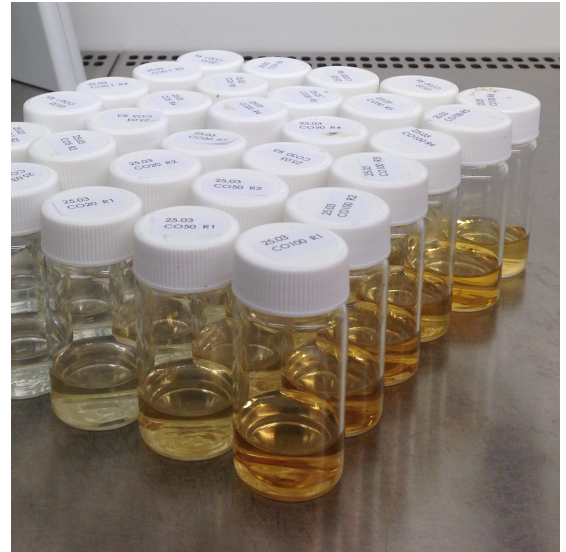


Bridging Theory and Experiments ~ Evolving Communities



**Max-Planck Institute for
Evolutionary Biology
18th - 22nd April**

Program for the Bridging Theory and Experiments: Evolving Communities

April 18, 2016

Contents

1	Workshop schedule	3
2	General information	4
2.1	Map of Plön	4
2.2	Travel	4
2.3	Hotel information	5
2.4	Lunch/Coffee	5
2.5	Dinner	5
2.5.1	Monday	5
2.5.2	Tuesday	6
2.5.3	Wednesday	6
2.5.4	Thursday	6
2.5.5	Plön	6
2.5.6	Lübeck	7
2.5.7	Kiel	7
2.6	WiFi	7
3	White Board Talks and Discussions	8
4	Abstracts	8
5	List of participants	26

1 Workshop schedule

<p>Monday</p> <p>14:00 Welcome and aims 14:15 Arne Traulsen 15:15 coffee 15:45 Thomas Bell 16:45 discussion in groups</p> <p>18:30 move to dinner at institute + discussion</p>	<p>Tuesday</p> <p>09:00 Joachim Krug 10:00 white board presentation introduction 10:10 coffee break 10:30 white board presentations</p> <p>12:30 lunch 14:00 Anna-Liisa Laine 15:00 discussion 15:30 coffee 16:00 present discussion results 17:00 move to dinner</p> <p>18:30 dinner + discussion</p>	<p>Wednesday</p> <p>09:00 Arjan de Visser 10:00 coffee break</p> <p>10:30 white board presentations</p> <p>12:30 lunch + discussion 14:00 discussion 15:00 boat trip</p> <p>17:00 dinner and discussion at Kash restaurant</p>	<p>Thursday</p> <p>09:00 Maria and Lutz 10:00 coffee break</p> <p>10:30 discussion</p> <p>12:30 lunch 14:00 Ursula Gaedke 15:00 discussion 15:30 coffee 16:00 present discussion results 17:00 move to dinner</p> <p>18:30 dinner+ discussion</p>	<p>Friday</p> <p>09:00 Joachim Hermisson 10:00 coffee break</p> <p>10:30 final discussion and summary for synthesis 12:30 lunch + departure</p>
---	--	---	---	---

2 General information

2.1 Map of Plön



2.2 Travel

You can reach Plön from Hamburg airport by public transport via Kiel or via Lübeck. We recommend to check out your individual travel plan on the official website of DB http://www.bahn.de/p_en/view/index.shtml.

- via Kiel: From 07:15, an hourly shuttle-bus departs from Hamburg airport to Kiel. Tickets can be bought directly in the bus (see also http://www.bahn.de/autokraft/view/angebot/kielius_en/kielius-ueb.shtml). From Kiel train station you can take the train to Lübeck or Lüneburg which also stops in Plön. The journey from Hamburg airport to Plön via Kiel takes a little more than 2 hours.
- via Lübeck: From Hamburg airport on Platform 2 take the Train S1 to Hamburg central station. In Hamburg Airport you can also find ticket machines from *DB*, where you can buy your ticket for the whole trip to Plön. From Hamburg central station you then take the train to Lübeck which usually departs from platform 6. In Lübeck you have to change into the train to Kiel which also stops in Plön. The journey via Lübeck takes between 2 and 3 hours.

2.3 Hotel information

The address of the hotel is Ölmühlenallee 3, 24306 Pln. You can reach it from the train station either by foot or by bus number 331 (stops Danziger or Fegetasche). For further information about the hotel, you can check their website <http://www.nordic-hotels.com/en/hotels/ploen-nordic-hotel-ploen/>.

2.4 Lunch/Coffee

- Between the sessions there will be a coffee break with coffee and snacks.
- Lunch will be provided in the institute.
- On Tuesday & Thursday we will go to a nearby restaurant for lunch; we will meet at 12:15 in front of the main entrance.

2.5 Dinner

On Monday, Tuesday, Wednesday and Thursday there will be dinner for the whole group. If you have any questions, ask *Maria* or *Lutz* for help.

2.5.1 Monday

- Location: Max Planck Institute
- Dinner starts at 18:30

2.5.2 Tuesday

- Location: "Prinzeninsel", a peninsula in the *Grosser Plöner See*, Grosse Insel 1, 24306 Plön
- Meeting time in front of the institute: 18:15
- Dinner starts at 19:00
- Meal and first drink is included

2.5.3 Wednesday

- Location: "Landgasthof Kasch", Dorfstrasse 60, Timmdorf/Malente
- meeting time in front of the institute: 14:30
- ferry departs from *Fegetasche* at 15:00
- transfer to the restaurant and back to the hotel will be organized

2.5.4 Thursday

- Location: "Restaurant alte Schwimmhalle", Schlossgebiet 1, 24306 Pln
- Meeting time in front of the institute: 17:30
- Dinner starts at 18:30
- Dinner includes a choice of 3 meals and the first drink

2.5.5 Plön

Plön is the capital of the Plön district in Schleswig-Holstein, Germany. It has about 8,700 inhabitants. Plön is almost an island in the middle of 5 different (but mostly connected) lakes. The biggest one, the *Grosser Plöner See* (Great Plön Lake), has a circumference of almost 40 kms. The town's landmark is Plön Castle, a chateau built in the 17th century on a hill overlooking the town.

