Genetics of Bark Beetles and Associated Microorganisms

5-6 September 2011, Sopron, Hungary

Programme and Book of Abstracts

Sopron, 2011

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Programme

4th Workshop on the „Genetics of Bark Beetles and Associated Microorganisms”

5 – 6 September 2011, Sopron, Hungary

Monday

11:00 Registration, location: Hotel Pannonia lobby
12:30 Lunch

14:00
Opening by Ferenc Lakatos and Christian Stauffer

14:30
Plenary lecture by A. I. Cognato, R. Olson, S. M. Smith, & B. H. Jordal: DNA identification of bark and ambrosia beetles

15:10
D. N. Avtzis, W. Arthofer, M. Riegler & C. Stauffer: Did *Wolbachia* influence the genetic structure of *Pityogenes chalcographus*?

C. Bertheau, H. Schuler, S. Krumböck, W. Arthofer & C. Stauffer: Hit or miss in phylogeographic analyses: the case of the cryptic NUMTs

P.H.W. Biedermann, D. L. Six, C. R. Currie & M. Taborsky: Fungus farming in the ambrosia beetle *Xyleborinus saxesenii*

C. Fraser, O. Brahy, P. Mardulyn & J.-C. Grégoire: Forest incest: Does the Great Spruce Bark Beetle (*Dendroctonus micans*) mate exclusively with its siblings?

19:00 Social evening

Tuesday

9:00
Plenary lecture by B. H. Jordal & A. I. Cognato: The first comprehensively sampled molecular phylogeny of Scolytinae

9:40
R. Schaidreiter, H. Schuler, S. Krumböck, C. Stauffer & C. Bertheau: Phylogeographic analysis of palearctic *Ips cembrae* populations

H. F. Anderson, B. H. Jordal, M. Kambestad & L. R. Kirkendall: Ecological genetics of a successful invasive generalist ambrosia beetle, *Xylosandrus morigerus*, in Costa Rica

T. S. S. Selvarajah, L. R. Kirkendall & B. H. Jordal: Ancient and recent range expansion in four globally distributed *Xyleborus* ambrosia beetles

F. Mayer, F. Piel, P. Mardulyn & J.-C. Grégoire: Phylogeography of two bark beetles: influence of two contrasted ecological strategies

12:00 Lunch

14:00 – 15:30
Open discussion The future of bark beetle genetics
moderated by A. I. Cognato, B. H. Jordal, C. Stauffer

16:00 – 18:00
Sightseeing Sopron

19:00 Icebreaker for the IUFRO meeting

Posters to be on view throughout the meeting

M. N. Andersson, J. M. Bengtsson , E. Grosse-Wilde, M. C. Stensmyr, Y. Hillbur, F. Schlyter, B. S. Hansson, C. I. Keeling, & J. Bohlmann: Olfactory Receptors in *Ips typographus*: Transcriptome from antenna analysed and preliminary compared to *Dendroctonus ponderosae* and *Tribolium castaneum* (Coleoptera: Curculionidae & Tenebrionidae)

A. Cassel-Lundhagen, N. Björklund, J. Wallén, F. Mayer & B. Långström: The spruce bark beetle (*Ips typographus*) followed its host – a two-way post glacial colonisation route into Scandinavia

Y. Kawasaki, H. Kajimura, C. Stauffer & F. Lakatos: Infection pattern of Wolbachia strains in Scolytinae

Oral presentations

Did *Wolbachia* influence the genetic structure of *Pityogenes chalcographus* (Coleoptera, Curculionidae)?

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The six-toothed spruce bark beetle *Pityogenes chalcographus* is an important pest infesting *Picea abies*. Strong intraspecific variation based on crossing studies and morphology was shown between northern and central European populations. Molecular studies verified this finding and it was hypothesized that postglacial history of *P. abies* influenced strongly the the genetic structure of *P. chalcographus*.

