Annual Report 2017

cbd
CENTRE FOR BIODIVERSITY DYNAMICS

Norwegian Centre of Excellence

NTNU – Trondheim
Norwegian University of Science and Technology

CBD IN SHORT

The aim of CBD is to produce research that will improve our ability to predict how changes in the environment, e.g. caused by human activities, affect the biological diversity at different organismal levels (gene, species and community). Our vision is to identify general principles and patterns which can be used to explain variation in biological diversity based on some basic properties of the systems. We will achieve this goal by a cross-disciplinary approach that integrates model development (focusing on stochastic effects), in-depth analyses of the dynamics of biological diversity in time and space in carefully selected study systems appropriate for examining model predictions and comparative analyses of extensive data sets.

CBD is organized into three research areas: (1) population ecology, (2) evolutionary biology, and (3) community dynamics. The overall approach is to implement stochastic models of single-species population dynamics into theories describing phenotypic evolution and community dynamics in fluctuating environments.

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COVER PHOTO:
The moose project on the island Vega is one of several long-term projects at CBD.
The picture shows a six year old bull, which is among the oldest bulls alive in the study area.
Photo: Endre Grüner Ofstad

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COMMENTS FROM THE DIRECTOR:
FIVE MORE YEARS OF EXCEPTIONAL RESEARCH

Bernt-Erik Sæther
Director CBD

In 2017, there was a considerable focus on the Midterm Evaluation of CBD. This was natural because the outcome of this evaluation would in practice decide whether the funding would continue during the last period of the centre, June 1 2018–May 31 2023. Fortunately, the evaluation committee gave CBD the highest score: exceptional. Consequently, the Steering Board of the Research Council of Norway decided on November 2 2017 to extend the funding also for the last period.

An important advantage of such a review is that it provides an external and objective perspective on the scientific activity at the centre. I am quite sure that in this case, everyone involved in running or steering CBD found the input from the evaluation committee very useful. I think the most important message from the evaluation committee was that the blending between biology and mathematical sciences – which is the core content of CBD – enables us to address questions in the international forefront of research. More importantly, the committee supported and encouraged further integration of the three Research Areas (Population Ecology, Evolutionary Biology and Community Dynamics). The committee even suggested that the quantitative approach characterizing most research at CBD had such high level of innovation and usefulness that CBD should take actions to develop into an international hub for education of researchers, to use such approaches in biodiversity

research. Furthermore, the committee suggested that the potential for obtaining groundbreaking results was especially high in the interface between evolutionary biology and community ecology. We found these and other recommendations from the committee very useful and started during the fall to implement them into actions.

As an example of this improved integration, I would like to highlight the studies of Opedal et al., who showed that herkogamy (the physical separation between male and female organs in hermaphroditic flowers), was able to genetically track selective optima defined by the pollinator reliability at a small geographical scale. This study really illustrates the importance of considering trophic interactions to fully understand evolutionary responses to changing environment.

A striking feature of the research published by the members of CBD during 2017 is that they reveal stronger integration between the different researcher groups at the centre. Most papers have now co-authors that belong to different research groups and a large part of them includes co-authors from more than one of the three research areas.

In 2017, researchers at CBD were awarded funding by the Research Council of Norway (RCN) for three new projects. In the call for free projects (FRIMEDBIO), the project *"Community dynamics in a rapidly warming high Arctic: trophic synchrony in time and space"* lead by researcher Brage Bremset Hansen was funded. Furthermore, the house sparrow project at the coast off Helgeland will be continued through the new project *"Spatial differentiation of a bird metapopulation: quantifying eco-evolutionary dynamics in space"* to the Director. Finally, researcher Geir H. Bolstad, NINA, was awarded a grant as Young Researcher Talent for the project *"The effects of life history genes on eco-evolutionary dynamics"*. I would also like to highlight PhD candidate Thomas Haaland, who received an Honorable Mention for the 2017 Student Paper of the Year award from *The American Naturalist*, which is one of the highest rated international journals in evolution and ecology.

Researchers at CBD have a large network of collaborators at other research institutions, both nationally and internationally. An important facilitator of this collaboration has been the project SUSTAIN (www.sustain.uio.no), which is a large integrated project funded by the Research Council of Norway. In this project, CBD is one of three principal nodes (the two other are the Centre for Ecological and Evolutionary Synthesis, University of Oslo, and the Department of Arctic and Marine Biology, UiT Arctic University of Norway). In January 2017, CBD organized its Second Annual Conference, in which 43 persons participated. As a part of the SUSTAIN project, researchers at CBD have stayed longer periods at other institutions both in Norway and abroad. Correspondingly, several SUSTAIN researchers from other institutions visited CBD. In my opinion, this project has been successful in building up interactions and collaborations, especially among Norwegian ecologists at early stages of their scientific career.

A more recent collaborator of CBD is the Norwegian Institute for Bioeconomy Research (NIBIO), specifically their research group on Landscape and Biodiversity. One outcome of this collaboration is that CBD is partner in the RCN–funded project *"The flowers and the bees – Solutions and tools for integrated sustainable planning to safeguard biodiversity in urban landscapes"*. The project is led by NIBIO and starts in early 2018. CBD is also collaborating with NIBIO on a PhD project related to spatial and temporal patterns of biodiversity.

On October 30 – November 2 2017, CBD organized the Eighth International Hole–Nesting Birds Conference (324 participants), as well as two international workshops. Such occasions have shown to be important for developing CBD's international links, especially among younger people in the beginning of their scientific career.

On September 1st 2017, the new dean for the Faculty of Natural Sciences, Øyvind Gregersen, became the leader of the Steering Board of CBD. On behalf of CBD, I would like to thank the former leader Anne Borg for all help and support during the crucial first period of the centre. In addition, I am grateful to CNRS research director, Ophélie Ronce, for accepting to be member of the Scientific Advisory Committee.

In 2017, professor Gunilla Rosenqvist, decided to leave CBD for a new position in Sweden. In addition to her research and teachning activities at all levels at the Department of Biology, Professor Rosenqvist was part of the CBD leader group. I strongly regret, but understand her decision. However, her great efforts to make CBD a socially well-functioning unit and in particular into rapidly integration of new members will be badly missed. However, I can promise her that genderequality issues will still be a major focus for the leadership of CBD.

Field work in an insular metapopulation of water voles (*Arvicola amphibicus*), off the coast of Helgeland.

MANAGEMENT

AND ADMINISTRATION:

THE LEADER GROUP

Bernt-Erik Sæther
Director
Professor

Steinar Engen
Deputy Director
Professor

Gunilla Rosenqvist
Professor
IBI

Ivar Herfindal
Leader, Research Area 1,
Researcher
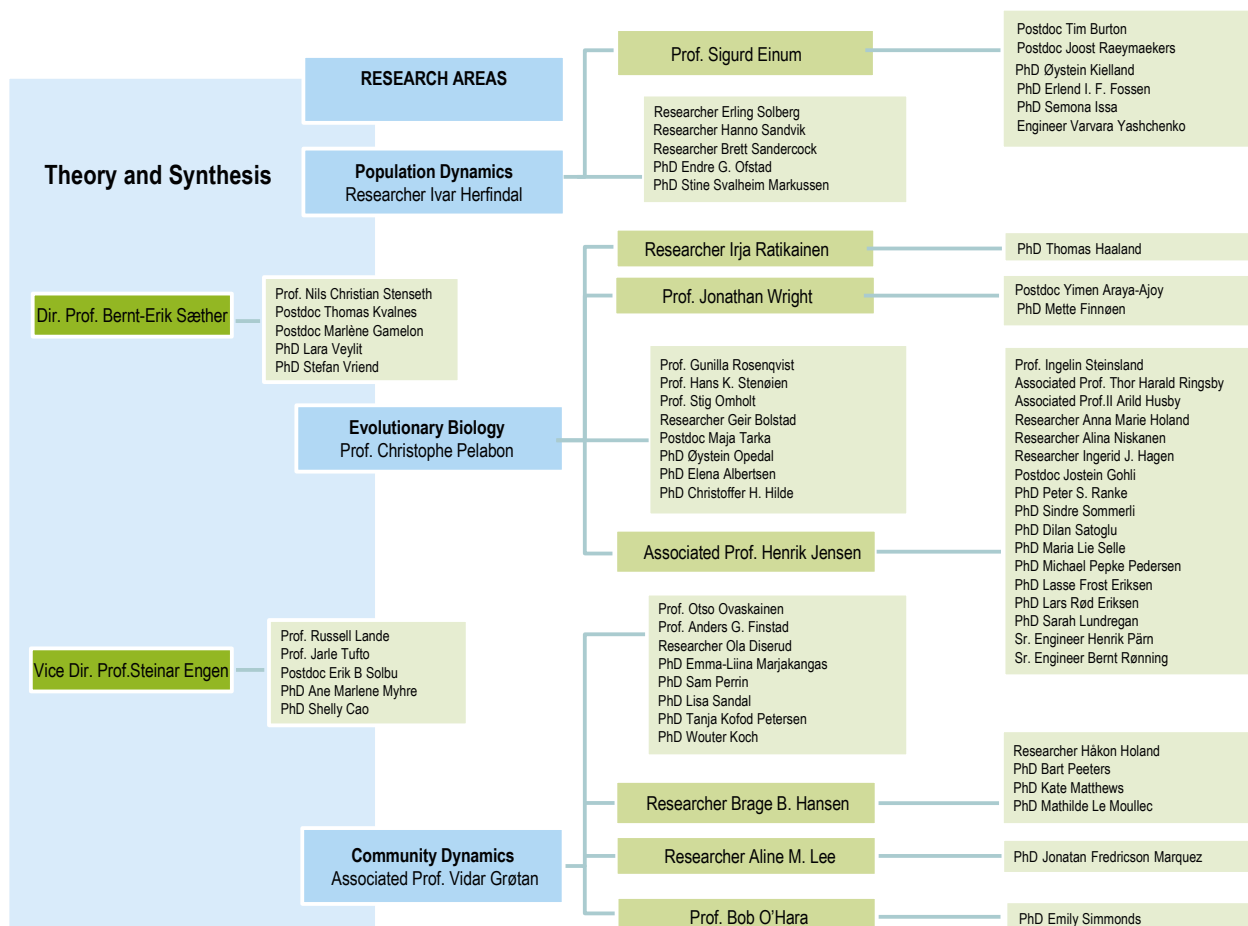
Christophe Pélabon
Leader, Research Area 2,
Professor

Vidar Grøtan
Leader, Research Area 3,
Associated Professor

Solveig Johnsen
Centre Coordinator

ORGANIZATIONAL CHART 2017

Theory and Synthesis

RESEARCH AREAS

Prof. Sigurd Einum
- Postdoc Tim Burton
- Postdoc Joost Raeymaekers
- PhD Øystein Kielland
- PhD Erlend I. F. Fossen
- PhD Semona Issa
- Engineer Varvara Yashchenko

Population Dynamics
Researcher Ivar Herfindal
- Researcher Erling Solberg
- Researcher Hanno Sandvik
- Researcher Brett Sandercock
- PhD Endre G. Ofstad
- PhD Stine Svalheim Markussen

Dir. Prof. Bernt-Erik Sæther
- Prof. Nils Christian Stenseth
- Postdoc Thomas Kvalnes
- Postdoc Marlène Gamelon
- PhD Lara Veylit
- PhD Stefan Vriend

Researcher Irja Ratikainen
- PhD Thomas Haaland

Prof. Jonathan Wright
- Postdoc Yimen Araya-Ajoy
- PhD Mette Finnøen

Evolutionary Biology
Prof. Christophe Pelabon
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- Prof. Hans K. Stenøien
- Prof. Stig Omholt
- Researcher Geir Bolstad
- Postdoc Maja Tarka
- PhD Øystein Opedal
- PhD Elena Albertsen
- PhD Christoffer H. Hilde

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- Prof. Ingelin Steinsland
- Associated Prof. Thor Harald Ringsby
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- Researcher Anna Marie Holand
- Researcher Alina Niskanen
- Researcher Ingerid J. Hagen
- Postdoc Jostein Gohli
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- PhD Michael Pepke Pedersen
- PhD Lasse Frost Eriksen
- PhD Lars Rød Eriksen
- PhD Sarah Lundregan
- Sr. Engineer Henrik Pärn
- Sr. Engineer Bernt Rønning

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- Prof. Jarle Tufto
- Postdoc Erik B Solbu
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- PhD Shelly Cao

- Prof. Otso Ovaskainen
- Prof. Anders G. Finstad
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- PhD Emma-Liina Marjakangas
- PhD Sam Perrin
- PhD Lisa Sandal
- PhD Tanja Kofod Petersen
- PhD Wouter Koch

Researcher Brage B. Hansen
- Researcher Håkon Holand
- PhD Bart Peeters
- PhD Kate Matthews
- PhD Mathilde Le Moullec

Community Dynamics
Associated Prof. Vidar Grøtan

Researcher Aline M. Lee
- PhD Jonatan Fredricson Marquez

Prof. Bob O'Hara
- PhD Emily Simmonds

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The Netherlands

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Research director
CNRS
University of Montpellier
France

SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

Current group members:
PI: Professor Bernt-Erik Sæther
Researcher Marlène Gamelon
Postdoc Thomas Kvalnes
PhD candidate Lara Veylit
PhD candidate Stefan Vriend

Aim: *To apply stochastic models to understand processes affecting the dynamics of populations and phenotypes in fluctuating environments.*

Bernt-Erik Sæther, Thomas Kvalnes and Marlène Gamelon. Not present Lara Veylit and Stefan Vriend.

The focus of this research group is to perform comparative analyses on larger data sets to examine how differences in life history affect population dynamics. Furthermore, this research groups aims to find the most appropriate study systems for parameterizing ecological and evolutionary models in all three RAs, which involves developing and maintaining a substantial network of international collaborators.