The town, nestled in the rolling, wooded lake district of Holstein Switzerland (Holsteinische Schweiz), also has importance in the tourism industry. We recommend a walk around the *Schöhsee* behind the Max Planck Institute, which takes around one to one and a half hours.

2.5.6 Lübeck

Lübeck is the second largest city of Schleswig-Holstein and is beautifully located at the river Trave. In the middle ages it was an important trading center and leading city of the *Hanse*, which controlled large shares of the northern European trade. Lübeck has a very nice old town (listed as a world heritage site), the well-known *Holstentor* and you can also visit the recently built *Hansemuseum*.

- Trains to Lübeck leave every 30 minutes, at hh:15 and hh:45.
- Trains back to Plön depart at hh:06 and hh:27 until 21:06 and afterwards at hh:01. The last train leaves Lübeck at 00:17.
- The train ride takes about 40 minutes.
- The day-ticket costs 19.10 EUR, and the group day-ticket for up to five persons costs 31.60 EUR.

2.5.7 Kiel

Kiel is the capital and most populous city in the northern German state of Schleswig-Holstein. Kiel lies approximately 90 kilometres north of Hamburg. Due to its geographic location in the north of Germany, the southeast of the Jutland peninsula, and the southwestern shore of the Baltic Sea, Kiel has become one of the major maritime centres of Germany. For instance, the city is known for a variety of international sailing events, including the annual Kiel Week, which is the biggest sailing event in the world. The Olympic sailing competitions of the 1936 and the 1972 Summer Olympics were held in Kiel.

- Trains leave every 30 minutes, hh:14 and hh:45.
- Trains back to Plön leave at hh:04 and hh:44. The last train departs in Kiel at 21:43.
- Train ride takes about 31 minutes.
- The day-ticket costs 13.90 EUR, and the group day-ticket for up to five persons costs 27.70 EUR.

2.6 WiFi

- WiFi is accessible for "eduroam" users in the institute.
- In case you do not have access to "eduroam", we will provide you with an account for our guest net.

3 White Board Talks and Discussions

We plan to have an unusual format to foster interactions and prepare for the synthesis. We will break into 5 teams and discuss problems handed out at the beginning of the discussion sessions. After one hour we will all gather again, such that each team has a few minutes to present their ideas on 1-2 slides.

4 Abstracts

Maria Abou Chakra & Lutz Becks

Theoretical Biology & Experimental Evolution

We will describe our collaboration and experience on the project "Eco-evolutionary feedback promotes Red Queen dynamics and selects for sex in predator populations"

Stuart Auld

Environment-driven variation in disease epidemics across replicate semi-natural communities

The strength and severity of disease epidemics depend on both the genotypic composition of host populations and on ambient biotic and abiotic environmental conditions. Controlled laboratory experiments have helped us dissect the role of environment and host genotype on infection phenotypes. However, even small levels of ecological complexity can dramatically influence environment-mediated effects on epidemics; this highlights the importance of identifying the mechanisms through which environment affects disease at the population level. We tested whether elevated ambient temperature or population mixing (or both) caused bigger disease epidemics in replicate artificial outdoor populations of the crustacean *Daphnia magna* and its natural sterilizing pathogen *Pasteuria ramosa*. Since *Daphnia* reproduce both sexually and asexually, we were able to establish twenty replicate *Daphnia* populations with an identical genetic composition. Epidemics were larger in unmixed populations than in mixed populations, and increased temperature led to increases in host investment in sexual reproduction. Peak parasite prevalence occurred before peak investment in sexual reproduction in the warmest populations. We are now genotyping both hosts and parasites collected after the epidemic to identify environment-mediated effects on the strength of parasite- and host-mediated selection and thus host-parasite coevolution. We will go on to examine eco-coevolutionary interactions across multiple years in each of our twenty populations.

Goekce Ayan

Experimental Evolution

I am interested in whether and how spatial structure of the environment play a role in de-

termining the extent of diversification and local adaptation. By using experimental evolution approach, I do microcosm experiments with a microbial predator (*Tetrahymena thermophila*) and prey (*Pseudomonas fluorescens* SBW25) model.

Susan Bailey

The effects of selection and mutation rate heterogeneity on parallel evolution

Parallel evolution - similar evolutionary changes arising in independently evolving populations, is often taken to be evidence of strong selection, however theory suggests that heterogeneity in mutation rate can be an equally important driver of parallelism. We explore the contributions of mutation and selection to the degree of parallelism at the gene-level in using data from experimentally evolved populations of *Saccharomyces cerevisiae* (Lang et al, Nature 2013). First focusing on the synonymous mutations, we use a probabilistic model to generate expectations for the distribution of mutations per gene, with and without heterogeneity in mutation rate. We show that a model incorporating heterogeneous mutation rates fits these data best. Shifting focus to the non-synonymous mutations, we then show that mutation rate heterogeneity is not sufficient to explain variation here and so, not surprisingly, selection also plays a role. We use maximum likelihood techniques to quantify the relative contributions of heterogeneity in mutation rate and selection that best explain these data, first under the assumption that mutations fix sequentially, and then allowing for the effects of clonal competition. We conclude that both mutation and selection play important roles in generating the patterns of parallelism observed in this experimental yeast system and discuss the generality of our results.

Thomas Bell

Adaptation of bacteria in simple and complex communities

Many studies have investigated how bacteria adapt to changing environments, but most have been conducted under simplified conditions, typically using model organisms in test tubes containing single populations. I have collected bacterial isolates from natural environments to investigate how bacteria evolve in multispecies communities under controlled conditions. I will discuss how adaptation proceeds simple communities containing up to 16 species, and how interspecific interactions alter the adaptive process. I will discuss how the evolution of species interactions depends on the makeup of the surrounding community. I will also present preliminary results showing how adaptation of focal species is altered when they are embedded within complex natural communities containing hundreds of species.

Joana Bernardes

Is epistasis the single reason behind heterosis?