The detection of *Wolbachia* in *P. chalcographus* populations put in question the validity of a host-based explanation of the phylogeographic patterns observed. *Wolbachia* are endosymbiotic bacteria and one common reproductive phenotype is cytoplasmic incompatibility (CI), which causes postzygotic sterility resulting in reproductive isolation when infected males mate with uninfected females. A nested PCR technique was employed in order to detect low titre *Wolbachia* infections. Although 35.5% of the individuals were infected by one and/or two strains, no distinct pattern of infection was revealed and infections were uncoupled from mitochondrial type. It is therefore unlikely that *Wolbachia* influenced the mitochondrial diversity of European *P. chalcographus* populations.

Ecological genetics of a successful invasive generalist ambrosia beetle, *Xylosandrus morigerus,* in Costa Rica

H. F. Anderson, B. H. Jordal, M. Kambestad & L. R. Kirkendall

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Although inbreeders are expected to show greatly reduced genetic variation, sibmating bark and ambrosia beetles are are strikingly successful in colonizing new regions. Many of the most common and abundant bark and ambrosia beetles tropical and subtropical forests are inbreeders, often exotic species.

One such invasive species is *Xylosandrus morigerus*. This tiny Asian native has spread to tropical forests around the world, including many small islands. In Costa Rica it is ubiquitous, breeding in twigs, small branches, vines, pods, and fallen leaves in primary as well as secondary forests. How can we explain this success?

Longterm inbreeding produces clone-like lineages. The ecological success of clonal lineages has been explained by two models, the frozen niche variation model (FNV) and the general-purpose genotype model (GPG). The former views clonal populations as assemblages of narrowly adapted specialist genotypes; the latter predicts that successful clones will be the most ecologically generalized.

We collected *X. morigerus* from contrasting eological situations, to test these two hypotheses. We found that two deeply diverged mitochondrial haplotypes coexist in Costa Rican populations, and that these two haplotypes do not differ in their association with various ecological factors. Overall the two haplotypes showed nearly complete overlap in resource utilisation and demonstrated that these genotypes have broad niches, supporting the GPG model. Clonal aspects of reproduction coupled with generalized host usage promote successful colonization of new habitats in distant regions by species such as this.

Hit or miss in phylogeographic analyses: the case of the cryptic NUMTs

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Phylogeographic studies call for attention as nuclear copies of mitochondrial DNA (NUMT) may generate erroneous results. We report the presence of NUMTs differing only by 1-3 bp from authentic mitochondrial haplotypes, consequently named cryptic NUMTs. In contrast to traditional NUMTs, for which reliable tools for detection are established, cryptic NUMTs question the validity of phylogeographic analyses based solely on mitochondrial DNA, like the one presented here on the European bark beetle *Ips typographus*. Caution is called since cryptic NUMTs might be responsible for haplotype richness found in several species, and the necessity of refined methods for NUMT detection is highlighted.

Fungus farming in the ambrosia beetle *Xyleborinus saxesenii* (Scolytinae: Curculionidae)

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Fungus gardens made by insects are not pure monocultures, but comparable to a community of interacting microbes with beneficial or detrimental effects to the farmers. These have been well studied for fungus farming ants and termites, but few studies have addressed the fungal community of ambrosia beetles and their interactions with particular species of fungi.

Laboratory studies showed that *Ambrosiella sulphurea* and *Fusarium merismoides* (Ascomycota) established first in new gardens of the wood-boring ambrosia beetle *Xyleborinus saxesenii* and were transmitted in spore-carrying organs by gallery founding females. These fungi usually dominated the microbial complex within the galleries. However, over time, five other fungal species appeared in gardens, of which two *Paecilomyces* species became increasingly abundant. Experiments showed that adults and brood induced growth of *A. sulfurea* that was characterized by massive fruiting structures (sporodochia). These fruiting bodies were a major part of the fungal layers growing on tunnel walls and seemed to be an essential component of beetle nutrition, as both egg and larval numbers were positively affected by their abundance. In contrary, *P. variotii* had a negative impact on larval numbers and led to the death of parental females by forming biofilms on their bodies. Our data suggests that two mutualistic, several commensalistic and at least one pathogenic filamentous fungus are associated with *X. saxesenii*. Fungal growth is probably regulated by different behaviour shown by adults and larvae.