Research Area 1 Population ecology

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Major scientific contributions

The effects of expected changes in climate on the population dynamics of dipper

In collaboration with researcher at the Centre for ecological and Evolutionary Synthesis (CEES) at the University of Oslo we have analysed how the pattern in the population fluctuations of the dipper will be altered by the expected changes in climate. One of the major challenges is to account for the combined effects of density dependence and age-structure as well as density dependent influences of climate on the population growth rate. We therefore used this unique long-term time series to build an Integrated Population Model, which enables us to include age-dependent climate effects as well as density dependence. Although warmer winters were associated with an increase of the mean size of the breeding population, density-dependent climate effects reduced the buffering capacity of the populations because cold winter weather occurring at high densities could cause severe reduction in population size. This illustrates the importance of using demographic models when predicting long-term ecological consequences of climate change.

r- and K-selection in age-structured populations

Density dependence plays an important role in regulation of the size of most natural populations. In order to integrate ecological dynamics with evolutionary processes, we focused on identifying whether density-dependent effects on the population dynamics affect the rate of phenotypic evolution. This is a major question in RA2. Lande et al. (2017) was able to show by analysis and simulation of age-structure that the stochastic dynamics of population size can be accurately approximated by a univariate model governed by three key demographic parameters: the intrinsic rate of increase and carrying capacity in the average environment, r and K, as well as the environmental variance in population growth rate. Including evolution in these three parameters, a new evolutionary maximization criteria was derived. An important implication of this result is that the magnitude of environmental stochasticity governs the classical tradeoff between selection for higher r versus higher K. However, selection also acts to decrease environmental stochasticity so the simple life-history tradeoff between r- and K-selection may be obscured by additional tradeoffs between them and environmental stochasticity. Under the classical logistic model of population growth with linear density dependence, life-history evolution in a fluctuating environment tends to maximize the average population size.

RECOMMENDED READING:

Gamelon, M., Grøtan, V., Nilsson, A.L.K., Engen, S., Hurrell, J.W., Jerstad, K., Phillips, A.S., Røstad, O.W., Slagsvold, T., Walseng, B., Stenseth, N.C. and Sæther, B.-E. 2017. Interactions between demography and environmental effects are important determinants of population dynamics. Science Advances 3, e1602298.

Lande, R., Engen, S. and Sæther, B.-E. 2017. Evolution of stochastic demography with life history tradeoffs in density-dependent age-structured populations. Proceedings of the National Academy of Sciences of the United States of America 114, 11582–11590.

Research Area 1 Population ecology

Research group: Eco-evolutionary dynamics

Current group members:
PI: Professor Sigurd Einum
Postdoc Joost Raeymaekers
Postdoc Tim Burton
PhD candidate Øystein N. Kielland
PhD candidate Semona Issa
PhD candidate Erlend I. F. Fossen
Engineer Varvara Yashchenko

Aim: *To improve understanding of links between ecological and evolutionary responses to environmental change through lab-based experimental approaches.*

Photo: Per-Harald Olsen
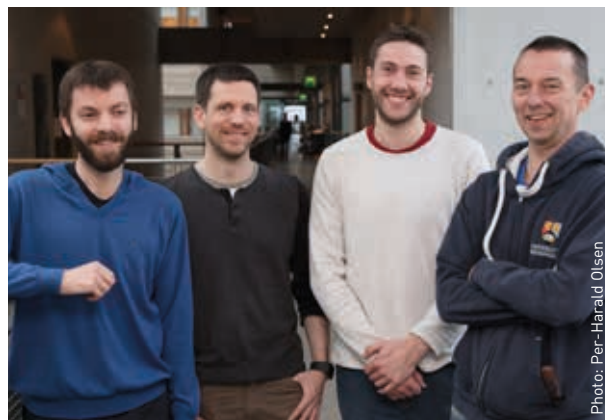
Erlend I. F. Fossen, Joost Raeymaekers, Øystein N. Kielland, Sigurd Einum.
Not present: Tim Burton, Semona Issa and Varvara Yaschenko.

Major scientific contributions

Our group has had a number of topics of interest during 2017. First, we have continued our work on characterizing within–population genetic variation in thermal reaction norms of various phenotypic traits as well as for population dynamic parameters. This is a topic that has received considerable efforts in our lab over the last few years, and the empirical work was to a large extent completed in 2017. We expect the first papers from this work to be published during 2018.

Second, we have been interested in the so–called temperature–size rule (TSR), i.e. the observation that ectotherms, and particularly aquatic ones, become smaller when developing at high temperatures. One of the most prominent hypothesis explaining this pattern has been that the challenge of obtaining sufficient amounts of oxygen limits ectotherm body size, and that this effect is more pronounced at higher temperatures where oxygen demand is higher. We have attempted to test this hypothesis using a combination of ecophysiological modelling and empirical measurements of metabolic rates and critical oxygen levels. This work is also continuing during 2018.

Third, we have continued method development and data collection on thermal tolerance. This is a trait that we expect is of high importance for ecological and evolutionary responses to the increasingly variable temperatures expected under climate change, and that we will continue to study in years to come. Fourth, through collaboration with ecotoxicologists we have studied how ecological interactions may influence the effects of toxic

substances. Toxicity assessments are usually conducted in highly standardized laboratory conditions, and extrapolating results of such studies to real environments is problematic because these studies overlook the potential for other components in the biotic community to influence the effects of toxins on focal organisms.

Finally, we have initiated the use of paleolimnological methods in our lab, whereby we collect sediment cores from lakes and use these to go back in time and obtain historical data on zooplankton communities. We believe that this will prove to be a very useful approach to quantify community dynamics in response to various environmental drivers. The Daphnia lab had its first PhD student completing in 2017. Øystein Nordeide Kielland successfully defended his thesis "Sources of variation in metabolism of an aquatic ectotherm" in December. Another of our PhD students (Erlend I. F. Fossen) had a 3 month research stay at KU Leuven (Belgium), where collaborative work was conducted to test for local adaptation to temperature by focusing on population dynamics parameters.

RECOMMENDED READING:

Kielland, Ø.N., Bech, C. and Einum, S. 2017. No evidence for thermal transgenerational plasticity in metabolism when minimizing the potential for confounding effects. Proceedings of the Royal Society B: Biological Sciences 284, 20162494.
Kielland, Ø.N., Bech, C. and Einum, S. 2017. Is there plasticity in developmental instability? The effect of daily thermal fluctuations in an ectotherm. Ecology and Evolution 7, 10567–10574.
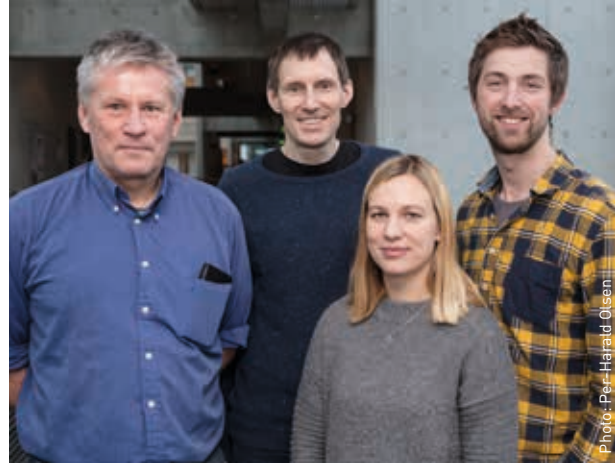
RESEARCH GROUP:
DEMOGRAPHIC RESPONSES TO A CHANGING ENVIRONMENT

Current group members:
PI: Researcher Ivar Herfindal
Researcher Erling J. Solberg
Researcher Hanno Sandvik
Researcher Brett Sandercock
PhD candidate Stine S. Markussen
PhD candidate Endre G. Ofstad

Aim: *To understand causes and consequences of demographic variation in time and space.*

Erling Solberg, Ivar Herfindal, Stine Svalheim Markussen, Endre Grüner Ofstad. Not present: Hanno Sandvik and Brett Sandercock.

Our main focus is related to the fact that individual traits and population properties vary in both time and space. Such variation can be caused by a range of factors, both natural and human-caused, and these factor often show complex interactions in time and space that are important to understand in face of a rapidly changing world. In 2017, the research activity of the group was mainly related to two projects: the Vega moose project, which is funded by the Norwegian Environment Agency, and the SUSTAIN project funded by the Research Council of Norway. The SUSTAIN project (Sustainable harvesting of renewable resources – an integrated approach across ecosystems) is a collaboration between CEES at the University of Oslo, the Arctic University of Norway in Tromsø, and CBD. Both projects have an applied focus in addition to dealing with fundamental ecological questions, and they both have harvesting as the main human influence on populations and species. However, whereas the Vega project perform detailed studies on one single population of moose, the SUSTAIN project involves analyses at larger spatial and ecological scales. Still, these two projects are becoming more and more integrated and it is becoming increasingly evident that a proper understanding of large-scale ecological processes requires detailed individual–based demographic data to constrain the range of variation in critical parameters.

Research Area 1 Population ecology

Major scientific contributions

The demography of harvested populations is a combination of natural variation in individual performance and harvest–induced mortality. Commonly, age– and sex–specific quotas are set based on management goals, e.g. to maximise production of calves, but there may be unexpected and unintentional consequences of such quotas. PhD candidate Stine S. Markussen has investigated the individual variation in vital rates in relation to harvest-induced mortality of male and female moose on Vega. There are persistent individual differences in reproductive performance in both males and females, which are closely related to the age at first breeding. Theoretical work suggests that individual heterogeneity may have population dynamical consequences, but the level of heterogeneity in the Vega moose population does not have any major influences on population properties such as time to extinction (Lee et al. 2017). However, these individual differences in reproduction generate harvest–induced selection. Because of the practice of not shooting cows that are accompanied by calves, the high–reproducing cows had a lower probability to be killed during harvest (Markussen et al. 2017). This generate positive covariation between reproduction and survival, and we are currently investigating how this affects important population properties such as effective population size, N_e. PhD candidate Endre G. Ofstad is relating such differences to behaviour, and particularly individual trade-off between food-rich habitats with a higher harvest mortality, and safer habitats with poorer foraging conditions. Preliminary results suggest that parts of the individual heterogeneity in vital rates of both males and females can be explained by behavioural decisions related to this tradeoff between food and safety.

Within the SUSTAIN project, we have mainly focused on the spatial scale of synchrony of different harvested species. Much of the research is still in progress, but has been presented at the SUSTAIN annual meetings and other workshops and conferences. One example is the spatial synchrony in early-life body mass of moose and domesticated reindeer, two species that are heavily influenced by management and harvesting. In many species, including ungulates, early–life body mass is one of the most sensitive life history traits, and we therefore expect a high synchrony in calf and yearling body mass over large distances corresponding to the high spatial autocorrelation in climate dynamics. However, the synchrony in these traits was surprisingly low. This seems to be caused by population–specific relationships between climate and body mass, where local environmental conditions or density dependence can affect the strength and direction of climate effects on body mass. This causes populations to be desynchronised even over short distances where climate fluctuations is highly correlated. Future research will investigate the role of harvesting on such spatial processes, as harvesting is the main driver of variation in density within and among populations in many wildlife species. Harvesting can therefore affect population synchrony directly (as shown by theoretical work by Steinar Engen and collaborators) and indirectly by affecting the strength of the climate effect on life history traits and population dynamics.

RECOMMENDED READING:

Markussen, S.S., Loison, A., Herfindal, I., Solberg, E.J., Haanes, H., Røed, K.H., Heim, M. and Sæther, B.-E. 2017. Fitness correlates of age at primiparity in a hunted moose population. Oecologia in press.

Lee, A.M., Sæther, B.-E., Markussen, S.S. and Engen, S. 2017. Modelling time to population extinction when individual reproduction is autocorrelated. Ecology Letters 20, 1385–1394.

Research Area 1 Population ecology

RESEARCH GROUP: STOCHASTIC THEORIES

Current group members:
PI: Professor Steinar Engen
Professor Russell Lande
Professor Jarle Tufto
Postdoc Erik Blystad Solbu
PhD candidate/Postdoc Ane Marlene Myhre

Aim: *To develop theories for the dynamics of populations, phenotypes and communities in fluctuating environments.*

This research group works at the interface between all the three RAs. The main approach here has been to extend the models developed to describe ecological dynamics to also include evolutionary processes as well as structural changes within ecological communities. Thus, this research group actively interact with members of most of the other research groups.
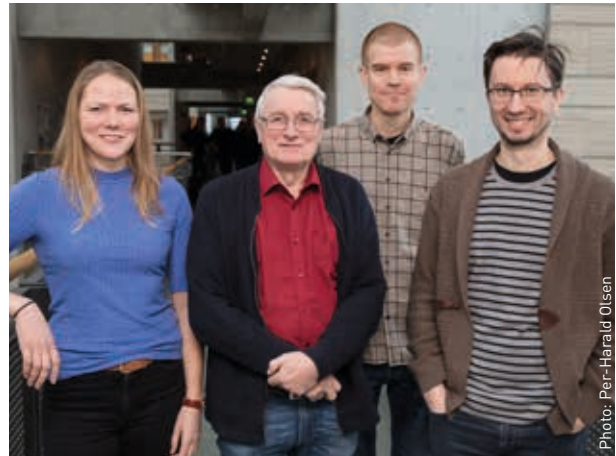
Ane Marlene Myhre, Steinar Engen, Jarle Tufto, Erik Blystad Solbu. Not present; Russell Lande.