Epistasis is one of genetic mechanisms that might explain heterosis. To identify how epistasis might influence the hybrid genome we set up to test the asexual fitness of partial haploid

hybrids. *Saccharomyces* species have chromosomes with different sizes, ranging from 230-1532000kb, and it is possible to substitute an entire chromosome from related species. We used partial haploid hybrids in *S. cerevisiae* background with one chromosome substituted by the correspondent *S. paradoxus* chromosome. Because the strains are haploids if there was a relation between the sizes of the genome substitution and their asexual fitness we could only attribute it to epistasis. Even though partial hybrids tended to perform better than the *S. cerevisiae* background, we did not find a relation between the size of the substitutions and the fitness of the partial hybrid. Thus, we can put aside a strong epistatic effect as the single explanation for heterosis.

Frederic Bertels

Parallel evolution of HIV-1 in a long-term experiment

One of the most intriguing puzzles in biology is the degree to which evolution is repeatable. The repeatability of evolution or parallel evolution has been studied in a variety of model systems, but has rarely been investigated with clinically relevant viruses. To investigate parallel evolution of HIV-1, we passaged two replicate HIV-1 populations for almost one year in each of two human T-cell lines. For each of the four replicate lines, we determined the genetic composition of the viral population at nine time points by sequencing the entire genome. Mutations that were carried by the majority of the virus population showed an extreme degree of parallel evolution. In one of our evolutionary lines, all 19 majority mutations also occur in another line but appear in a different order. This repeatable pattern of HIV-1 evolution is indicative of a predictable process, which is maximally inconsistent with evolutionary neutrality.

Karen Bisschop

The community context of ecological specialisation

Biodiversity is currently being lost at an unprecedented rate due to environmental changes at different scales in space and time. In order to cope with these changes, organisms are continuously challenged to adapt to novel conditions. This process of adaptive evolution is referred to as ecological specialisation and is hypothesised to be strongly impacted by the community context. The effect of competition and a homo- or heterogeneous environment on the local adaptation of spider mites (*Tetranychidae*) will be investigated during experimental evolution. By means of parameterised individual based model, i foresee to quantify the relative importance of ecological setting and evolution for the observed population dynamics.

Marvin Boettcher

RNA translation before the steady state

The TASEP, shorthand notation for totally asymmetric simple exclusion process was initially developed as a stochastic model for mRNA translation: In the translation process ribosomes

attach to a initiation site (initiation), move along the RNA while appending amino acids to the chain (elongation) and exit the RNA molecule after progressing to the last codon and releasing the protein (removal). The TASEP has subsequently attracted a lot of attention, since it can be applied to a variety of systems, including molecular transport, traffic, or spread of epidemics, and can be treated analytically in multiple cases. In biological systems, however, recent evidence, i.e. the correlation of several translation quantities and transcript length, suggests that extensions to the TASEP might be required to correctly capture those previously unknown features of translation. We examine the influence of ribosome reinitiation on translation, that is the releasing ribosome directly initiates again without leaving into the ribosome pool, by using an implementation of the TASEP with the Gillespie algorithm. In contrast to previous work we explicitly take the initial phase, before steady state is reached, into account, since mRNA molecules start translation without attached ribosomes. For realistic biological parameters the translation does not necessarily reach a steady state, since reinitiation considerably prolongs the time until steady state is reached and mRNA lifetime is comparatively limited. We demonstrate that including reinitiation creates a strong length dependency on both ribosome density on the transcript and protein yield from a single transcript.

Primrose Boynton

Selection pressures on wild yeast populations

Saccharomyces cerevisiae is a well studied model organism, but its natural history is poorly understood. I study selection pressures on wild *Saccharomyces* populations including interactions with other microbes, adaptation to abiotic conditions, and bet hedging.

Arjan de Visser

Chance and necessity in the evolution of an antibiotic resistance enzyme

Evolution is inherently stochastic due to chance events, such as mutations, but not fully random due to deterministic consequences of natural selection and developmental constraints. A better understanding of the factors and conditions that increase the predictability of evolution may help to control the evolution of unwanted phenotypes, such as antibiotic-resistant pathogens. In my talk, I will show how chance and necessity affect the evolution of a notorious antibiotic resistance enzyme, TEM-1 β -lactamase. We study the evolution of this enzyme in the presence of third-generation cephalosporin cefotaxime, using laboratory in vitro and in vivo evolution experiments. These studies broadly explore the evolvability of cefotaxime resistance, and address how both developmental constraints of this enzyme (pictured by its fitness landscape) and the supply of new mutants together determine the repeatability of evolution. In particular, I will show how mutations with exceptionally large effects on resistance, developmental constraints caused by strong interactions between mutations at different positions, and a large population size all introduce evolutionary constraints that increase the repeatability of evolution of cefotaxime resistance. Surprisingly, we find that small populations sometimes reach higher

resistance than populations up to 1,000 times larger in size, suggesting an important role of chance events for long-term adaptation.

Elias Ehrlich

The trade-off shape matters its effects on intraspecific trait variation in a predator-prey system

Trade-offs between functional traits emerge not only among but also within species resulting in intraspecific trait variation which provides the basis for evolutionary processes. The exact cost-benefit relationship between two traits is described by the trade-off shape which may be concave, linear or convex. We use a predator-prey model involving an intraspecific trade-off between growth and defence among three prey genotypes to explore short- and long-term effects of the trade-off shape on standing intraspecific trait variation. Linear trade-offs promote long-term coexistence of all prey genotypes based on neutrality. In contrast, concave and convex trade-offs reduce the initial trait variation in the long-term. Almost linear trade-offs (slightly concave or convex) enable co-occurrence of all prey genotypes on shorter but ecologically relevant time scales due to a delayed competitive exclusion. Our results reveal that examining the shape of the trade-off allows an understanding of how intraspecific trait variation can be maintained.

Rachael Evans

Evolving microbial communities for biofuel production

Lignocellulose is a promising substrate for biofuel production due to its abundance and high sugar content. However, due to the recalcitrance of lignocellulose, industrial degradation is an expensive and energy intensive process. This project aims to utilise experimental community evolution to produce bacterial communities able to efficiently degrade lignocellulose. Several bacterial strains have been isolated from compost and assayed against various carbon sources to determine their enzymatic activities. These bacteria will be evolved in communities of varying diversity on both simple and complex substrates to determine the best method for improving lignocellulolytic activity. Constituent species will be isolated regularly from communities and assayed to determine how their individual activities and their interactions with other species are changing. The productivity of communities will be measured regularly and those showing the most improved productivity will be analysed using metagenomics, proteomics and transcriptomics to determine the molecular reasons for increased productivity. Using these techniques, enzymes which appear to be playing a role in increasing community productivity will be expressed and characterised to determine potential industrial applications. This project offers interesting opportunities to not only discover enzymes with lignocellulosic activities but to also gain insight into how both diversity and substrate affect the evolution of bacterial strains within a community.