DNA identification of bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae)

A. I. Cognato, R. Olson, S. M. Smith, & B. H. Jordal

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Bark and ambrosia beetles are ubiquitous in forests worldwide and contribute to the decomposition of dead vegetation. Although most species are benign, some species cause great economic and ecological damage to forests. In addition to destruction caused by native scolytines species, introductions of exotic bark beetle species continuously threaten native forests throughout the world. Exotic scolytines are among the most frequently intercepted species from shipping dunnage and packing crates. Despite the vigilance of port authorities many species elude inspection and establish populations in non-native lands. Detection and identification of scolytine species is particularly difficult for the immature stages, due to the lack of morphological diagnostic characters and adults of tropical species due to poor knowledge of their species diversity. In an effort to help identify scolytines, a DNA identification system is developed using 600 base pairs the 5' portion of the mitochondrial cytochrome oxidase I gene. A preliminary database of >350 species is created including > 35 genera and >70 species. Phylogenetic analysis of these data indicate that species and many genera are monophyletic. This suggests that DNA identification of scolytines is possible and accuracy of species identification will increase with the increase of scolytine sequences in this database.

Forest incest: Does the Great Spruce Bark Beetle (*Dendroctonus micans*) mate exclusively with its siblings?

C. Fraser, O. Brahy, P. Mardulyn & J-C Grégoire

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The Great Spruce Bark Beetle (*Dendroctonus micans*) has an intriguing life history, with an apparently purely endogamous mating system. Gravid females bore solitary egg galleries beneath the bark of spruce trees. The gregarious larvae initially feed together but, at the onset of pupation, separate into individual niches. As young adults they gather together again in the brood chamber to mate. Except under outbreak conditions, brood chambers are isolated and rarely intersect; this system ensures that mating is purely among siblings. However, observations of reproductively viable adult males flying through the forest raises the question of whether exogamous matings can and do occur for *D. micans*. We aim to use a combination of laboratory and field experiments, and genetic techniques, to test whether: 1) multiple matings can occur; 2) such matings lead to some or all progeny being sired by the less-related latecomer (e.g., via sperm competition); 3) females would preferentially mate with less-related males; and 4) exogamous matings increase progeny fitness. We will use microsatellite markers to determine paternity. Although several useful polymorphic loci have already been isolated, we will additionally use next-generation 454 sequencing technology to enhance the microsatellite library for this species.

The first comprehensively sampled molecular phylogeny of Scolytinae

B. H. Jordal & A. I. Cognato

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Bark and ambrosia beetles include more than ten percent of the total weevil diversity and vary enormously in their adaptations to a subcortical lifestyle. Comparative analyses of evolutionary transitions in key ecological and biological traits are therefore particularly informative for this group of beetles. Progress in such analyses is largely dependent on a resolved and well supported phylogeny, which is thus far not available. Hyperdiverse clades such as those of Scolytinae are intriguingly difficult to resolve, particularly so for the deepest splits in the group. This presentation focuses on recent progress in establishing a phylogeny of Scolytinae, and to place the subfamily within the advanced weevils. Analyses of the four nuclear genes EF-1α, CAD, ArgK and 28S, the mitochondrial gene COI, and 128 morphological characters have firmly concluded that Scolytinae is a monophyletic group, albeit with uncertain relationships to Platypodinae and Cossoninae. Further analyses within Scolytinae were based on the same five gene fragments, including 199 scolytine species in 147 genera representing 24 of the currently 27 recognized tribes in the subfamily. Despite the inclusion of 3694 nucleotides from five unlinked genetic loci, resolution at deeper nodes was poor. The most interesting and well supported results included the monophyly and sometimes basal position of Scolytini, the basal position of the 100 Myr fossil genus Microborus not grouping with the other Hexacolini, the nested position of Scolytoplatypus in the remaining of Hexacolini, the nested position of Hylastini in a clade consisting of boreal conifer associated taxa (Tomicus, Dendroctonus, Hylurgus), a nested position of Premnobius in Ipini, and a sister relationship between the latter and Dryocoetini that includes a nested Xyleborini. Well supported monophyletic tribes sampled for more than two genera included only Hypoborini, Bothrosternini, Corthylini, Crypturgini, Xyloterini, and sometimes Micracini that was separated into one African and one American clade.

