alba phenotype in Colias butterflies, and its evolution

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Colors and patterns in nature often have known adaptive value and are considered a visual representation of the selection process; therefore they provide important evolutionary insight. Butterflies in the genus Colias exhibit color variation both among, but more interestingly, within species. A color dimorphism, called Alba exists in females of many Colias species. This dimorphism causes a change in the wing ground color, from yellow-orange to white. The Alba allele is known to affect female physiology, behavior, fecundity, and overall fitness. Therefore, it is an excellent model for ecological genomic research and its study can provide evolutionary insight into the role of color variation within and among species. Unfortunately, the genetic and molecular mechanisms that control this color variation remain unknown. We currently have sequenced pooled samples of Alba and orange C. eurytheme females, each at >= 50X genomic coverage. I am currently constructing a de novo assembly of the C. eurytheme genome and using candidate genes to investigate genetic differences between these two color morphs.