Photo: Per-Harald Olsen
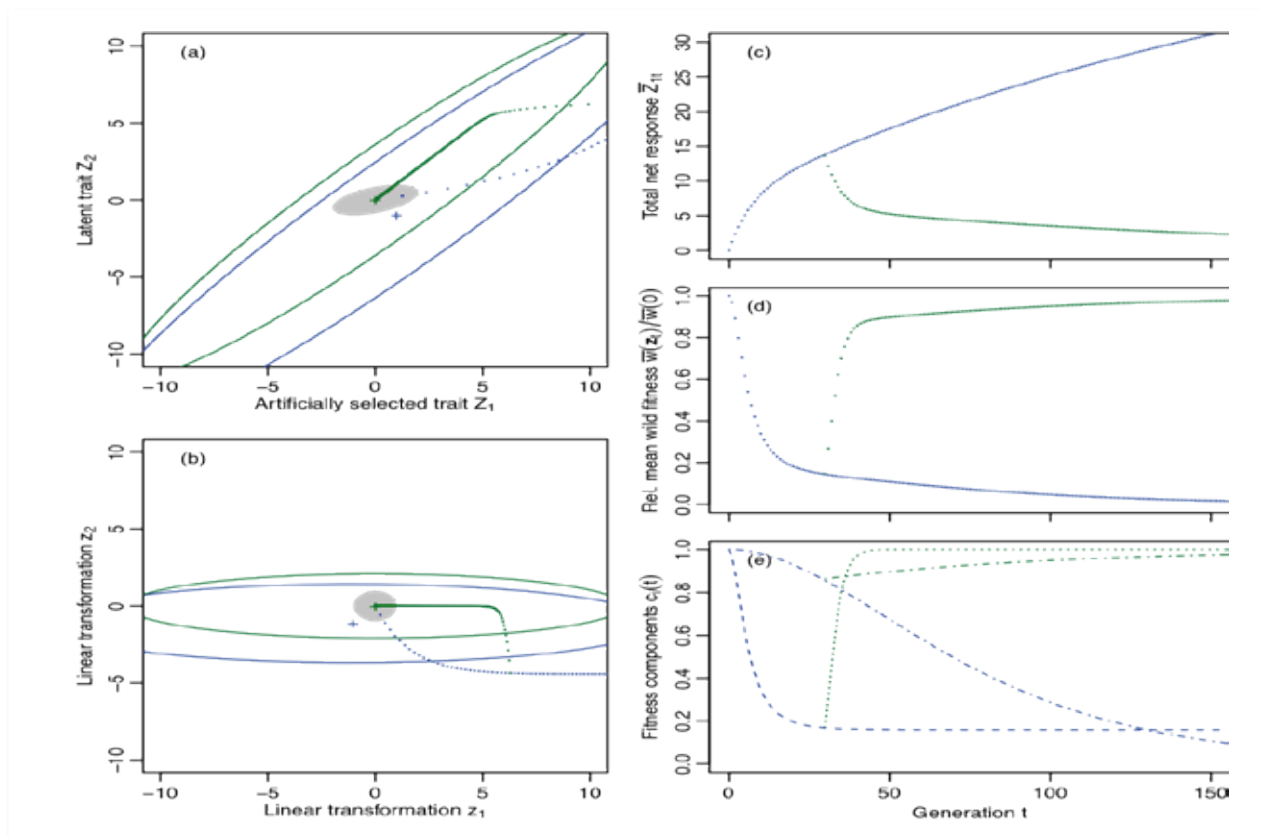
Fig. 1. Trait trajectories and evolution of relative mean population fitness for a bivariate version of the model of fitness cost due to domestication (Tufto et al. 2017).

Research Area 1 Population ecology

Major scientific contributions

Sustainable harvest in a spatially structured environment

As part of CBD's input to the large integrated project SUSTAIN an important focus for the theoretical work has been to develop harvest model for a sustainable exploitation of spatially structured populations. In an age–structured model including two age classes, juveniles and adults, and with density regulation, age–specific dispersal, stochasticity in vital rates and proportional harvesting, Engen et al. (2017) showed how to simulate the joint density fields of the age classes and derive results for the spatial scales of all spatial autocovariance functions for densities. In this model, the optimal harvesting strategy in the deterministic case is to harvest only juveniles when their relative value (e.g. financial) is large, and otherwise only adults. Including fluctuations in the environment change this general result. With increasing environmental stochasticity, there is an interval of increasing length of values of juveniles relative to adults where both age classes should be harvested. Harvesting generally tends to increase all spatial scales of the autocovariances of densities.

Loss of wild fitness during domestication

Farmed Atlantic salmon and other domesticated species continually escaping and interbreeding with wild relatives impose a detrimental migration load on wild populations. As domesticated stocks become increasingly different as a result of artificial and natural selection in captivity, fitness of escapees in the wild is expected to decline, reducing the effective rate of migration into wild populations (e.g. Bolstad et. al. 2017). Recent theory (e.g. Huisman and Tufto, 2012) suggests that this may alleviate and eventually eliminate the resulting migration load. If true, this would of course be good news for the sustainability of the aquaculture industry.

A new theoretical multivariate model (Tufto, 2017) shows that this view is likely to be too simplistic, however. The model considers trait and wild fitness evolution resulting from the joint effects of artificial selection and natural multivariate correlational Gaussian selection in the captive environment. Some alignment between the adaptive landscapes in the wild and in captivity is assumed (Fig. 1a, fitness contours shown as green and blue ellipses, respectively) reflecting the assumption that similar functional constraints and optimization principles are likely to apply in both environments. Initially, the evolutionary trajectory (Fig. 1a, blue dotted curve) is dominated by the effects of artificial selection causing a fast initial decline

in fitness of escapees in the wild (Fig. 1d, blue dotted curve, generations 1-20). In later phases, through the counteracting effects of correlational stabilizing natural selection in captivity (Fig. 1a, blue ellipse), the mean phenotype is pushed in directions of weak counteracting stabilizing selection, allowing a sustained response in the trait subject to artificial selection (Fig. 1c, blue dotted curve). In generally, observable evolutionary changes (Fig. 1c and d) are shown to involve fast and slow phases over different characteristic time scales associated with the strength of stabilizing natural selection acting on a set of decoupled, independently evolving linear transformations (Fig. 1b) of the original traits (Fig. 1a). These phases are associated with slower rates of decline in wild fitness of the domesticated stock (Fig. 1d, generations 20-150), suggesting that escapees are likely to impose a considerable migration load on wild populations in the foreseeable future.

The model also provides novel interpretations of patterns often seen in artificial selection experiments. Typically, a sustained but decelerating response is observed with an initial rapid regression towards the initial mean after relaxation of artificial selection similar to prediction of the current model (Fig. 1c, green dotted curved). Even though a sustained response to artificial selection is often observed, fitness can reach a plateau in some experiments (similar to Fig. 1d, blue curve).

RECOMMENDED READING:

Bolstad, G.H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O.H., Fiske, P., Jensen, A.J., Urdal, K., Næsje, T.F., Barlaup, B.T., Florø-Larsen, B., Lo, H., Niemelä, E. and Karlsson, S. 2017. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nature Ecology & Evolution 1, 0124.

Engen, S. 2017. Spatial synchrony and harvesting in fluctuating populations: Relaxing the small noise assumption. Theoretical Population Biology 116, 18–26.

Huisman, J., and J. Tufto. 2012. Comparison of non-Gaussian quantitative genetic models for migration and stabilizing selection. Evolution 66, 3444–3461.

Tufto, J. 2017. Domestication and fitness in the wild: A multivariate view. Evolution 71, 2262–2270.

Research Area 2 Evolutionary biology

RESEARCH GROUP: EVOLUTIONARY DYNAMICS OF QUANTITATIVE TRAITS

Current group members:
PI: Professor Christophe Pélabon
Professor Gunilla Rosenqvist
Postdoc Maja Tarka
Researcher Geir Hysing Bolstad
PhD candidate Elena Albertsen
PhD candidate Øystein H. Opedal
PhD candidate Christopher H. Hilde

Aim: *Analyse the effects of the genetic architecture of complex characters on their evolutionary dynamics in fluctuating environments.*

This group is testing predictive models for the evolutionary dynamics of quantitative traits in a fluctuating environment, focusing especially on the role of the genetic architecture and evolvability on phenotypic evolution. An important research activity of this group is to assess the theoretical validity of the measurements used in the evolutionary theory. The group has published two papers on the subject in 2017 and organized a workshop on measurements.

Christope Pélabon, Gunilla Rosenqvist, Elena Albertsen, Christoffer Høyvik Hilde, Maja Tarka. Not present: Øystein H. Opedal, Geir H. Bolstad.

Photo: Per-Harald Olsen

Figure 1 *Dalechampia scandens* populations in north-western Costa Rica and their assignment to genetic clusters. The neighbour-joining tree indicates the phylogenetic relationships among the populations, and is colour coded according to the main genetic cluster assigned for each population. This map shows that *D. scandens* populations are largely isolated genetically when more than 20 km apart.
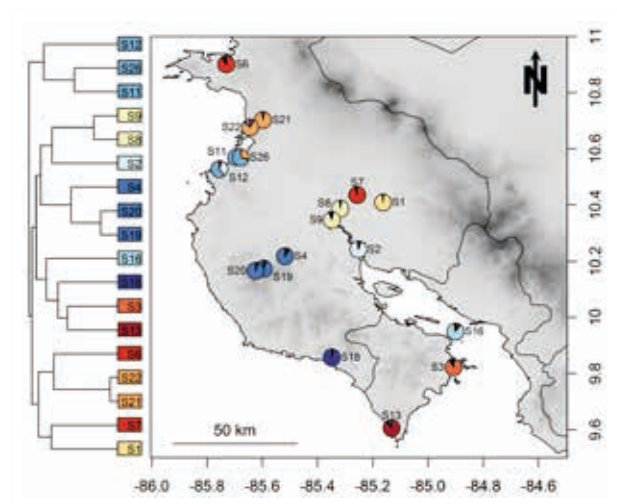
Figure 2 Representation of the concept of adaptive inaccuracy. Relationship between trait values, relative fitness and load assuming the quadratic fitness function $W(z;\theta)/W(\theta;\theta) = 1-s(z-\theta)^2$ in blue. The distribution of trait values (horizontal histogram), with mean given by μ, are transformed into a distribution of relative fitness values (vertical histogram) using the quadratic fitness function with an optimum at trait value θ. The green arrow labelled "At pop. mean" refers to the fitness accrued at the population mean. From Armbruster et al. 2017.

Research Area 2 Evolutionary biology
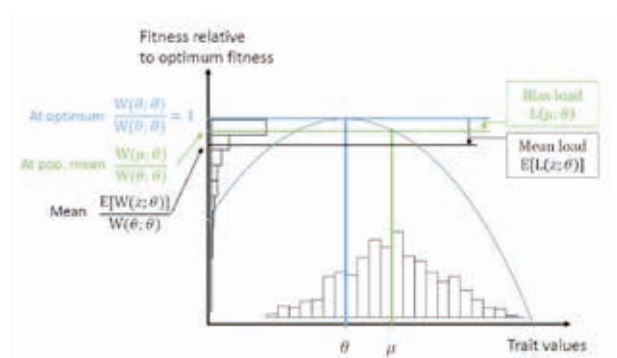
Major scientific contributions

Evolution of flower morphology in a fluctuating environment

Variation in pollinator availability is expected to strongly influence the evolution of herkogamy and dichogamy, the separation in space and time, respectively, between the male and female functions of flowers. Indeed, while herkogamy is beneficial when pollinators are abundant because it favours outcrossing, it becomes detrimental when pollinators become scarce, because it prevents self-pollination and thereby reproductive assurance. By affecting the level of self-fertilization, herkogamy is also expected to affect the genetic structure of the populations and their susceptibility to inbreeding depression. Using *Dalechampia scandens*, a neotropical vine, we have been testing several of these hypotheses. In two publications we have first shown that, contrary to expected, gene flow resulting from pollination by Euglossine bees was limited to certain nearby populations within continuous forest blocks, while long-distance gene was extremely limited. Furthermore, within population, gene flow was biased towards nearby plants (Opedal et al. 2017a, Figure 1). In a meta-analysis with 27 natural populations of 17 species including our own study species, we also showed that herkogamy is a particularly evolvable trait that should rapidly respond to changes in the pollinator environment (Opedal et al. 2017b). These results confirm that the correlation between floral traits promoting autonomous selfing and variation in the pollinator fauna observed among populations of *Dalechampia scandens* in Costa Rica (Opedal et al. 2016) revealed the rapid evolution of herkogamy and that floral traits influencing mating systems can track variation in adaptive optima generated by variation in pollinator reliability.

Measurement theory in evolutionary biology

Measurement is the process by which we assign numbers to attributes of entities so that the mathematical relationship among numbers captures empirical relationships among the attributes of interest. Only appropriate measurements and analyses that respect the nature of the measurements can lead to correct conclusions about the world. While the process of measurement has received a great deal of attention in physics, actual measurement practices in biology frequently falls short of the ideal, leading to incorrect conclusions that can derail fields for years. During the past year, the group has worked on different aspects of measurements in evolutionary biology and more specifically on the importance of scale when measuring functional traits such as heterostyly and herkogamy, two traits particularly important in the evolution of floral plants.

A first important contribution of the group regarding measurement theory in 2017 was the publication of a paper in New Phytologist (Armbruster et al. 2017), where we proposed a new measure of reciprocity (the correspondence of locations of pollen placement on, and stigma contact with, pollinators in heterostylous flowers) based on theory that relates floral morphology to reproductive fitness. This method establishes a scale based on adaptive inaccuracy, a measure of the fitness cost of the deviation of phenotypes in a population from the optimal phenotype (Pélabon et al. 2012). Inaccuracy allows the estimation of independent contributions of maladaptive bias (mean departure from optimum) and imprecision (within-population variance) to the phenotypic mismatch (inaccuracy) of heterostylous morphs on a common scale (Fig. 1). In this contribution, we also show how previous indices of reciprocity have been derived without consideration to the properties of measurements. Although applied to the derivation of an index related to floral traits, this approach is general and can be applied to many traits.

A second important contribution of the group was the organization of the workshop on measurements in biology and medicine (see below).

RECOMMENDED READING:

Armbruster, W.S., Bolstad, G.H., Hansen, T.F., Keller, B., Conti, E. and Pélabon, C. 2017. The measure and mismeasure of reciprocity in heterostylous flowers. *New Phytologist 215*, 906–917.

Opedal, Ø.H., Albertsen, E., Armbruster, W.S., Pérez-Barrales, R., Falahati-Anbaran, M. and Pélabon, C. 2016. Evolutionary consequences of ecological factors: pollinator reliability predicts mating-system traits of a perennial plant. *Ecology Letters 19*, 1486–1495.

Opedal, Ø.H., Falahati-Anbaran, M., Albertsen, E., Armbruster, W.S., Pérez-Barrales, R., Stenøien, H.K. and Pélabon, C. 2017. Euglossine bees mediate only limited long-distance gene flow in a tropical vine. *New Phytologist 213*, 1898–1908.