Phylogeography of two bark beetles: influence of two contrasted ecological strategies

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The last 700 000 years are well known to have had a drastic effect on European organisms by periodic alternations between glacial periods and short warm and wet intervals. So far, very few studies have focused on histories of well-adapted-to-harsh-climate species, like the boreo-montane ones. The European spruce bark beetle (*Ips typographus*, Curculionidae: Scolitinae) and the great European spruce bark beetle (*Dendroctonus micans*, Curculionidae: Scolitinae) are both Palaearctic boreo-montane species and they share same hosts: all trees from the genus *Picea*. However, they exhibit obvious differences in their life-history traits reflecting contrasted ecological strategies: *I. typographus* is exogamous, secondary in endemic conditions, known to disperse far away and attacks trees in mass by producing aggregation pheromones. Its strategy can be categorized as well adapted to scarce resources, variable in space and time. On the other side, *D. micans* mates among siblings, is always primary, rarely observed in flight and a solitary colonizer. Living like a parasite of trees, it evolved toward a cryptic and well adapted to stable condition strategy. This presentation highlights the impact of such differences on haplotype networks of these species. Samples from the whole Europe were sequenced for the mitochondrial marker COI (1200 bp). To confirm the mitochondrial results, a subset of the samples was also sequenced for 4 nuclear markers (coding genes: EF1a, G6PD, Wingless and Arginine kinase, sized between 600 and 900 bp). As expected, our results show contrasted haplotype networks. *I. typographus* networks (mitochondrial and nuclear) reveal to be poorly structured but expose a high number of polymorphisms. On the other hand, *D. micans* COI network is extremely structured and nuclear networks show an extreme low level of polymorphism. Unexpected similarities suggest a same differentiation history between Asian and European populations.

Phylogeographic analysis of palearctic *Ips cembrae* (Coleoptera, Scolytinae) populations

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Ips cembrae is an economically important pest species on *Larix* spp. in the Palearctics. According to a publication based on mitochondrial DNA *I. cembrae* hardly revealed genetic differentiation within Europe. However, European and Asian populations were significantly separated confirming the Asian populations as own taxonomic entity namely *I. subelongatus*. These findings are important regarding the decision making in forest management and sanitary measures in timber trade.

This master thesis was designed to study European and Asian populations with mitochondrial and nuclear markers. Mitochondrial data surprisingly revealed higher haplotypic richness than the previous study and this discrepancy might be caused by pseudogenes or the influence of the maternally inherited endosymbiont *Wolbachia*. In addition, nuclear data are in agreement with the mitochondrial marker revealing a clear distinction between Asian and European larch bark beetle populations.

Ancient and recent range expansion in four globally distributed *Xyleborus* ambrosia beetles

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Some of the more ubiquitous and widespread species of scolytine ambrosia beetles belong to the genus *Xyleborus*. Their common occurrence on remote oceanic islands and frequent introductions to new continents via important trade routes indicate that many species are superior colonizers of distant biomes. Facilitated by an advantageous inbreeding reproductive system, in which siblings mate before dispersal, they seem pre-adapted for wide distribution by recurrent colonizations of remote areas. If so, phylogeographical patterns should indicate not only dispersal during recent times, but also during more ancient times before human transport of wooden products around the globe. We tested this hypothesis in a comparative context, analyzing the population genetic structure and phylogeography of four species in *Xyleborus*, including *X. ferrugineus*, *X. affinis*, *X. perforans* and *X. volvulus*. Molecular evidence from the mitochondrial COI gene and the nuclear gene Elongation factor–1α revealed that the four species are each monophyletic and likely single species with globally wide distributions. These data furthermore demonstrated range expansions in both ancient and recent times for all species. Despite clear evidence for multiple recent introductions to new continents, all species were surprisingly strongly structured geographically. Genetic diversity within populations was generally high, further documenting the historical contribution from multiple introductions and the long term coexistence of genetically diverged populations.