Urusla Gaedke

The interplay between biomass and trait dynamics helps to understand observed plankton dynamics

Depending on the different facets of biodiversity (e.g. genetic, phenotypic, and species diversity), individuals, populations and communities possess an inherent flexibility which allows them to adjust to ambient conditions improving their fitness. This influences their dynamics and consequently those of the entire food web. Given such feedback loops between biomass and trait dynamics, the responses of food webs to altered conditions are yet very difficult to understand and to predict, but of outstanding importance for fundamental and applied ecology. To overcome these limitations, we use flexible, trait-based approaches rather than classical static species-based approaches where rigid properties are assigned to each species independent of ambient conditions. The models reveal that a potential for trait variation alters the dynamics remarkably, e.g. classical predator-prey cycles may be silenced by fast trait changes, producing e.g. anti-phase or cryptic cycles. We could understand and reproduce the plankton dynamics observed in Lake Constance only when accounting for trait variation enabling a mutual adjustment of interacting trophic groups on an ecologically relevant time scale. Otherwise, substantial deviations occurred. The potential for intraspecific trait changes may also be highly relevant for species coexistence. Moderately strong intraspecific trait variation occurring within ecological time strongly enabled coexistence of numerous species since they became temporally more similar or dissimilar depending on the actual amount of stabilizing and equalizing forces.

Jenna Gallie

Synonymous mutations in nature

Summary: Despite their lack of effect on protein sequence, synonymous mutations have been shown to exert a multitude of effects on organismal phenotype and fitness. We are investigating how and why synonymous mutations accumulate in a natural context, through unravelling the effects of various synonymous mutations in three divergent strains of *Pseudomonas fluorescens* (SBW25, A506 and Pf0-1).

Chaitanya Gokhale

Theoretical Evolutionary Biology

I am interested in understanding the role and interplay of ecology and evolution, together, in the proliferation of a species and/or between species interactions. The main tools I use for the same are deterministic and stochastic processes, probability theory and computer simulations.

Katrin Hammerschmidt

The mode of group interaction affects the transition to multicellularity

The transition to multicellularity is central to the emergence of biological complexity. During the transition, groups of cells must acquire the capacity to reproduce so that they can participate in evolution by natural selection. While a reproductive life cycle is necessary for a transition to multicellularity, it is not sufficient. Here I present experiments that enabled groups of the bacterium *Pseudomonas fluorescens* to reproduce via a developmental life cycle that decoupled fitness at the cell and group level. Two ecological frameworks that differ in the way in which groups interact will be contrasted. The mode of group interaction affects the strength and outcome of selection operating at the group versus cell level. The structure of the metapopulation therefore has implications for the potential of groups of cells to transition to multicellularity.

Ellie Harrison

Tripartite interactions between phage, bacteria and plasmid shapes the trajectory of evolution

Mobile genetic elements play a major role in bacterial evolution. Bacteriophages (phages) are key bacterial predators and impose strong selection for resistance while elements such as conjugative plasmids facilitate adaptation through horizontal gene transfer but also place a strain on the cell, often reducing host fitness. We investigate how simultaneous interactions between bacteria, phage and plasmid alter the ecological and evolutionary outcomes of the tripartite interaction. We find that antagonistic coevolution between the bacteria, *Pseudomonas fluorescens*, and phage SBW25?2 can drive the extinction of the mercury resistance mega-plasmid, pQBR103, from bacterial populations when plasmids are purely parasitic. Under selection for plasmid bound traits however, plasmid carriage limited bacteria-phage coevolution; bacteria and phage evolved lower resistance and infectivity respectively and bacteria evolved high rates of mucoidy, a form of weak phage resistance. Gene expression data suggests that that subtle effects on bacterial regulation due to plasmid carriage primes the bacteria towards this evolutionary path. Our findings demonstrate how species interactions can have evolutionary consequences for bacteria beyond those observed in simple pairwise interactions.

Giannina Hattich

Eco-Evolutionary Dynamics in competing marine phytoplankton communities

In a community, responses to an environmental stressor (e.g. ocean acidification) can act on different levels. These levels include changes in the species composition (ecological processes), genotypic composition (evolutionary processes) and phenotypic plasticity. In recent years it has been shown that the evolutionary and ecological processes involved in shaping communities can act on similar time scales and can thus interact with each other. Phytoplankton species represent optimal candidates to work with in eco-evolutionary experiments they have short generation times, they can be cultured and their ecology for many species has been well described. To disentangle the eco-evolutionary dynamics in a competing marine phytoplankton

community we work with two different species including *Emilinia Huxleyi* (coccolithophore) and *Chaetoceros affinis* (diatom). The different species are kept under controlled experimental conditions and their response to ocean acidification in a competing environment will be assessed. We expect that under high CO₂ conditions the diatoms will be less affected compared to the coccolithophores. Coccolithophores are calcifiers (their shells contain CaCO₃) and higher CO₂ concentrations could impair their ability to calcify. The Price Equation Model will help us understand the quantitative contribution of evolutionary and ecological adaptation to ocean acidification

Joachim Hermisson

Evolutionary Rescue: How to adapt when you really need it

When a new environmental challenge drives a population towards extinction it can still hope to rescue itself by speedy adaptation. We then have a race between the population dynamics of a population with dwindling size and the evolutionary dynamics, which may create an adaptive "rescue type" just in time. The probability of successful evolutionary rescue depends in interesting ways on the genetics of the rescue type and on the ecological setting. I will discuss, in particular, two factors: i) the role of population structure for rescue and ii) the role of the genetic architecture if rescue depends on adaptation at more than a single locus.