Opedal, Ø.H., Bolstad, G.H., Hansen, T.F., Armbruster, W.S. and Pélabon, C. 2017. The evolvability of herkogamy: Quantifying the evolutionary potential of a composite trait. *Evolution 71*, 1572–1586.

RESEARCH GROUP: LINKING ECOLOGICAL AND GENETIC DYNAMICS

Current group members:
PI: Associate professor Henrik Jensen
Professor Stig W. Omholt
Professor Ingelin Steinsland
Associate Professor Thor Harald Ringsby
Associate Professor Arild Husby (20 %)
Researcher Ingerid J. Hagen (NINA)
Postdoc Alina Niskanen (Guest researcher from the University of Oulu)
PhD candidate Peter S. Ranke
PhD candidate Sindre L. Sommerli
PhD candidate Dilan Saatoglu
PhD candidate Maria L. Selle
PhD candidate Michael P. Pedersen
PhD candidate Sarah Lundregan
Engineer Henrik Pärn
Engineer Bernt Rønning

Bernt Rønning, Peter Sjolte Ranke, Thor Harald Ringsby, henrik Pärn, Sindre Sommerli, Alina Niskanen, Henrik Jensen, Ingerid J. Hagen.
Not present: Stig W. Omholt, Ingelin Steinsland, Arild Husby, Jostein Gohli, Dilan Saatlogu, Marie Selle Lie, Sarah Lundregan.

Aim: *To improve our understanding of interactions between ecological and genetic dynamics.*

Our research group produces knowledge targeting key questions at the interface between RA1 and RA2. In particular, our goals are to examine how spatiotemporal variation in population dynamics (including the effects of density dependence, environmental stochasticity and dispersal) interact with phenotypic variation and evolutionary dynamics, and the role of genetic variation in these interactions. To achieve our goals we combine state-of-the-art genomic tools with development and application of novel statistical methods to analyse individual–based data on fitness–related phenotypic traits, life history traits, and fitness components. Our main study systems are several intensively studied natural vertebrate metapopulations, including house sparrows, water voles and arctic foxes. We also provide molecular genetic resources and assistance needed by other research groups in all three RAs at CBD. Furthermore, the empirical individual based data on phenotypic traits, fitness, and genetic variation we produce are (1) needed to parameterize and test models developed by other research groups at CBD and (2) attractive for scientists who wish to use our unique data in international and national collaborative projects that test hypotheses and answer questions in various fields in biology.

Figure 1.Release of house sparrows during an artificial selection experiment in northern Norway (Kvalnes et al. 2017; Photo by Henrik Jensen).

Research Area 2 Evolutionary biology

Major scientific contributions

Selection and evolutionary dynamics in natural populations

Understanding how life history characters affect population dynamics (aim of RA1), and how selection may result in evolutionary change in fluctuating environments (aim of RA2) are fundamental goals in evolutionary biology. Using individual data from three of CBD's long-term study populations of house sparrows at the coast of Helgeland, we investigated the evolvability of body size and whether there exists an intermediate phenotype with higher mean individual fitness than more extreme phenotypes across years in a variable environment (Kvalnes et al. 2017). To answer these questions we carried out an eleven-year experiment with four years of artificial selection for large and small body size, respectively. The experiment caused strong selection in the imposed directions, which resulted in significant evolutionary responses at both the phenotypic and genetic levels that closely followed the predicted responses from quantitative genetic theory. However, artificial selection was counteracted by reduced production of recruits in offspring of artificially selected parents. This resulted in weak natural selection against extreme trait values. Consequently, the significant responses to artificial selection were followed by a significant return toward pre–experimental means at both the phenotypic and genetic levels. The results of this study demonstrate that selection may lead to rapid evolution of natural populations in fluctuating environments. Furthermore, we show that natural selection may favour an intermediate phenotype in wild populations. By manipulating the observed link between phenotypes and the environment, such selection experiments in the wild clearly have a great potential to reveal novel insights into adaptive evolutionary dynamics under natural conditions.

Effects of demographic variance on the rate of loss of genetic variation

Knowing what factors affect the distribution of genetic variation within and between populations is important in order to understand evolutionary processes and the viability of endangered populations. The effective population size (Ne) is a key parameter linking RA1 and RA2 because it depends on a population's demographic processes, and determines the rate of loss of genetic variation due to genetic drift and inbreeding. This interaction was the main topic for the thesis brilliantly defended by dr. Ane Marlene Myhre in June 9 2017, after being scrutinized by professor R.S. Waples and dr. Luis-Miguel Chevin.

Using data from CBD's long–term studies of 13 house sparrow populations in the wild, we estimated contemporary Ne, and examined causes for variation in Ne/N ratios between these populations that differed in age–structure, sex ratio, and inter–individual variation in survival and fecundity (Stubberud et al. 2017). Our results draw attention to the applicability of sensitivity analyses in population management and conservation. In addition to being of vital importance in management of endangered populations and species, knowing which demographic processes that affect Ne/N most will improve our understanding of how demography affects evolution through its influence on the interaction between genetic drift and selection.

Effects of translocation on demographic processes

Translocation of individuals to augment small populations facing risk of extinction is an important conservation tool. When translocations are carried out, they are expected to increase the size and reduce any negative effects of inbreeding and genetic drift in the local population. Consequently, translocation should result in higher population growth rate by influencing population dynamics (RA1) as well as genetic dynamics (RA2).

In order to investigate how translocated individuals influence the demography of the population they are introduced to, we carried out an experiment where we translocated house sparrows from one distant metapopulation into another (Ranke et al. 2017). In our experiment, the resident individuals served as a reference to the performance of translocated individuals. We found evidence for assortative mating based on origin, revealed by fewer parentages between translocated males and resident females than expected, and lower total number of fledglings produced by such pairs. The reproductive success of translocated males was positively related to the size of a sexual ornament in males, such that only translocated males with a large ornament were as successful as resident males. However, offspring with parents of different origin had higher survival than offspring with parents of the same origin, which suggests hybrid vigour. The contribution of resident and translocated individuals to the stochastic component of the long–run growth rate of the population was similar; neither the mean individual contributions in fitness nor the demographic variance differed between the two groups. Thus, this experiment shows that translocated individuals may have a similar demographic influence on the growth of local populations as resident individuals. However, hybrid vigour with respect to offspring recruitment seemed to partially decrease the negative fitness consequences of the assortative mating based on origin.

Genetic basis of ecologically important characters

To understand the interaction between ecological (RA1) and evolutionary (RA2) processes in single species as well as in communities (RA3) we need to know the genetic basis of traits involved in adaptation. Despite its importance, we still have a poor understanding of how processes at the molecular genetic level (e.g. evolutionary responses in genes), relate to processes at the phenotypic level (e.g. selection due to changes in the environment).

A prerequisite to be able to study evolution at the genetic level is that genomic resources exist for the species under study. To this end, we have assembled a high-quality reference genome for one of our main model species, the house sparrow (Elgvin et al. 2017). Information from the reference genome was used with high-density Single Nucleotide Polymorphism (SNP) genotype data in a Genome Wide Association Study (GWAS) to map genes for fitness-related morphological characters (Silva et al. 2017). In our study, we also included similar genomic and phenotypic data from collared flycatchers in Sweden, and demonstrated that the proportion of variance explained by each chromosome was positively related to the chromosome size for most traits in both species. Furthermore, we found two significant associations, for bill length in house sparrows and tarsus length in collared flycatchers, but these explained less than 3% of the phenotypic variation. Thus, our results indicate a polygenic basis for morphological traits. These results suggest that selection is likely to have considerable consequences for eco-evolutionary dynamics because selection will affect many genes spread across an organism's genome. This implies that genomic techniques can be useful to provide a better understanding of short–term evolutionary change of phenotypic traits in natural populations.

RECOMMENDED READING:

Elgvin, T.O., Trier, C.N., Tørresen, O.K., Hagen, I.J., Lien, S., Nederbragt, A.J., Ravinet, M., Jensen, H. and Sætre, G.-P. 2017. The genomic mosaicism of hybrid speciation. *Science Advances 3*, e1602996.

Kvalnes, T., Ringsby, T.H., Jensen, H., Hagen, I.J., Rønning, B., Pärn, H., Holand, H., Engen, S. and Sæther, B.-E. 2017. Reversal of response to artificial selection on body size in a wild passerine. *Evolution 71*, 2062–2079.

Ranke, P.S., Skjelseth, S., Pärn, H., Herfindal, I., Pedersen, Å.A.B., Stokke, B.G., Kvalnes, T., Ringsby, T.H., Sæther, B.-E. and Jensen, H. 2017. Demographic influences of translocated individuals on a resident population of house sparrows. *Oikos 126*, 1410–1418.

Silva, C.N.S., McFarlane, S.E., Hagen, I.J., Rönnegård, L., Billing, A.M., Kvalnes, T., Kemppainen, P., Rønning, B., Ringsby, T.H., Sæther, B.-E., Qvarnstrom, A., Ellegren, H., Jensen, H. and Husby, A. 2017. Insights into the genetic architecture of morphological traits in two passerine bird species. *Heredity 119*, 197–205.

Stubberud, M.W., Myhre, A.M., Holand, H., Kvalnes, T., Ringsby, T.H., Sæther, B.-E. and Jensen, H. 2017. Sensitivity analysis of effective population size to demographic parameters in house sparrow populations. *Molecular Ecology 26*, 2449–2465.

Figure 2. Having a large black badge on the throat and chest (a sexual ornament), was found to be more important for the reproductive success of translocated male house sparrows than resident males in a translocation experiment in northern Norway (Ranke et al. 2017; Photo by Henrik Jensen).

Research Area 2 Evolutionary biology
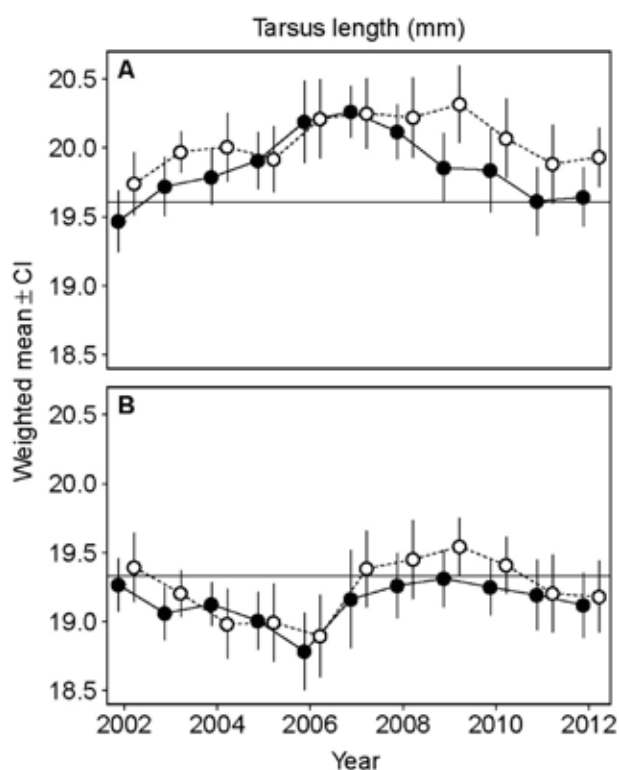
Research Area 2 Evolutionary biology

Figure 3. An artificial selection experiment on large and small body size (i.e. tarsus length) was carried out from 2002 to 2005 in two natural house sparrow populations at the coast of northern Norway (Kvalnes et al. 2017). The experiment resulted in phenotypic responses that closely followed the predictions from quantitative genetic models. During the seven years following the artificial selection, the mean body size and estimated breeding values in the populations gradually returned towards their pre–experimental means. The horizontal lines are the mean body size for each population across sexes prior to the first selection episode.
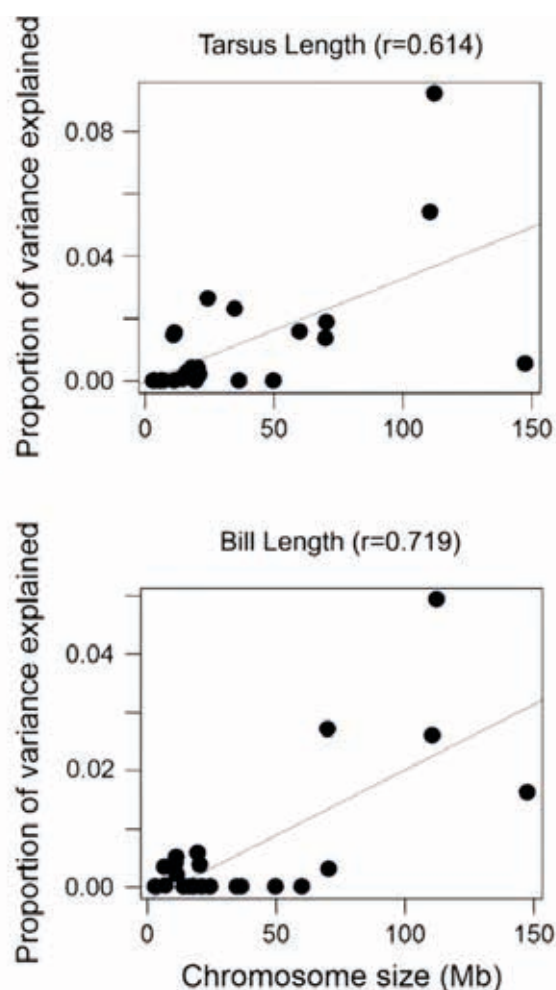

Figure 5. For many morphological traits in house sparrows, such as tarsus length and bill length, the proportion of variance explained by a chromosome is positively related to the chromosome size, suggesting a polygenic basis for these traits (Silva et al. 2017).

Figure 4. In a large-scale translocation experiment in house sparrows (Ranke et al. 2017), we found a stronger relationship between the size of a sexual ornament (the size of the black badge on males' throat and chest) and the number of fledglings produced in translocated males (n = 29; filled circles and solid line) than in resident males (n = 42; open circles and dashed line).