Posters

Olfactory Receptors in *Ips typographus*: Transcriptome from antenna analysed and preliminary compared to *Dendroctonus ponderosae* and *Tribolium castaneum* (Coleoptera: Curculionidae & Tenebrionidae)

M. N. Andersson, J. M. Bengtsson , E. Grosse-Wilde, M. C. Stensmyr, Y. Hillbur, F. Schlyter, B. S. Hansson, C. I. Keeling, & J. Bohlmann

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We have identified putative olfactory receptor (OR) genes in a non-model insect, the bark beetle *Ips typographus*. Next-generation sequencing methods (454 GS/FLX and Solexa) were used to analyze the antennal transcriptome. Bioinformatic analyses revealed 40 open reading frames that, with a high probability, encoded ORs. RACE PCR (Rapid Amplification of cDNA Ends) was deployed to extend eight of these sequences in 3'-direction, and reverse transcriptase PCR was used to verify antennal expression. Transmembrane prediction indicated that candidate proteins of sufficient length contained multiple transmembrane domains, in a pattern typical for olfactory receptors. RT-PCR confirmed expression in the antennae for 5 of 8 extended gene fragments.

Candidate ORs were compared to ORs of *Tribolium castaneum*, the only other beetle with identified OR genes from a genome and to the Mountain Pine Beetle *D. ponderosae* for which a transcriptome is available at Univ. British Columbia, Canada.

Like ORs in other insect species, those in *I. typographus*, in general, demonstrated a low level of sequence similarity. A dendrogram based on sequence similarity indicated that ORs from *D. ponderosae* and *I. typographus* form bark beetle-specific subgroups, distinct from other subgroups dominated by ORs from *T. castaneum*. This suggests a clear extension of bark beetle OR function. However, a few groups included receptors from all species, implying some degree of conservation among Coleopteran ORs.

The spruce bark beetle (*Ips typographus*) followed its host – a two-way post glacial colonisation route into Scandinavia

A. Cassel-Lundhagen, N. Björklund, J. Wallén, F. Mayer & B. Långström

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It has been widely agreed that spruce and the spruce bark beetle colonized the Scandinavian peninsula after the last glaciation from the north, i.e. via Finland and round the gulf of Bothnia. Thus, it has been assumed that the spruce bark beetle followed its host and adapted to the harsh climate prevailing close to the Arctic circle along the immigration route. However, recent findings also indicate that the spruce have crossed the Baltic sea from the Baltic region into southern Sweden. We aimed at testing if also the spruce bark beetle had taken this geographic "short cut". 359 individuals, representing northern, eastern and central Europe, were collected and a 698 bp long fragment of the mtDNA COI gene were sequenced and analysed. Our data verify that the spruce bark beetle has followed the same colonisation routes as the spruce. We found that most of the bark beetles found in southern Sweden have low genetic variability and has mainly colonized from the southeast via the Baltic states. In contrast, those populations residing in the north are considerably more genetically variable and appear to have colonized mainly from the north via Finland. We find no support for a glacial refugium in northern Europe. Rather, the glacial refugium is likely the same for the whole north European region.

Infection pattern of *Wolbachia* strains in Scolytinae

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The subfamily Scolytinae is a large taxonomic group with approximately 6000 species worldwide, including bark and ambrosia beetles, and is associated with various microorganisms. In the present study, we have examined endocellular bacteria, *Wolbachia*, in 24 beetle species of Japan, Europe (Austria, Hungary, Germany) and USA. First, diagnostic PCR of the wsp gene demonstrated that haplodiploid/sib mating species were infected with *Wolbachia* at significant higher rates than diploid/random mating species. Second, molecular phylogenetic analysis showed that three *Wolbachia* strains (wScol 1-3) existed in different beetle species, in addition to three species-specific strains infecting *Xylosandrus germanus*. Two of five genes in *Wolbachia* genome were highly homologous between wScol 1 and wScol 2, predicting their ancestral strains might have recombined with each other. Finally, comparison of phylogenetic trees of the beetles and *Wolbachia* indicated a clear discordance in divergence patterns, suggesting multiple horizontal transfers of *Wolbachia* into each beetle species rather than co-speciation between them. We conclude that *Wolbachia* is not likely to drive the beetles into haplodiploidy but to favor haplodiploidy or other ecological features such as female-biased sex ratio.

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