Jasmijn Hillaert

The evolution of an optimal size distribution in food webs

Size is a crucial factor in explaining variation in metabolic rate between individuals. On its turn, metabolic rate interacts with crucial aspects of organisms such as their developmental strategies and dispersal, thereby shaping an individual's life history. Because of the size dependency of both life history and dispersal, we expect habitat fragmentation to induce a strong selection pressure on the mean size and its variance on species associated in food webs. The inclusion of size evolution among- and within species within food webs is thus essential to understand the trait-distribution of species belonging to different trophic levels in spatially structured populations and communities. Such evolutionary responses are then again expected to feedback on food web properties and functioning. Starting from a simple individual-based resource-consumer model we demonstrate how variation in habitat fragmentation affects the optimal size distribution within food webs of incremental complexity. In the future, we hope to validate our results by collecting experimental data.?

Teppo Hiltunen

Studying eco-evolutionary community dynamics with experimental microbial systems

The consumer-resource relationship is central to population biology and evolutionary ecology. Recent research has demonstrated that evolutionary change can happen rapidly and on the same

time scale as ecological processes affecting community dynamics qualitatively. I will present recent experimental data on eco-evolutionary community dynamics obtained with microbial model systems. In addition to focusing on more fundamental role of evolution on ecological community dynamics, I will present work that have more applied value such as how we need to take eco-evolutionary community dynamics into account if we wish to fully understand the antibiotic resistance problem.

Weini Huang

Stochastic dynamics of frequency dependent interactions in species evolution and coevolution

Stochastic approaches lead to a plethora of new properties, reaching from simple extinctions of (sub)populations due to random drift to the stable maintenance of population cycles which could not remain in corresponding deterministic models. These patterns become even richer, if we consider feedback between ecological and evolutionary dynamics. For example, the carrying capacity may change due to interactions of different phenotypes or genotypes, which in return changes the selection pressure on these types and the rate of new types to arise. Here we present our stochastic model about the frequency dependent interactions of those phenotypes/genotypes under demographic fluctuations either in one species or in the context of predator-prey coevolution. Our results show that stochastic fluctuations have a significant impact on the evolutionary outcomes both in small and large populations. In addition, the coevolution of two species can further change the population dynamics and constrain the diversity level, compared with the evolution of a single species.

Thijs Janzen

Trait-based community assembly in savanna trees and cichlid fish

The relative importance of niche-based (e.g., competitive or stress-based) and stochastic (e.g., random dispersal) processes in structuring ecological communities is frequently analyzed by studying trait distributions of co-occurring species. While filtering processes, such as the exclusion of stress-intolerant species from particular habitats, increase the trait similarity between co-occurring species, other processes, such as resource competition, can limit the similarity of co-occurring species. Comparing the observed trait distribution patterns in communities to null expectations from randomized communities (e.g., a draw of the same observed richness from the regional pool) therefore gives a first indication of the dominant process driving community assembly. However, such comparisons do not inform us about the relative contribution of these different processes in shaping community compositions in case of their joint operation (a likely scenario). Using an Approximate Bayesian Computation approach, we have developed a new method that allows inference of the relative importance of dispersal, filtering, and limiting similarity processes for the assembly of observed communities with known species and trait composition. We demonstrate our new method on two very different community datasets, one regarding savanna tree communities sampled along a strong rainfall and fire gradient in a South

African savanna, and the other regarding cichlid fish communities sampled along the shores of Lake Tanganyika, Zambia.

Toni Klauschies

Trait adaptation promotes supersaturated species coexistence

Species can adjust their mean phenotypes in response to selection due to genetic variation or adaptive phenotypic plasticity. We studied the combined influence of the speed and the potential range of trait adaptation on species coexistence in a multi-species predator-prey model with well-established trade-offs. Prey species differ in their maximum growth rate and vulnerability to predation and predator species in their minimum food demands and selectivity for prey items. We show that in the absence of trait adaptation most species got excluded because niche differences did not compensate for species fitness inequality. In contrast, sufficiently large and fast trait adaptation strongly promoted species coexistence by decreasing species-level average fitness differences among species while maintaining sufficient niche differences. Finally, very large trait adaptation yielded unstable species coexistence since niche differences were strongly reduced. Hence, we find an optimum in the potential range of trait adaptation promoting stable species coexistence. Most crucial, we show that trait adaptation may enable supersaturated species coexistence over a wide range of parameters and thus may contribute to resolve the paradox of the plankton. Hence, when aiming for a complete understanding of the relationship between biodiversity and foodweb dynamics we have to account for the ubiquitous intraspecific trait changes and thus flexibility of organisms.

Joachim Krug

Epistasis and genotypic complexity in Fisher's geometric model: Theory and applications

Fisher's geometric model (FGM) was originally introduced to argue that complex adaptations must occur in small steps because of pleiotropic constraints. When supplemented with the natural assumption of additivity of mutational effects on phenotypic traits, it provides a versatile and conceptually simple mechanism for the emergence of genotypic epistasis from the nonlinear mapping of phenotypes to fitness. In recent years FGM has therefore become a standard reference point for the interpretation of experiments on evolutionary adaptation, and as such it illustrates the search for common principles at the interface between theoretical and experimental work in this field. Here I present the results of a recent study of pairwise epistasis between randomly chosen beneficial mutations in a multicellular fungus, which provides support for the predictions of FGM and allows to estimate the model parameters from data. To put these results into context, I then describe theoretical work aimed at clarifying the relationship between genotypic and phenotypic complexity in the model. Somewhat surprisingly, it will be shown that the ruggedness of the genotypic fitness landscapes induced by FGM generally decreases with increasing phenotypic dimensionality. The talk is based on joint work with Sungmin Hwang, Su-Chan Park, Sijmen Schoustra and Arjan de Visser.