RESEARCH GROUP: MODELLING BEHAVIOUR IN STOCHASTIC ENVIRONMENTS

Current group members:
PI: Researcher Irja Ida Ratikainen
PhD candidate Thomas Haaland

Aim: *To increase understanding of behavioural and life history strategies in stochastic environments.*

We are a small research group with strong collaborations both within CBD, but also internationally. Our main project is "Evolutionary responses to variable and unpredictable environments" a "Young talented researchers" project from the Norwegian Research Council. This currently combines several modelling techniques to investigate evolution of epigenetic information use, plasticity and learning, insurance and bet–hedging of both behaviour and life history strategies, all in variable and unpredictable environments. Our contribution to the research program of CBD is therefore primarily in RA2.

Photo: Per Harald Olsen

Irja Ida Ratikainen and Thomas Haaland.

MAJOR SCIENTIFIC CONTRIBUTIONS

Adaptations to unpredictable environmental fluctuations represent some of the most intriguing problems in evolutionary biology and some of the most relevant for the understanding of biodiversity dynamics in the light of climate change. At the individual level, this involves the use of 'insurance' strategies against the most severe effects of extreme environments. However, across generations it is usually predicted that genotype fitness is maximized in the form of 'bet–hedging' adaptations. We have created a simple model demonstrating that in a population where individuals can evolve insurance strategies, bet–hedging strategies become unnecessary. In a different model, individuals use a reaction norm to match their phenotype to the fluctuating environment. Here we show that different types of environmental variation will select for very different use of information from different sources, including both own sampling of the environment and information transmitted from parents about the environments they experience. Parental stress is also shown to contribute important information to the offspring. Also in this simulation, parents may

evolve diversification bet–hedging strategies, but offspring will generally evolve to disregard any such parental effects.

In a second series of models that were published in American Naturalist by Thomas Haaland et al. in 2017, we have shown that parental investment should be adjusted according to partner quality, but that the response is highly dependent on the exact partner effect on either investment costs or offspring fitness. These results are important because parental investment can contribute both to evolution by sexual selection but also to natural selection because parental investment decisions can either enhance or reduce individual quality differences.

RECOMMENDED READING:

Haaland, T.R., Wright, J., Kuijper, B. and Ratikainen, I.I. 2017. Differential allocation revisited: When should mate quality affect parental investment? *American Naturalist 190*, 534–546.

Research Area 2 Evolutionary biology

RESEARCH GROUP: ADAPTATIONS TO (UN)PREDICTABLE ENVIRONMENTAL CHANGE

Current group members:
PI: Professor Jonathan Wright
Postdoc Yimen Araya-Ajoy
PhD candidate Mette Helene Finnøen

Aim: *To explore adaptive evolution in fluctuating environments.*

This RG is run by Wright, and contributes to the research program of CBD primarily in RA2. Working at the interface between theoretical and empirical research, we are involved in a wide range of activities, from developing formal mathematical models to conducting observational and experimental studies on wild populations in the field and laboratory. A variety of research approaches are therefore applied to understanding the evolution of the hierarchical structure of variation in life history, morphological, physiological and behavioural traits.

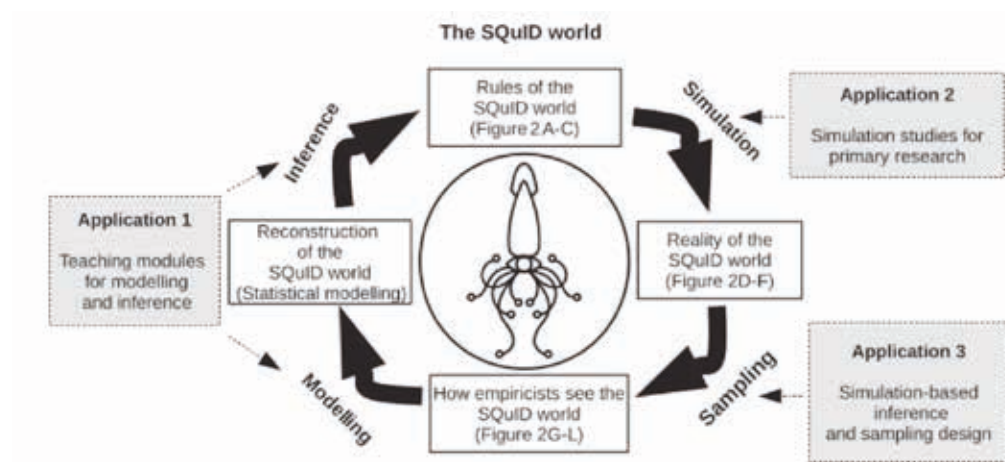Jonathan Wright, Yime Araya-Ajoy
and Mette Helene Finnøen.

Figure 1. The SQuID world. For explanation, see the main text. SQuID, Statistical Quantification of Individual Differences.
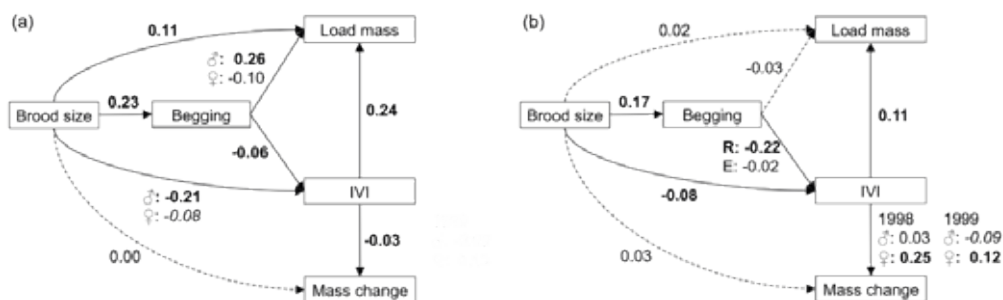

Figure 2. Summary of Westneat *et al.* (2017) results from separate analyses of the impact of experimentally enlarged brood size on two aspects of parental provisioning behaviour (inter-visit interval [IVI] and load mass), average nestling begging at the previous visit (begging) and changes in parental body mass (mass change) across two consecutive visits on **(a)** means and **(b)** residual variances in pied flycatchers. Arrow direction indicates independent to dependent variable; arrows with bold numbers indicate strong support (credible intervals not overlapping zero), arrows with italic numbers indicate some support (credible intervals slightly overlapping zero) and dashed black lines indicate little support for a non-zero relationship. Sex, brood size (Reduced vs Enlarged) and year differences are indicated when they existed

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Major scientific contributions

Exploring the hierarchical structure of phenotypic variation – a mixed model approach

Phenotypic variation exists in and at all levels of biological organization: variation exists among species, among individuals within populations, and in the case of labile traits, within individuals. Mixed–effects models represent ideal tools to quantify multilevel measurements of traits and are being increasingly used in evolutionary ecology. Mixed–effects models are relatively complex, and three main issues may be hampering their proper usage: (i) the relatively few educational resources available to teach new users how to implement and interpret them, (ii) the lack of tools to ensure that the statistical parameters of interest are correctly estimated, and (iii) conceptual developments on the ways they can be used to address specific biological questions. During the last year, members of this group have developed and explored the use of mixed effect models for quantifying patterns of phenotypic variation at different levels of hierarchical organization. We advocate the use of particular types of mixed effect models to study heritability and repeatability of plasticity (Araya-Ajoy & Dingemanse 2017) and assortative mating (Class et al. 2017). Furthermore, we developed a simulation-based tool (SQuID) that can be used for research and educational purposes (Allegue et al. 2017). This simulation tool creates a virtual world inhabited by subjects whose phenotypes are generated by a user-defined phenotypic equation, which allows easy translation of biological hypotheses into quantifiable parameters (see Fig.1).

The current framework is suitable for simulation studies, determining optimal sampling designs and making simulation-based inferences to aid in the interpretation of empirical studies. It is also a teaching tool for biologists interested in learning, or teaching others, how to implement and interpret linear mixed–effects models when studying the processes causing phenotypic variation.

Exploring multiple levels of phenotypic variation in means as well as variances

Evolutionary theory concerning life histories and foraging in the context of provisioning offspring generally makes predictions about mean trait values, but some circumstances might favor changes in the variance of parent and offspring traits. We analyzed data on free-living pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*) experiencing a brood size manipulation (Westneat et al. 2017; Mathot et al. 2017). We used double hierarchical generalized linear models to investigate patterns in means and variances of provisioning, brood begging, and parental mass. As predicted by life history theory, parents with enlarged broods of intensely begging nestlings fed at higher rates and delivered more food per unit of time. They also delivered food at a more consistent rate. This contradicts the prediction from variance–sensitive foraging theory, because only in a year with insufficient food availability did great tit parents facing higher brood demand choose more variable foraging options. Indirect evidence suggests that reduced variance in trip time arose from shifts in parental time budgets. Exploratory analyses of the flycatcher data revealed patterns in residual variance of both nestling begging and parental mass changes, with enlarged broods begging less consistently and female body mass changes being more variable after longer foraging trips. In this way we were able to show that parent pied flycatchers simultaneously adjust means and variances in multiple aspects of their provisioning effort to changes in brood demand and that these responses might be linked with nestling begging and changes in parental body mass (Fig.2). Research in our group thus highlights the importance of adopting sophisticated statistical approaches to biological hierarchies of phenotypic (co)variation in order to fully understand the implications of evolutionary theory.

RECOMMENDED READING:

Allegue, H., Araya-Ajoy, Y.G., Dingemanse, N.J., Dochtermann, N.A., Garamszegi, L.Z., Nakagawa, S., Réale, D., Schielzeth, H. and Westneat, D.F. 2017. Statistical Quantification of Individual Differences (SQuID): an educational and statistical tool for understanding multilevel phenotypic data in linear mixed models. Methods in Ecology and Evolution 8, 257–267.

Araya-Ajoy, Y.G. and Dingemanse, N.J. 2017. Repeatability, heritability, and age-dependence in the aggressiveness reaction norms of a wild passerine bird. Journal of Animal Ecology 86, 227–238.

Class, B., Dingemanse, N.J., Araya-Ajoy, Y.G. and Brommer, J.E. 2017. A statistical methodology for estimating assortative mating for phenotypic traits that are labile or measured with error. Methods in Ecology and Evolution 8, 1910–1919.

Mathot, K.J., Olsen, A.-L., Mutzel, A., Araya-Ajoy, Y.G., Nicolaus, M., Westneat, D.F., Wright, J., Kempenaers, B., Dingemanse, N.J. and Wong, B. 2017. Provisioning tactics of great tits (Parus major) in response to long-term brood size manipulations differ across years. Behavioral Ecology 28, 1402–1413.

Westneat, D.F., Mutzel, A., Bonner, S. and Wright, J. 2017. Experimental manipulation of brood size affects several levels of phenotypic variance in offspring and parent pied flycatchers. Behavioral Ecology and Sociobiology 71, 91.

Research Area 2 Evolutionary biology

Research group: Community Dynamics

Current group members:
PI: Associate professor Vidar Grøtan
Professor Otso Ovaskainen
Professor Bob O'Hara
Senior researcher Ola Diserud
Associate Professor Anders Gravbrøt Finstad
PhD candidate Emma-Liina Marjakangas
PhD candidate Sam Perrin
PhD candidate Lisa Sandal
PhD candidate Tanja Petersen
PhD candidate Wouter Koch

Aim: *To examine how community dynamics in time and space of different taxa along ecological gradient are affected by environmental stochasticity.*
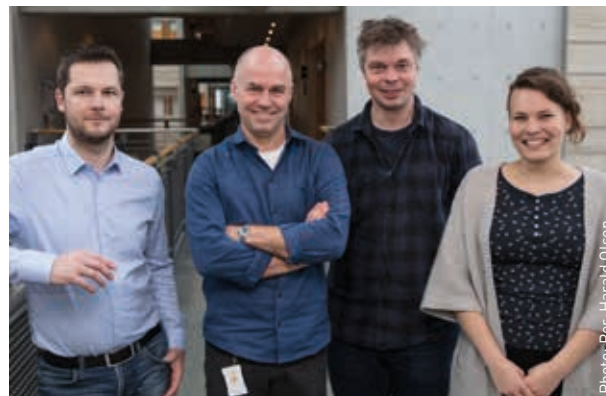
Vidar Grøtan, Ola Diserud, Anders G. Finstad, Emma-Liina Marjakangas.
Not present Otso Ovaskainen, Sam Perrin, Lisa Sandal, Tanja Kofod Petersen, Wouter Koch.

Major scientific contributions

One of the key challenges in community ecology is to model and estimate the strength of species interactions in space and time. Recent developments of Otso Ovaskainen and collaborators (Tikhonov et al. 2017) have shown that Joint Species Distribution Models (JSDM) can become important new tools for estimating species associations (residual co–occurrence patterns after accounting for environmental niches), provided that large data sets are available.
The use of these approaches is also likely to increase the predictive power of species distribution models by accounting for such associations. This is supported by several analyses published in several papers by Ovaskainen and collaborators which have examined the performance of this statistical framework, using both simulated and real data. Thus, these statistical methods provide a new tool for ecologists who wish to investigate the dependency of interspecific interactions on environmental context using non–manipulative observational community data. This approach can be applied to answer fundamental questions in community ecology about how species interactions shift in changing environmental conditions, as well as to predict future changes of species interactions in response to global change. A summary of the potential avenues that opens for future studies is found in Ovaskainen et al. (2017a)

As a practical illustration of the application of this approach, Abrego et al. (2017) analysed data on the occurrences of 98 wood–inhabiting fungal species in managed and natural forests in northern Spain. In

this study, they addressed the question whether the positions of wood-inhabiting fungal species within the interaction networks influenced their responses to forest management. By using a joint species distribution model that partitions variation in species occurrences among environmental (i.e. resource availability) and biotic (i.e. species–to–species associations) predictors. This study demonstrated that in addition to the direct loss of resource-specialized species, forest management has indirect effects mediated through interactive associations, strongly indicating that species with strong associative links to other species are especially sensitive to forest management.

Ovaskainen et al. (2017b) also a developed a new approach to estimate interaction matrices based on time series data from species rich communities. This approach is based on the assumption that the influences of the other species on the dynamics of a focal species can be summarized through a few community–level drivers, which is those linear combinations of species abundances that are most relevant in determining the future growth rates of all the species. Biologically, community–level drivers can for example represent the total abundance of all species (coefficients of linear combination equal for all species), the total biomass of the community (coefficients proportional to mass of each species), or different functional groups (coefficients non-zero only for a particular functional group). The effects of these community–level drivers was estimated in a way that they

best explain the data jointly for all species. To do so, one approach related to latent variable modelling was applied, which has recently emerged in the ecological literature as a tool for estimating large co–occurrence matrices from snapshot data with joint species distribution models. Analyses of both simulated as well as time series data from real communities showed that this approach was able to estimate species interactions matrices quite well (Fig. 1).

RECOMMENDED READING:

Tikhonov, G., Abrego, N., Dunson, D., Ovaskainen, O. and Warton, D. 2017. Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods in Ecology and Evolution 8*, 443–452.

Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B.-E. and Abrego, N. 2017. How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proceedings of the Royal Society B: Biological Sciences 284*, 20170768.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F.G., Duan, L., Dunson, D., Roslin, T. and Abrego, N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters 20*, 561–576.

Abrego, N., Dunson, D., Halme, P., Salcedo, I. and Ovaskainen, O. 2017. Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. *Oikos 126*, 259–268.
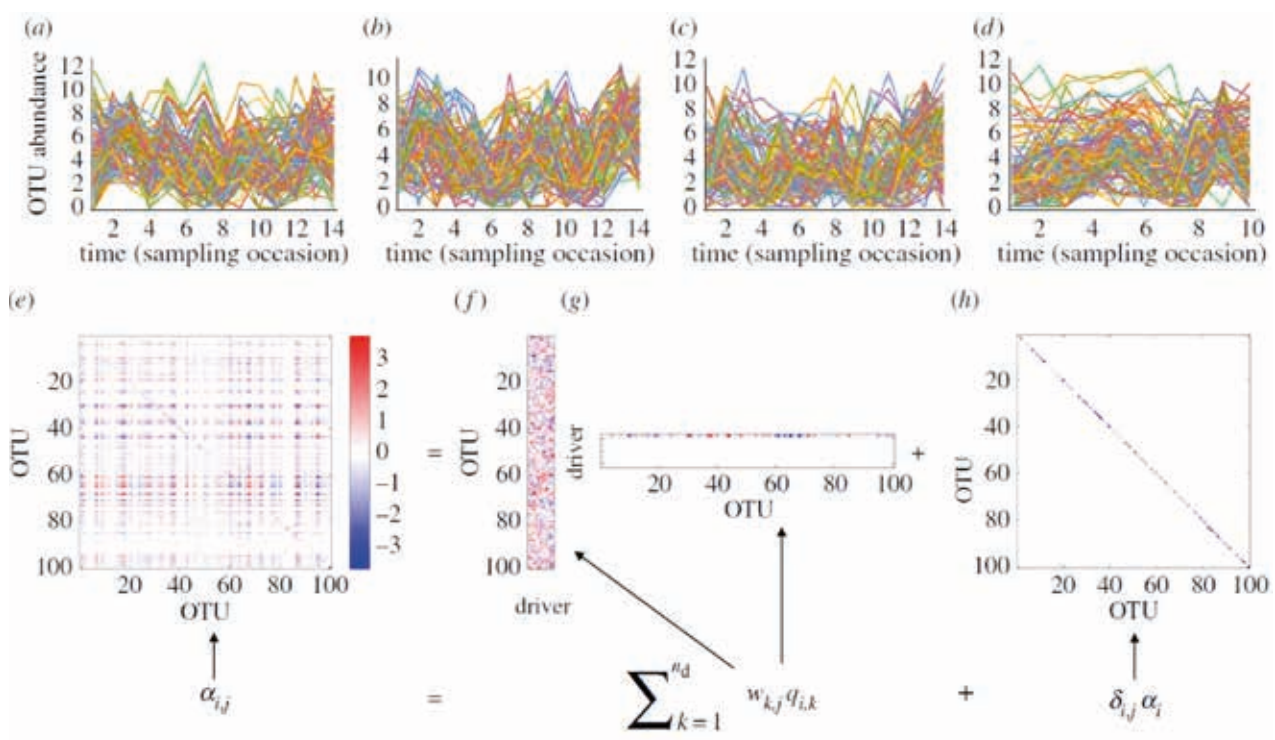

Figure 1. Community–level drivers-model fitted to empirical data on aquatic microorganisms. Panels (a–d) illustrate the $\log(x + 1)$-transformed time series data for the 100 most abundant species on the four study sites. Panels (e–h) illustrate how the matrix of interactions among species are estimated The interaction matrix is shown in panel (e) is constructed through matrices representing the contributions of the species to the community-level drivers ($w_{k,j}$, shown in panel f), the influences of the drivers to the species ($q_{i,k}$, shown in panel g) and terms modelling within-species density dependence (a_i , shown in panel h).

Research group: Dynamics of Arctic ecosystems

Current group members:
PI: Researcher Brage Bremset Hansen
Postdoc Håkon Holand
PhD candidate Mathilde Le Moullec
PhD candidate Bart Peeters
PhD candidate Kate Layton Matthews

Aim: *To combine demographic modelling of key species and multi–species stochastic approaches to disentangle how community dynamics are influenced by shared versus species–specific environmental noise linked to climate change.*

Bart Peetes, Mathilde Le Moullec, Brage Bremset Hansen, Kate L. Matthews, Håkon Holand.

In December 2017, we received a grant from the FRIPRO program at the Research Council Norway, funding the cross–disciplinary project ´Community dynamics in a rapidly warming high Arctic: trophic synchrony in time and space (INSYNC)´ for the period 2018-21. This project aims to combine field experimental approaches with time series analyses to explore how major climate drivers of key ecosystem components shape spatiotemporal dynamics of the entire tundra community. Collaborators include University of Aberdeen, United Kingdom, University of Groningen, the Netherlands, University of Iceland, CNRS Montpellier, France, Norwegian Meteorological Institute, Oslo, and University Centre Svalbard.

Major scientific contributions

We are currently in a process where we test and evaluate the different methodologies and experimental setups that we apply in our population and community dynamic approaches. For instance, extremely few *in situ* time series data are available from tundra vegetation at high latitudes, and in a paper by Karlsen et al (2017, Environmental Research Letters) we presented new and improved methodology for using remote sensing (NDVI) data as proxy for annual plant productivity back in time (Fig. 1). Furthermore, in a paper published in Wildlife Biology, Le Moullec et al. (2017) compared the accuracy and applicability of different methods for monitoring abundances of reindeer, as a first step towards assessing (changes in) their distribution and total abundance across Svalbard. In this bottom–up trophic system, it turns out that reindeer are distributed in space simply according to local vegetation productivity (NDVI). The close links between climate drivers and key ecosystem components are, in turn, likely to play an important role in shaping spatiotemporal community dynamics on the tundra (Fig. 2).
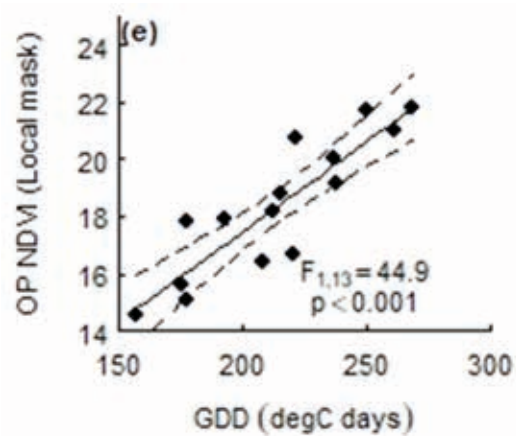

Figure 1. A new remotely sensed proxy for vegetation productivity is closely related to summer weather (Karlsen et al. 2018).

RECOMMENDED READING:

Karlsen, S.R., Anderson, H.B., van der Wal, René and Hansen, B.B. 2017. A new NDVI measure that overcomes data sparsity in cloud-covered regions predicts annual variation in ground-based estimates of high arctic plant productivity. Environmental Research Letters, in press.

Le Moullec, M., Pedersen, Å.Ø., Yoccoz, N.G., Aanes, R., Tufto, J. and Hansen, B.B. 2017. Ungulate population monitoring in an open tundra landscape: distance sampling versus total counts. Wildlife Biology 2017, wlb.00299.
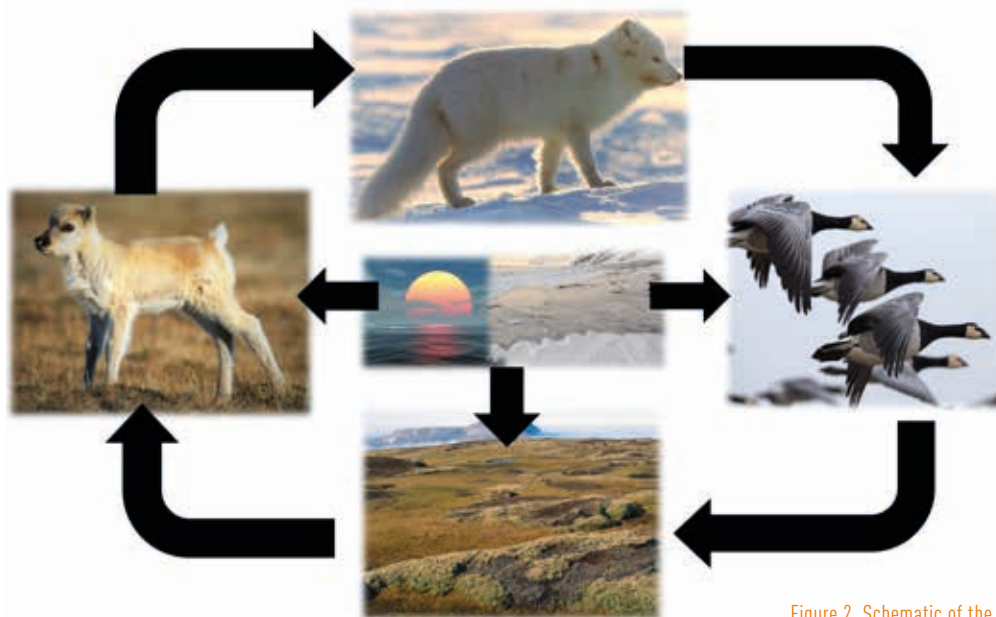

Figure 2. Schematic of the trophic tundra system in Svalbard.

Research Area 3 Community dynamics

RESEARCH GROUP: MODELLING OF THE DYNAMICS OF SPECIES INTERACTIONS

Current group members:
PI: Researcher Aline Magdalena Lee
PhD candidate Jonatan Fredricson Marquez

Aim: *To understand stochastic population dynamics in the presence of species interactions, using a combination of theoretical modelling and data analysis.*

Aline M. Lee and Jonatan Fredricson Marquez.

MAJOR SCIENTIFIC CONTRIBUTIONS

Major scientific contributions from this group include new insight into how best to model population dynamics when individuals are not all the same.

In nature, individual reproductive success is seldom independent from year to year, due to factors such as reproductive costs and individual heterogeneity. However, population projection models that incorporate temporal autocorrelations in individual reproduction require estimation of a large number of parameters, making them impractical when populations are small or data sparse. We have shown that failing to explicitly account for such individual reproductive autocorrelations will in most cases cause only very small biases in stochastic population growth and extinction risk. This was confirmed using a range of parameterizations, including a case study using moose data, indicating that standard age–structured models should perform well even in the presence of such autocorrelations (Lee et al. 2017b).

Adult individuals that do not breed in a given year also occur in a wide range of natural populations. We have

shown that the common practice of basing population models on breeders can substantially inflate estimates of population growth if individuals that skip breeding in a given year can later return to breed (Lee et al. 2017a).

The group is now focusing on understanding population dynamics and distributions in the presence of interspecific interactions and environmental noise. This involves both developing new theory through modelling, and studying specific assemblages of species, in particular fish in the Barents sea.

RECOMMENDED READING:

Lee, A.M., Reid, J.M. and Beissinger, S.R. 2017. Modelling effects of nonbreeders on population growth estimates. *Journal of Animal Ecology 86*, 75–87.
Lee, A.M., Sæther, B.-E., Markussen, S.S. and Engen, S. 2017. Modelling time to population extinction when individual reproduction is autocorrelated. *Ecology Letters 20*, 1385–1394.
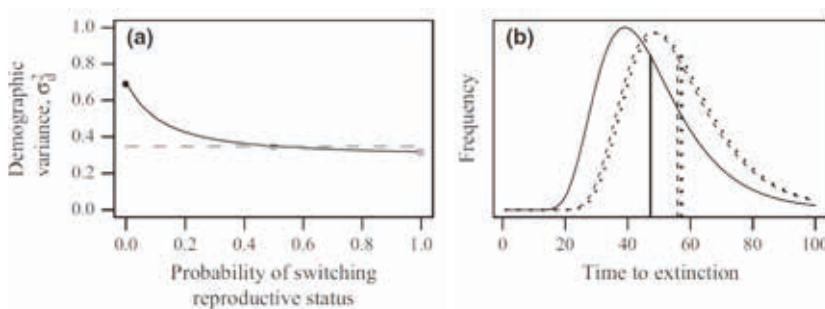

Figure. Estimated demographic variance (a) and distribution of time to extinction (b) from a model with reproductive autocorrelations (solid line) compared to those from a standard age structured model (grey dashed line), as the probability of switching between producing 0 and 1 offspring varies. Note that the probability of switching has to be extremely low for the time to extinction to be noticeably shortened.

PHD ESSAYS

Thomas Haaland

FIRST STEPS OF A CAREER IN SCIENCE

Already as part of my MSc at NTNU, I experienced a lot of what CBD had to offer. As both of my supervisors were involved in the Centre, I presented my work there twice, and got to know many of the PhD students there. While I had initially planned on doing my PhD somewhere else than NTNU (having been here for Bachelor and Master's), my supervisor got a large grant including a PhD position just as I was finishing my Master's, and encouraged me to apply for it. It seemed too good an opportunity to pass up – I could easily tell that CBD would be a good place to work and develop as a scientist, and of course it helped that I was enjoying life in Trondheim (friends, partner, outdoor activities, social activities, etc.) enough that staying here for another four next years would be great. I also get a long extremely well with my supervisors and value their scientific ambitions, guidance and cooperation a lot.