Anna-Liisa Laine

Variation in within-host pathogen communities: causes and consequences

Pathogens are prevalent across all ecosystems and they may have strong negative effects on their hosts. Hence, there is a pressing need to understand risks of infection and how these evolve. To date, host-pathogen interactions have been largely viewed within the one host-one parasite framework although in reality the same host may be attacked by a myriad of pathogenic microbes. As molecular tools have become increasingly available for the study of parasites, we now know that a single host individual can support a highly diverse pathogen community. However, remarkably little is known about the factors that determine which pathogens co-occur within the same host individual and how they interact. Theoretically the resulting interaction has been proposed to range along a continuum where at the one end we find superinfection with a single strain gaining dominance of the entire host, and at the other end of the continuum we find coinfection. For a long time the empirical study of disease dynamics under coinfection lagged behind theoretical predictions due to the methodological challenges of directly observing coinfection dynamics. However, given recent developments in sequencing technologies, it is now possible to accurately characterize the true diversity of within host pathogen communities and to quantify how infection dynamics change under co-infection. Moreover, in recent years technological advances have enabled a new class of multivariate models for ecology, with the potential to study correlation patterns across taxa at the same time as studying environmental variables, to tease the two apart to unravel the determinants of within-host pathogen communities. In my talk I will present a case study of within host pathogen diversity, and give an overview of what are the current opportunities and gaps in knowledge in understanding the causes and consequences of variable within-host pathogen communities.

Romana Limberger

Testing for reciprocal effects of competition and adaptation in a deteriorating environment

Adaptation may rescue species from extinction in changing environments. Most experiments that have tested for evolutionary rescue have focused on single species. In nature, however, species are part of diverse communities and species interactions might affect adaptation to environmental change. In a selection experiment with algae species, we tested if adaptation to salt stress affects and is affected by interspecific competition. We propagated monocultures of six algae species at low and gradually increasing salt concentrations and tested for adaptation in terms of monoculture growth rate and of competitive ability. Of the six algae species, the diatom *Nitzschia* and the green alga *Pseudokirchneriella* adapted to high salt conditions in terms of monoculture growth rate. After the selection experiment, we also assembled communities either from low- or from high-salt lines and quantified the changes in species abundances in low- and high-salt assay environments. We found higher persistence of high-salt than low-salt lines in high-salt assays only for *Pseudokirchneriella*, but not for *Nitzschia*, suggesting that adapta-

tion in terms of monoculture growth rate does not necessarily translate in increased competitive ability. For two species we also tested if presence of a competitor during the selection experiment affected adaptation to salt stress. We propagated the green alga *Scenedesmus* and the cyanobacterium *Anabaena* in monocultures and as pair in low and increasing salt concentrations and tested for adaptation in reciprocal transplant experiments after 46 serial transfers. None of the two species adapted to salt stress, neither when growing as monoculture nor as pair during the selection experiment. However, salt history affected competitive ability of *Anabaena*, with high-salt lines of *Anabaena* having reduced competitive ability in benign conditions.

Luisa Listmann

Eco-Evolutionary Dynamics in competing marine phytoplankton communities

In a community, responses to an environmental stressor (e.g. ocean acidification) can act on different levels. These levels include changes in the species composition (ecological processes), genotypic composition (evolutionary processes) and phenotypic plasticity. In recent years it has been shown that the evolutionary and ecological processes involved in shaping communities can act on similar time scales and can thus interact with each other. Phytoplankton species represent optimal candidates to work with in eco-evolutionary experiments they have short generation times, they can be cultured and their ecology for many species has been well described. To disentangle the eco-evolutionary dynamics in a competing marine phytoplankton community we work with two different species including *Emilinia Huxleyi* (coccolithophore) and *Chaetoceros affinis* (diatom). The different species are kept under controlled experimental conditions and their response to ocean acidification in a competing environment will be assessed. We expect that under high CO₂ conditions the diatoms will be less affected compared to the coccolithophores. Coccolithophores are calcifiers (their liths contain CaCO₃) and higher CO₂ concentrations could impair their ability to calcify. The Price Equation Model will help us understand the quantitative contribution of evolutionary and ecological adaption to ocean acidification

Wolfram Moebius

Spatial expansions of populations in heterogeneous environments

The invasion of a new territory by a population is a transient process that is characterized by an advancing population front and leaves its footprints in the populations genetic structure. We here study the effects of finite-sized regions with poor growth conditions on the population fronts dynamics and on the genetic diversity at the front as well as in the established population. We address this problem using a bottom-up approach, focusing on the shape of the population front in simplified geometries. A combination of experiments, theory, and simulation allows us to gain insight into the front dynamics and evolutionary dynamics. Specifically, we use a model system in which bacteriophage T7 spreads on a lawn of *E. coli*, which includes patches

of resistant *E. coli* posing obstacles for plaque growth. Defined obstacles can be created using a printing assay, which helps us to study the front dynamics quantitatively. The front dynamics has a pronounced effect on the genetic composition of the population; using an *E. coli* model and stochastic simulations, we describe an effect of geometry-enhanced genetic drift, complementary to founder effects occurring in the presence of spatial bottlenecks. Based on these findings, we are making and testing predictions for environments with many obstacles, focusing on front speed as a function of obstacle size and density. In addition, we will outline how experiments with phage T7 may help understand the evolutionary dynamics in these complex environments.

Bogna Pawlowska

Quantitatively Defined Spatial Structure Explains the Relationships between Population Density and Cooperation

How cooperative behaviour evolves and is maintained remains a central question in evolutionary biology. The essence of the problem is the following: how can a group of individuals that engage in cooperative behaviour resist invasion by cheats, who do not pay the cost of cooperation but still reap the reward? It has recently been recognised that microorganisms display an impressive spectrum of cooperative behaviours contributing to important functions such as food acquisition, evasion of host immunity and antibiotic resistance, to name a few. We know that ecology of the environment (spatial structure and resource availability) and population demography (size) profoundly affect microbial cooperation. However no consistent relationship between population demography and cooperation has yet emerged. We hypothesise that this is due to differences in the way ecology of the environment is considered in empirical studies. We test this hypothesis by developing a flexible theoretical framework in which ecology and population demographics can be systematically manipulated. This uncovers a complex range of scenarios that favour cooperation, capable of reconciling previous conflicting results from the literature. Having a simple and consistent measure of spatial structure within is key to understanding a complex interplay between ecology and demographics and their effects on cooperation.