I am doing a theoretical project investigating adaptations to variable and uncertain environments. There is a lot we do not know about how evolution shapes organisms when the climate or other conditions change between and within generations. Especially in the field of behavioral ecology, this has often been overlooked. I therefore aim to build and analyze models that show how organisms cope with variation and uncertainty.

It is an interesting project because of how general it is, and because it has the potential to link together many areas of biology that have been a bit disconnected. It is a very open project, which I have been free to take in any direction I wanted. It's also a project that leaves a lot of doors open for the next step in my career, because it involves looking into a lot of different fields, and the work is very applicable to new systems. A great strength of CBD is the scientific width of people's backgrounds, so there is always someone to discuss problems, ideas and projects with, and that's a major advantage in a project that's as general as this one. When faced with new questions and systems, I can easily start looking at it with modelling eyes to clarify how some of the problems work out. Hopefully I can also be of use and help for the others at the Centre as one of the relatively few with this kind of competence.

My only published paper so far is of the project I did for my Master's degree. I'm very proud of this one (I'll include it here since it was also as part of CBD) as it was published in the American Naturalist, involved international collaboration, a very long and challenging review process (from which I learned a lot), and has given rise to many new potential projects and papers.

Thomas Haaland presenting at the 2017 Congress of the European Society for Evolutionary Biology (ESEB) in Groningen, The Netherlands.

Photo: Fredrik Jutfelt

Michael Pepke Pedersen

THE BEGINNING OF UNDERSTANDING THE END: AVIAN TELOMERE RESEARCH AT CBD

Telomeres, the short repetitive DNA sequences protecting the ends of chromosomes in most organisms, are degraded due to cell division and oxidative stress, inducing senescence. They may thus represent an important physiological mechanism mediating fundamental life–history tradeoffs between growth, survival and reproduction. The emerging field of telomere ecology therefore holds great potential for integrating evolutionary biology, population dynamics, physiology and maybe even community ecology (to complement the research areas of CBD). My PhD project at CBD combines large–scale fieldwork and laboratory work in a unique attempt to test evolutionary hypotheses about the role of telomeres in nature. Rather conveniently, this nature is found in an attractive insular setting near CBD, where the house sparrow abounds.

The advantages of studying this ubiquitous and versatile *éminence grise* (ˈgråspurvˈ in Norwegian) clearly outweighs its vulgar nature. However, the true strength of CBD's house sparrow project lies in its continuity (having just celebrated its 26th field season anniversary), its relevance to the ongoing biodiversity crisis, and the interdisciplinary knowledge it has gathered. Thus, the ancient commensal relationship between man and house sparrow has advanced at CBD in terms of mutual understanding. To me, CBD is no longer a cannabinoid abbreviation (not to mention the lacking English translation of NTNU furthermore unbestowed of intranational associations), but a hallmark of *excellence*: Being familiar with the institution of ˈCenters of Excellenceˈ within my Nordic sphere of interest and the competences (people) and opportunities (for funding and *serendipity*) they have generated elsewhere, I was happy to join CBD in 2017 with no reservations. In addition, the cold, mid-Norwegian environment surrounding CBD fosters clear thinking and an international escapism unparalleled on the continent; combined with the respect for early–career scientists at CBD, the distinction between business and pleasure is easily erased.

My lab work has allowed me to combine practice (things work, but you don't know why) and theory (you know things, but they don't work) so that nothing works and no one knows why. However, as a Chinese saying (pre-dating Mao, who led a military campaign against house sparrows) goes: "A bird does not sing because it has an answer. It sings because it has a song". My studies nevertheless indicate that telomere length might be an indicator of individual phenotypic quality reflecting a more subtle cost of growth. Ongoing studies at CBD will show whether a causal mechanism with transgenerational fitness consequences is at play and how telomeres, like a molecular thread of destiny, can ensure a happy ending to your chromosomes as well as your life.

Photo: Mary Ngo

House sparrow (juvenile) and Michael Pepke Pedersen (adult) interacting on the island of Lovund, Helgeland, in northern Norway.

Ever tried fitting a goose in a plastic box?Catching and ringing barnacle geese at the study site in Ny-Ålesund, Svalbard with the University of Groningen field team.

Kate Layton Matthews

#WORKHARD_SKIHARD

My masters at the University of Zurich was my first step into the field of demography and population dynamics. Upon hearing of the work of some members at CBD, I felt this was a natural step further into the field of population dynamics, to join a group with such experts in the field as Bernt-Erik, Steinar and Vidar. Additionally, the position offered at CBD allowed me to pursue my (almost) life-long fascination with the dynamics of Arctic populations and climate change, thus combining a wealth of expert knowledge with the opportunity to work with unique study species and systems. Furthermore, as someone who has already had the fortune to study abroad, I recognised the added value of the opportunities CBD could provide in terms of international workshops, conferences, allowing me to make new connections and gain new ways of thinking.

My PhD is focused on explaining the changes we observe in the dynamics of a population of barnacle geese, at their breeding grounds in high Arctic Svalbard. Specifically, I want to understand what is really driving the variation we see in survival and reproduction; is it mostly caused by density dependence, changes in climate or even other species at the breeding grounds? Additionally, I am exploring how individual variation, for example in age at first reproduction or body condition, can ultimately influence population fitness.

I was always looking for a project where I could advance my understanding of statistical and modelling techniques, as well as contributing work that is actually relevant in the real world. Understanding how migratory geese are responding to climate change and the potential need for future management is certainly a topical problem. Thus, by being part of such a dynamic environment with many people from different fields within ecology and evolutionary biology, I have gained a huge amount of, not only practical techniques, but also inspiration for different projects that I had not even thought of. The whole aim of a PhD or even research in general, is to make as many links as possible with people, projects and even disciplines and for me this was the huge strength of a centre like CBD, which has provided me with numerous ideas and new approaches to answering biological questions.

In this process of writing up the first paper of my PhD on density dependence in barnacle geese, I realised that in the last year and a half I have gone from zero knowledge of Bayesian modelling to developing an integrated population model and tackling some really challenging issues in this field. This is not meant as a pat on the back so to say, but rather a comment on the importance of having so many people to discuss issues with at the centre. Having so many outlets for discussion, such as our weekly PhD meetings, seminars and an internal conference last year really allowed for me to gain some hugely valuable feedback and, perhaps more importantly, constant motivation.

Mathilde le Moullec

The great life of a Arctic wanderer PhD at CBD

It has been over three years since I was hooked into the dynamic centre for biodiversity studies! The corner of this diverse world that made me the most passionate is the Arctic biome. While studying my Master's, I met Brage B. Hansen who was a great co-supervisor and with whom I wished to continue studying a PhD. I was successful in obtaining a position, thanks to the NTNU faculty, following a presentation on the Svalbard ecosystem, of course. So... let's say that my arrival at this centre of excellence was because of Brage. I was far from imagining the endless opportunities CBD gave me to build a solid start in science.

Mathilde Le Moullec found love on Svalbard; the annual reindeer capture program in Ny-Ålesund.

The CBD has fed my inspiration in the multidisciplinary fields of ecology. You are exposed daily to topics from genes to communities, from the tropics to the high-arctic. The education provided by the centre is unique for developing a robust background in study design and statistics, which is indispensable for the critical analysis of science. You are pushed to build your own independent way of thinking, which is, to me, the most important. Especially for a young scientist, the CBD grew more dynamic two years ago, when numerous PhD students were employed. Only energetic and amazing people were hired! The atmosphere is great inside and outside the CBD walls, climbing, skiing, cabin brainstorming, playing laser tag... During long winter evenings, I now dream up future grant projects linking population ecology and evolution. But first priority is my PhD.

My PhD touches the field of estimation of species abundance in space and time. First, local and long–term monitored sites on Svalbard enabled me to investigate the accuracy of methodologies for counting reindeer and for reconstructing vegetation production in permanent plots using annual ring-growth of polar willows. Then, roaming around Svalbard backpacking or sailing, I applied these methodologies to the full range of the endemic Svalbard reindeer and the polar willow. Finally, obtaining large–scale and long–term time series enabled me to study the population synchrony of two high–arctic keystone species in the context of the Moran theory.

If there is a study I am particularly pleased about, it is the spatiotemporal patterns of growth synchrony in the polar willow. It started with the spirit for expedition, then came the challenges to start a dendrochronology laboratory to read ring growth from "the most difficult" shrub on earth, as I was told when learning the methodology in Alaska. Together with Lisa (my Master's student at the time, now a PhD student at the CBD) and co-authors, we were able to show that ring growth of the polar willow not only represented above–ground biomass production of the very species, but of the entire vascular plant community. By reaching unstudied remote places, we could reconstruct past fluctuations in primary production. This study is the first to demonstrate the role of climate in synchronizing Arctic primary production over large distances, with implications for energy flow through high–arctic food webs. To build this project from the ground up, I needed facilities, help in the laboratory, synchrony experts, the SQUID workshop, conferences [...], which were all provided by the CBD. All that I needed to do was "do it"!

Emma-Liina Marjakangas

I STILL CAN'T BELIEVE I DO THIS FOR A LIVING!

I arrived in Trondheim almost three years ago, not as a PhD candidate, but as an intern. I wanted to learn more about statistical methods in ecology, and CBD was the place of my choice for that. During a coffee break on my fourth day of the internship, Vidar asked Otso and Nerea whether they knew someone in Finland that would be interested in applying for an open PhD position at NTNU Sustainability (and CBD). Since combining conservation biology and statistics was exactly what I wanted to do, I was trying very hard to find the words to politely scream "MEEEE!", but Otso was faster and pointed at me. Within that coffee break the four of us had laid out a project plan, and a week later I submitted it.

That plan included all things the things I could have dreamt of and even more. My PhD project is focused on the effects of forest fragmentation on species interactions. More specifically, I study (with help of latest community dynamics models) how interaction patterns change along fragmentation gradients and how species traits and relatedness affect the patterns. My study system is in coastal Brazil and it is a highly fragmented biodiversity hotspot. Often people ask what my study species is. The answer is: all of them. I use databases on occurrences of various organisms, including (but not restricted to) birds, trees, bats, rodents, primates, bees, flowering plants and butterflies. During the PhD, I get to be part of many large–scale initiatives to conserve global biodiversity

and ecosystem services (e.g. NTNU Sustainability and ATLANTIC Forest Initiative). In addition to that, I get paid to learn new things and to travel to one of the most biodiverse ecosystems on this planet.

Working on this project simply wouldn't be possible outside CBD. In addition to the obvious advantages of being so close to where the development of latest statistical methods to analyze such huge community data sets happens, the centre provides opportunities to keep a young researcher's skills up to date. We learn from each other by arranging R-seminars, Tuesday lunch talks, weekly PhD meetings, international workshops, lønningspils, and just by sharing the office with people from different fields of ecology and mathematics.

My personal learning curve has been exponential since I started working at NTNU. For example, so far in 2018, my small personal victories include learning how to use the university computer cluster and getting the largest analysis running after an almost year of trying. There are days when nothing works and Matlab only produces error messages, but the feeling when managing to solve those problems outweighs the earlier frustrations. The best thing about the working environment at CBD is that there is always room for sharing both the frustrations and the 'yay' moments with others. We have mandatory coffee breaks every morning to make sure of that.

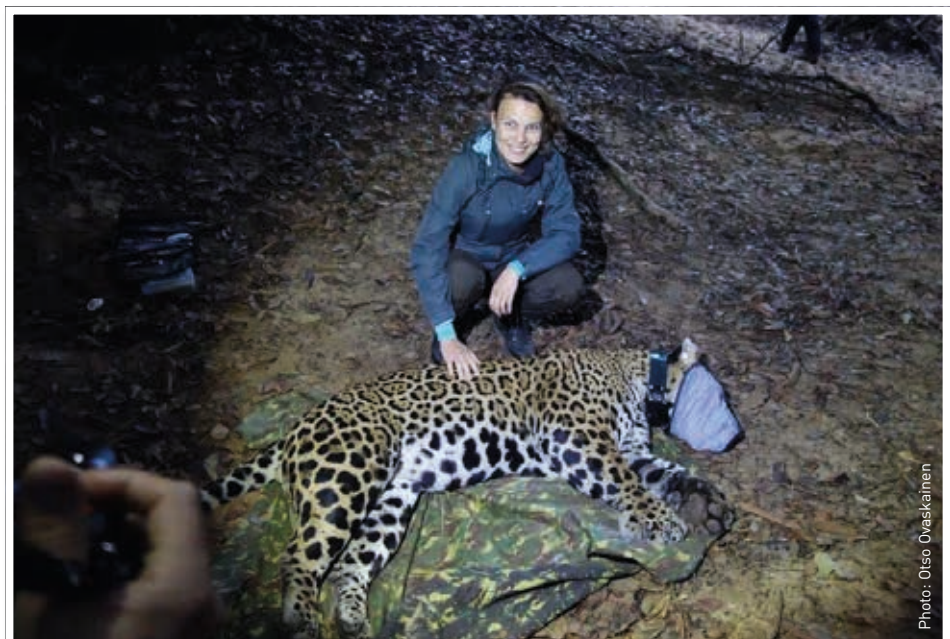Joining the local researchers for radio collaring jaguars in Pantanal.

Photo: Otso Ovaskainen

WORKSHOPS AND CONFERENCES

EIGHTH INTERNATIONAL HOLE-NESTING BIRDS CONFERENCE

From October 30th to November 2nd, 2017, CBD (Stefan Vriend, Bernt-Erik Sæther), together with Ben Sheldon (Edward Grey Institute, University of Oxford) and Marcel Visser (NIOO-KNAW), hosted the Eighth International Hole-Nesting Birds Conference. This meeting brought together nearly 100 leading scientists, research students and citizen scientists covering 37 different institutes and 16 different countries to exchange and share their experiences in hole-nesting bird research.

The field of hole-nesting bird research has a long and fundamental history. The studies by Kluijver in the Netherlands, and Lack and Perrins in the United Kingdom on great tits and blue tits in the 1950s were the first individual–based studies of vertebrates in the wild, and are the longest running field studies to this day. These pioneering studies provided the foundation for entire research fields. Many other researches followed the lead of Kluijver, Lack and Perrins and started to record individual life histories to study population dynamics and demography. The availability of long–term, individual–based data in a large geographical range enabled researchers to use hole-nesting birds as a model species to address fundamental questions in a wide range of scientific disciplines – from physiology to behaviour and evolutionary biology, and from population dynamics to climate change.

Hole-nesting birds have been important study organisms for researchers at CBD. The house sparrow metapopulation off the coast of Helgeland, and international collaborations on other hole-nesting bird systems have been a great source of data to answer research questions in various research fields.

The Eighth International Hole-Nesting Birds conference provided the right opportunity to share the newest findings in hole-nesting bird research at CBD. At the same time, the great and friendly atmosphere enabled participants to experience the variety of themes, to establish new contacts and to start new collaborations in hole-nesting bird research.

Participants at the Eight International Hole-nesting Birds Conference sharing their research during the poster session.

Participants on the measurement workshop.

Workshop on measurement practice in life sciences and medicine

Professor Christophe Pelabon arranged a workshop from June 7th to 9th about measurements. This was a collaboration with David Houle at Florida State University, US. Although awareness of the problems related to measurements has emerged in the past years, there is still place for progress. The aim with this workshop was to assess the generality of measurement issues in biology and explore measurement practice in several fields in life sciences and medicine.

The workshop recruited leading practitioners in areas such as biomedical research, community ecology, behavior and molecular biology who were willing to explain the measurement choices that they and others make, and to discuss whether lapses in measurement practice hamper good science in their fields. In total, the workshop hosted more than 33 participants from 12 different countries.
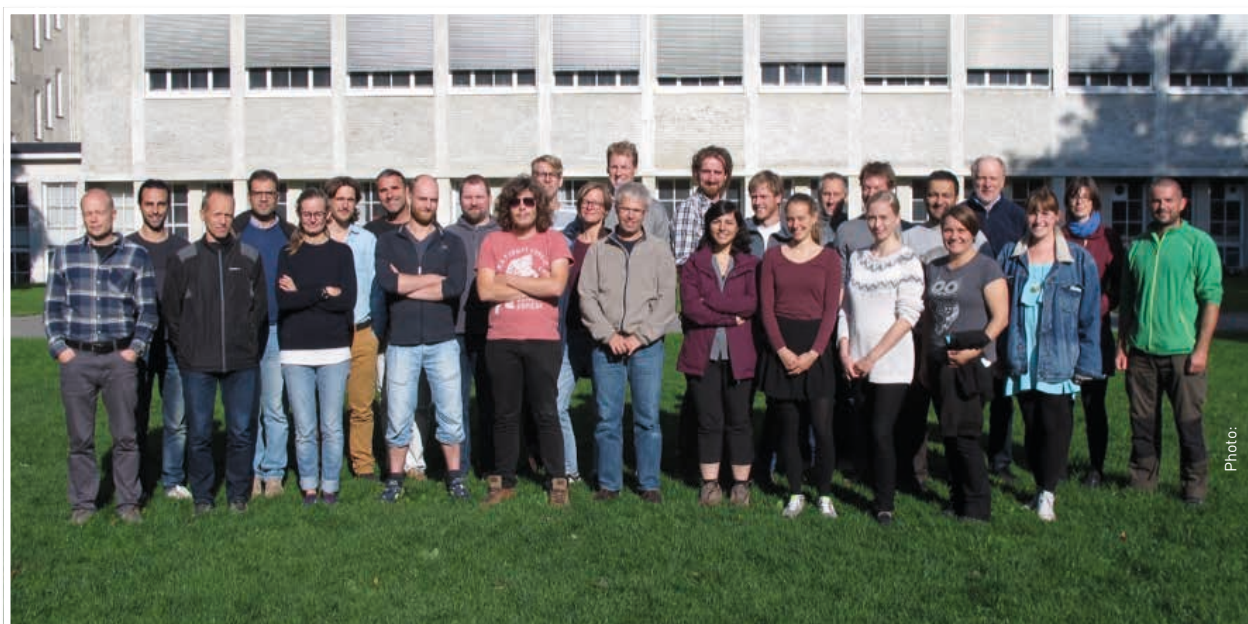
Participants on the IPM workshop.

Workshops on Stochastic population dynamics and Bayesian integrated population modelling (IPM) using JAGS

A PhD-course composed of the two workshops "Stochastic population dynamics" and "Bayesian integrated population modelling (IPM) using JAGS" was given 28th August–1st September and 4th September–8th September 2017 at CBD. Participants were required to attend both workshops as well as pass an oral exam in order to get credits for the course. It was also possible to attend one or both of the workshops without signing up for the PhD course.

Ecologists have become increasingly aware of the benefits of thinking in terms of separating their models into an observational process and a state process, when estimating parameters from data. The first part of the course introduced theoretical models for stochastic population dynamics as well as state-of-the-art applications of the theoretical framework. Participants also got hands-on experience in performing related statistical analyses. While the first part of the course focused on the theory behind population dynamical processes, such as the influence of stochasticity and age structure on demographic processes, the second part focused on how state-of-the-art Bayesian Integrated Population modelling (IPM) may allow and improve estimation of parameters of such processes. IPM allows great flexibility in construction of statistical models that simultaneously account for the specifics of the various data available and the population dynamical process studied.

Nine PhD candidates followed the PhD course (7 from CBD, 1 from NINA and 1 from NIMBU). The workshop "Stochastic population dynamics" attracted 21 participants (14 from CBD, 5 from other Norwegian institutions and 2 international). The IPM workshop also had 21 participants, of these 9 were from CBD, 8 from other Norwegian institutions and 4 participants were international.

NATIONAL AND INTERNATIONAL COLLABORATION

One of the characteristics of the research at CBD is that it often involves extensive international and national collaboration with research groups at other institutions. Almost every week during the term at least one international researcher has visited CBD, in addition to that 5 researchers have spent longer periods (> 1 month) at CBD. The national collaboration has in 2017 been especially developed through the project SUSTAIN, resulting in frequent visits of researchers between the three principal nodes CBD, CEES at the University of Oslo and the Department of Arctic and Marine Biology, UiT Arctic University of Norway, Tromsø.

In 2017, the strong collaboration between researchers studying hole–nesting birds was intensified, especially through the project "Evolution in a changing climate" funded by the Research Council of Norway. An important step to develop this collaboration was organizing of the Eighth International Hole-Nesting Birds Conference in Trondheim (see above). In May 2017, a delegation of Brazilian researchers visited CBD to develop further scientific interactions between Norway and Brazil in biodiversity research.

In 2017, we initiated the CBD lecture series in which distinguished researchers were invited to give open lecturers aimed for a wider audience. This monthly lecture scheme has been very successful. In addition to providing a series of stimulating talks summarizing the state of art on several important research questions, social events related to these visits have been important to strengthen the interactions among researchers also within CBD.

Several members of the CBD have been on longer research stays abroad during 2017. In particular, members of the research group "Dynamics of Arctic Ecosystems" have been active in performing long–term visits to other research institutions (B. Peeters 3 months in Guelph/Canada, B. B. Hansen 3 months and K. L. Matthews 3 weeks in Groningen/NL).

Popular Science

Also in 2017, researchers at CBD appeared quite frequently in public media. In total, 20 oral presentations were made for a public audience and 6 popular scientific papers were written. In fact, the results by Thomas Kvalnes and collaborators on artificial selection in house sparrows made into the main national news.

List of CBD lecturers 2017

- Professor Erik Svensson, Lund University, Sweden

- Professor David Reznick, University of California, USA

- Dr. Roberto Salguero-Gómez, University of Oxford, UK

- Professor Jon Ågren, Uppsala University, Sweden

- Dr. Marjo Saastamoinen, University of Helsinki, Finland

- Dr. Martin Lind, Uppsala University, Sweden

- Professor Hanna Kokko, University of Zurich, Switzerland

- Professor Luc de Meester, KU Leuven, Belgium

- Associate professor Jörgen Ripa, Lund University, Sweden

Dissertations

Three PhD candidates defended their thesis at CBD in 2017:

June 2nd: **Øystein Hjorthol Opedal**: *"The evolution of herkogamy: pollinator reliability, natural selection, and trait evolvability"*

Opponents: Professor Susan Mazer, University of California, Santa Barbara, USA
                   Professor Stefan Andersson, Lund University, Sweden

June 9th: **Ane Marlene Myhre:** *"Effective size of density dependent populations in fluctuating environments"*

Opponents: Senior Scientist Robin S.Waples, National marine Fisheries Service, Washington, USA
                   Researcher Luis-Miguel Chevin, Centre d'Ecologie Functionnelle & Evolutive, Montpellier, France

December 13th: **Øystein Nordeide Kielland**: *"Sources of variation in metabolism of an aquatic ectoterm".*

Opponents: Professor Neil Metcalf, University of Glasgow, UK
                   Professor Dag O. Hessen, University of Oslo, Norway

KEY FIGURES 2017

GENDER EQUALITY

In 2017 CBD had one female professor, Gunilla Rosenqvist and two associated female professors, Ingelin Steinsland, NINA and Irja Ida Ratikainen, IBI. So there is still a strong male biased in the sex-composition among the core-members of the Centre.

At the end of 2017, 45% of the PhD Candidates and Postdoc were female, but there is a tendency that female postdocs are fewer then the males.

Recruiting female to scientific careers after termination of the postdoc-period is also a challenge, so the male researchers are redundant in the centre mix.

It is a central focus for the leadership of CBD to strengthen the recruitment of female to position at all levels because we strongly believe that a balanced sex-ratio generates an environment the will facilitate excellence in research. We will therefore continue to actively recruit female researchers to CBD and will in collaboration especially with the Department of Biology propose different actions to achieve this goal. We hope this will facilitate future recruitment also of females to senior positions at CBD

KEY FIGURES

Key numbers in CBD	2017
Staff	
Senior Researchers	25
Postdoctor	7
PhD-candidates	26
Adm./Tech Staff	6
All staff at CBD	64
Scientific advisory Board	6
Results	
Journals	90
Anthologies	
Reports	113
Media attentions	10
Books/chapters	2
Costs and funding	**in thousand**
Operational costs CBD	30 718
Funding	
NINA	750
NFR	18 850
NTNU	11 868
Operational costs Associated projects	15 276

CBD MEMBERS

PhD Candidates

Ane Marlene Myhre
PhD candidate IBI/CBD

Elena Albertsen
PhD candidate CBD

Erlend Fossen
PhD candidate IBI

Mathilde Le Moullec
PhD candidate IBI

Peter Sjolte Ranke
PhD candidate CBD

Endre Grüner Ofstad
PhD candidate CBD

Stine Svalheim Markussen
PhD candidate IBI

Kate Layton-Matthews
PhD candidate IBI

Lara Veylit
PhD candidate CBD

Øystein Nordeide Kielland
PhD candidate IBI

Øystein Hjorthol Opedal
PhD candidate IBI

Emma-Liina Marjakangas
PhD candidate IBI

Thomas Haaland
PhD candidate IBI

Bart Peeters
PhD candidate CBD

Christoffer Hilde
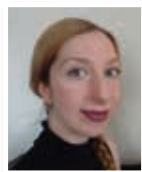PhD candidate CBD

Jonatan Fredricson Marquez
PhD candidate CBD

Michael Pepke Pedersen
PhD candidate CBD

Lisa Sandal
PhD candidate CBD

Sam Perrin
PhD candidate VM

Sarah Lundregan
PhD candidate IBI

Semona Issa
PhD candidate IBI

Shelly Cao
PhD candidate CBD

Sindre Sommerli
PhD candidate CBD

Tanja Kofod Pedersen
PhD candidate VM

Lars Rød-Eriksen
PhD candidate NINA

Lasse Frost Eriksen
PhD candidate NINA

Wouter Koch
PhD candidate Norwegian Biodiversity Information Centre

Dilan Saatlogu
PhD candidate IBI

Maria Lie Selle
PhD candidate IME

Mette Finnøen
PhD candidate IBI

PostDocs

Maja Tarka
Postdoc CBD

Marlène Gamelon
Postdoc CBD

Olivia Langhammer
Postdoc IBI

Erik Blystad Solbu
Postdoc CBD

Thomas Kvalnes
Postdoc CBD

Jostein Gohli
Postdoc CBD

Yime Araya-Ajoy
Postdoc CBD

RESEARCHERS

Brage Bremseth Hansen
Researcher CBD

Håkon Holand
Researcher CBD

Tim Burton
Researcher IBI

Alina Niskanen
Guest researcher

Aline M. Lee
Researcher CBD

Ingerid Julie Hagen
Researcher NINA

Ivar Herfindal
Researcher CBD

Ola Diserud
Sr. Researcher
NINA

Erling Johan Solberg
Sr. Researcher
NINA

Geir Hysing Bolstad
Researcher II
NINA

Hanno Sandvik
Researcher
NINA

Brett Sandercock
Researcher
NINA

PROFESSORS / ASSOCIATE PROFESSORS

Vidar Grøtan
Ass. Professor
IBI

Bob O'Hara
Professor
CBD

Steinar Engen
Professor CBD/IME

Otso Ovaskainen
Professor (50%)
IME

Arild Husby
Ass. Professor (20%)
CBD

Sigurd Einum
Professor
IBI

Jonathan Wright
Professor
IBI

Ingelin Steinsland
Professor
IME

Thor Harald Ringsby
Ass Professor
IBI

Jarle Tufto
Professor
IME

Henrik Jensen
Ass. Professor
IBI

Anders Gravbrøt Finstad
Ass. Professor
VM

Stig William Omholt
Professor
Division Director
Faculty of Medicine

Russel Lande
Professor
CBD
(45 %)

Hans K. Stensøien
Professor
VM

Irja Ida Ratikainen
10% Ass Professor IBI,
90% Researcher CBD

TECHNICAL STAFF

Linn-Karina Selvik
Engineer
IBI

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SCIENTIFIC PRODUCTION

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