Jorge Peña

Waiting for volunteers: endogenous group formation and the evolution of public goods provision

Game-theoretic models of the evolution of cooperation often assume that group size is constant or that its distribution is fixed. However, in many natural systems group formation can be endogenous in a way that the group size distribution depends on the level of cooperation in the population. Examples include social microbes producing adhesive proteins, bark beetles attacking host trees, burying beetles preparing and burying carcasses, and social carnivores participating in collective hunting or confrontational scavenging. Here, we explore the evolutionary consequences of endogenous group formation in a volunteer's dilemma. In our model, individ-

uals are sequentially recruited by focal groups until the critical number of cooperators needed to provide the collective good is reached. Our rule of group formation generates predictions that are in stark contrast to those resulting from the standard volunteer's dilemma. In particular, protected polymorphisms are impossible and the invasion barrier for cooperator mutants is less severe at sufficiently low cost-to-benefit ratios. Our results highlight the importance of explicitly accounting for endogenous processes of group formation in social evolution.

Yuriy Pichugin

Model of the decoupling between cell and group fitness

The evolution of multicellular life forms from unicellular types requires that collectives acquire Darwinian properties such that they can participate directly even if only marginally in the process of evolution by natural selection. When this occurs, the fitness of collectives stands to decouple from (become independent of) the fitness of cells. The kinds of selective regimes that facilitate this decoupling are unclear. Here, we describe a multi-level selection model based on the experimental study of Hammerschmidt et al (Nature, 2014) that allows investigation into the effects of different selection regimes. We show that fitness decoupling is likely to occur when cells and collectives manifest traits that allow selection to work in an orthogonal manner at the level of cells and collectives.

Philippe Remigi

Lineage selection and the evolution of cancer

Cheat-suppressing mechanisms in metazoans are complex adaptations. Of particular importance are mechanisms of development that control cell growth and limit, through apoptosis, opportunities for unchecked proliferation; also important are mechanisms that confer capacity to distinguish self from other and to effect punishment against rogue types. Additional developmental mechanisms limiting conflicts and suppressing possibilities for cheating, include reproduction via a single-cell bottleneck and germ line sequestration. Our current efforts are focused on understanding how such mechanisms evolve, and the selective causes for their evolution. During the earliest stages in the evolution of multicellularity, concomitant with manifestation of Darwinian properties at the level of nascent collectives, selection began to shift focus to the higher (collective level). Of the many consequences, the fitness of lower level units became increasingly aligned with that of the collective. Mechanistically this likely involved the emergence of developmental mechanisms controlling cell division and suppressing the opportunity for selection at the lower (cell) level to disrupt the collective. I will describe a project designed to test this hypothesis using bacterial populations. In a previous experiment, simple cooperating lineages of bacteria were propagated under a selective regime mimicking primitive life cycles, which rewarded collective-level fecundity. Selection fostered fitness decoupling between collectives and individual cells: although evolved bacterial strains had a slower growth rate (individual-cell fitness), their ability to form stable collectives and to cycle through the

selection regime increased. This adaptive behaviour at the collective level was dependent on lineage selection acting at the time scale of life cycles. Adaptation to life cycles was also associated with an elevated mutation rate, which is expected to generate tensions between the fitness of cells and collectives, via the evolution of cancerous cell types. Using a combination of theory and experiments, we will investigate the selective conditions that we predict have favoured the evolution of developmental mechanisms controlling the proliferation of single cells. Additionally, we have incorporated into the project an experimental test of an idea to explain Petos paradox, namely, that selection acting at the level of nascent multicellular organisms may have driven the evolution of cancer-suppressing mechanisms in a size-dependent manner.

Claus Rueffler

A general condition for adaptive genetic polymorphism in temporally and spatially heterogeneous environments

Both evolution and ecology have long been concerned with the impact of environmental variability on levels of diversity. We model the evolution of a quantitative trait under selection that fluctuates in both space and time, and derive an analytical condition for when these fluctuations promote genetic diversification through adaptation to different environmental conditions. As ecological scenario we use a generalized island model with soft selection within patches in which we incorporate generation overlap. We allow for arbitrary fluctuations in the environment including spatio-temporal correlations. Using the concepts of invasion fitness and evolutionary branching, we derive a simple and transparent condition for the adaptive evolution and maintenance of genetic diversity. This condition relates the strength of selection within patches to expectations and variances in the environmental conditions across space and time. Our results unify, clarify, and extend a number of previous results on the evolution and maintenance of genetic variation under fluctuating selection. Individual-based simulations show that our results are independent of the details of the genetic architecture and whether reproduction is clonal or sexual. The onset of increased genetic variance is predicted accurately also in small populations in which alleles can go extinct due to environmental stochasticity.

Thomas Scheuerl

Evolutionary dynamics of diverse bacterial communities in nature

A key challenge to understand future ecosystem function and services is how natural selection drives evolution in multi species communities. A broad range of studies inform us how single species evolve in response to various environmental selection pressures. However, nature is usually infinitely more complex and species are embedded within many other species with which they interact while struggling with the abiotic environment. How does interaction within communities affect species evolution in new environments and what is the effect of this on the ecosystem? To understand how evolution and natural ecological complexity might play in concert it is necessary to conduct experiments investigating species embedded in natural

communities. Here we present an experiment using 22 common bacterial isolates embedded in 9 different natural bacterial communities and follow evolutionary changes over a six month period. We show how selection responses of seven different traits, spanning morphological and physiological characters, are depending on biotic interactions and shifts in community structure. These data give deep insight how important naturally common species evolve in response to a broad range of ecological interactions. Our data will allow prediction of ecosystem responses when selection is amended by biotic interaction under abiotic disturbance.

Sijmen Schoustra

Microbial ecology of Zambian fermented products: evolution of microbial communities

Analogous to well-known fermented products such as yoghurt, wine, beer and sauerkraut, Zambia has many endogenous fermented products. The fermentation processes are ancient and result in safe products with an increased nutritional value and an increased shelf life than the raw materials. The microbiology of fermentation in these traditional foods is largely unknown and represents an outstanding opportunity for addressing both fundamental and practical questions of wide concern and is very suitable for a thesis project. In particular, why are the microbial communities in these fermented products so stable and what mechanisms prevent the invasion of novel strains such as pathogenic bacteria. These questions represent long-standing issues in community ecology and evolutionary biology, namely, what makes natural microbial communities both diverse and stable over the long-term. I will present results on the species composition and community dynamics of field sampling and laboratory (experimental evolution) results.

Hinrich Schulenburg

C. elegans as a model host to study microbe community evolution

Multicellular organisms are usually host to a species- and individual-rich microbial community. Host and its microbiota often influence one another's fitness and may act as a unit of selection during evolution. Even though there is accumulating evidence on the multifaceted interactions between host and microbiota, it is less clear whether these associations really form a unit of selection. What is needed is a versatile experimental system, which allows us to test the theoretical predictions and particularly the evolutionary importance of such associations - both at the level of the microbial community alone and also its interaction with the host. During my presentation, I will highlight the nematode *C. elegans* as a powerful host system for such an experimental approach, as it can be easily used in evolution experiments in combination with molecular and phenotypic characterizations of the interaction. I will provide examples from our own work and also that of others, showing the insight gained on microbe evolution and host-microbe dynamics.

Arne Traulsen

Modeling the evolutionary dynamics of cancer

The somatic evolution of cancer is an example where predictive models are desirable. Typically, such dynamical models require dynamical data as input. This kind of data is difficult and sometimes even be impossible to obtain. Collaboration between cancer biologists and theorists requires long term efforts from both sides. I will discuss three examples of collaborations in this context: In the first one, the theoretical input is miniscule, but the result can be of crucial interest. In a second project, we show additional insight can be obtained from the combination of dynamical models and data. In a third project, an example will be given where dynamical data is no longer required and a single snapshot is sufficient to estimate the parameters of the model.

Noemi Woltermann

The shape of trade-offs for eco-evolutionary dynamics

Although the patterns and processes that underlie population and community dynamics have been studied extensively over the past decades, we still do not fully understand what general mechanisms drive the dynamics observed in nature and how we can explain variation. In the interplay of trait variation within a population and population dynamics in ecological systems, trade-offs have been observed as playing a crucial role. A common trade-off observed in planktonic systems is between being defended against predation and growth rate. This phenomenon has been studied also in respect of eco-evolutionary dynamics. We want to enhance the understanding of trade-offs in this system by looking at the role of different shapes of trade-offs theoretically and experimentally. Hereby we want to understand how, in an ecological time-frame, the shape of a trade-off influences eco-evolutionary dynamics in a predator-prey system.

Meike Wittmann

Rapid evolution facilitates regional coexistence of species engaged in local priority effects

Early-arriving species at a habitat patch often have an advantage over later-arriving species and can exclude them from the patch. Such priority effects can temporarily enhance beta diversity by promoting community divergence, but eventually cause regional extinctions and reduce gamma diversity. Previous research suggests that such systems are stable only if species are continuously supplied from an external species pool or a spatial refuge, often an unrealistic assumption. Here we argue that rapid evolution may allow regional species coexistence despite local priority effects. Using simple metacommunity models, we show that species engaged in priority effects via habitat modification can coexist regionally if sensitivity to habitat modification evolves under a trade-off with competitive ability. Because resistance is costly, regionally common species tend to become sensitive to heterospecific habitat modification and thereby allow rare species to recover. This eco-evolutionary buffering of rare species appears especially

likely when many small communities are connected by infrequent dispersal.

5 List of participants

Abou Chakra, Maria	abouchakra@evolbio.mpg.de
Auld, Stuart	s.k.auld@stir.ac.uk
Ayan, Goekce	ayan@evolbio.mpg.de
Bailey, Susan	susan.f.bailey@gmail.com
Becks, Lutz	lbecks@evolbio.mpg.de
Bell, Thomas	thomas.bell@imperial.ac.uk
Bernardes, Joana	bernardes@evolbio.mpg.de
Bertels, Frederic	frederic.bertels@gmail.com
Bisschop, Karen	karen.bisschop@ugent.be
Boettcher, Marvin	boettcher@evolbio.mpg.de
Boynton, Primrose	pboynton@evolbio.mpg.de
Bumann, Silke	s.bumann@evolbio.mpg.de
de Visser, Arjan	arjan.devisser@wur.nl
del Arco, Ana	anadelarco@ugr.es
Ehrlich, Elias	eehrlich@uni-potsdam.de
Evans, Rachael	re638@york.ac.uk
Gaedke, Urusla	gaedke@uni-potsdam.de
Gallie, Jenna	gallie@evolbio.mpg.de
Gokhale, Chaitanya	gokhale@evolbio.mpg.de
Greig, Duncan	d.greig@evolbio.mpg.de
Gruber, Heike	gruber@evolbio.mpg.de
Hammerschmidt, Katrin	khammerschmidt@ifam.uni-kiel.de
Harrison, Ellie	ellie.harrison@york.ac.uk
Hattich, Giannina	ghattich@geomar.de
Hermisson, Joachim	joachim.hermisson@univie.ac.at
Hillaert, Jasmijn	jasmijn.hillaert@ugent.be
Hiltunen, Teppo	teppo.hiltunen@helsinki.fi
Huang, Weini	huang@evolbio.mpg.de
Janzen, Thijs	janzen@evolbio.mpg.de
Klauschies, Toni	tklausch@uni-potsdam.de
Krug, Joachim	krug@thp.Uni-Koeln.DE
Laine, Anna-Liisa	anna-liisa.laine@helsinki.fi
Limberger, Romana	romana.limberger@eawag.ch
Listmann, Luisa	llistmann@geomar.de
Moebius, Wolfram	wolfram.moebius@gmail.com
Pawlowska, Bogna	Bogna.Pawlowska@exeter.ac.uk
Peña, Jorge	pena@evolbio.mpg.de
Pichugin, Yuriy	pichugin@evolbio.mpg.de
Remigi, Philippe	p.remigi@massey.ac.nz
Rueffler, Claus	claus.rueffler@ebc.uu.se
Schenk, Hanna	schenk@evolbio.mpg.de
Scheuerl, Thomas	t.scheuerl@imperial.ac.uk
Schoustra, Sijmen	sijmen.schoustra@wur.nl
Schulenburg, Hinrich	hschulenburg@zoologie.uni-kiel.de
Sieber, Michael	misieber@uni-potsdam.de
Theodosiou, Loukas	theodosiou@evolbio.mpg.de
Traulsen, Arne	traulsen@evolbio.mpg.de
Wittmann, Meike	meike.wittmann@univie.ac.at
Woltermann, Noemi	woltermann@evolbio.mpg.de