cbd
CENTRE FOR BIODIVERSITY DYNAMICS

Annual Report 2016

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 different 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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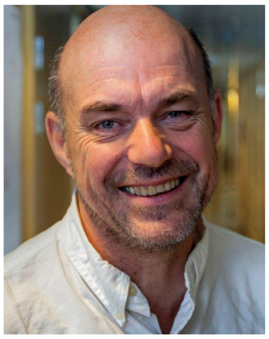
DIRECTOR'S COMMENTS



Bernt-Erik Sæther
Director CBD

In 2016 CBD experienced a boost in the number of publications with 100 papers published. This mainly reflects that projects established early in the project period of CBD now start to provide results, as well as extended collaborations among research groups. In addition, the increase in the scientific staff during 2014 and 2015 have now started to be reflected in the number of additional publications in 2016. An important contribution was the book by Otso Ovaskainen and collaborators entitled *Quantitative Ecology and Evolutionary Biology*, published by Oxford University Press. In 2016 CBD scientists published in leading general journals such as *Nature* (2), *Nature Communications* (2) and *Science* (1), as well as in general biological journals such as *American Naturalist* (1), *Proceedings of the Royal Society of London B* (4) and *Trends in Ecology and Evolution* (1). Many of the most important contributions were published in leading journals in ecology or evolution, such as *Ecology* (2), *Ecology Letters* (1), *Evolution* (5), *Journal of Animal Ecology* (6), *Journal of Ecology* (1), *Journal of Evolutionary Biology* (1), *Methods in Ecology and Evolution* (6), *Molecular Ecology* (2), *Oecologia* (1) and *Oikos* (5).

2016 was a year when CBD continued to grow in size in terms of number of new people, mostly because of funding of several new research projects. It also became a year of consolidation for many of our on-going research projects. For the first stage of the project period, we chose a flat organizational structure, which essentially resulted in the centre being organized as a collection of separate research groups. One disadvantage of such an organizational structure was that as the research groups grew larger they tended to become more independent from one another, making it increasingly difficult to establish collaborations across groups. This issue was brought to our attention by the Scientific Advisory Committee during their meeting in February 2016 in Trondheim, where they stated that "the uniqueness of CBD as a centre of excellence is its focus on general questions that require synthesis and collaboration among different research disciplines". Therefore, in order to facilitate more integrated multi-disciplinary approaches across more narrowly focused research groups, the Steering Board asked the Director of CBD to implement a more hierarchical organizational of the centre, which involved making senior researchers responsible for the research in each of the three Research Areas (RA).

As a consequence of the recommendation from the Steering Board, a new leader group of CBD was formed in early 2016, consisting of Bernt-Erik Sæther (Centre Director), Steinar Engen (Deputy Centre Director), Solveig Johnsen (Centre Coordinator), Gunilla Rosenqvist (communication, gender equality and external contacts), Ivar Herfindal (Research leader RA1: Population ecology), Christophe Pèlabon (Research leader RA2: Evolutionary biology) and Vidar Grøtan (Research leader RA3: Community dynamics). The first task of the leader group was to develop an action plan to encourage multidisciplinary interactions within CBD, and this has now been implemented from spring 2016. This involved an evaluation and analysis of the centre by the consultancy firm "Mind the Gap", which has broad competence in organization development, especially of companies based upon knowledge and innovations. A concrete outcome of the evaluation report was the development of individual research plans for all senior members at the centre. We also focused on creating more social arenas where all members of the centre could interact, such as a 2-day seminar on the coast of Trøndelag and a one-day presentation of all PhD-projects. I believe these actions have had a substantial impact on all members of the centre by improving the focus and identifying their activities in relation to each other and to the overall research goals of CBD.

CBD has a high proportion of females among its PhD candidates and postdocs, but experiences the common problem of losing females from science during or after a postdoc-period. As highlighted in the action plan, we organized a workshop on "Genderinequality in science" in November in Trondheim. The workshop involved a combination of local and international speakers who provided a general overview of this problem, as well as fruitful discussions about the specific challenges and solutions for CBD. As an outcome of this workshop, an action plan for improving gender equality at CBD will be developed, along with further seminars and workshops on this topic.

A number of important contributions to the overall research goals of RA1 were published in 2016. Many of these papers were related to the effects of age-dependence on the population growth. A comparative analysis of avian population dynamics showed that variation in population size affects different vital rates in a similar way when the population approached the carrying capacity, even though the species included in the analyses showed large differences in ecology (Sæther et al. *Nature Communications*). Another example involved an analysis of an age-structured model by Gamelon et al. published in *Ecology*. Here it was shown that the contribution of different age-classes to the growth of a great tit population depended on the combined effect of how individuals of different ages affected the density dependences, and on how they were affected themselves by individuals in other age-classes. These analyses operationalized the concept of critical age classes, which were facilitated by applying the flexible Integral Population Model approach (see the book by Kery and Schaub, *Bayesian Population Analysis Using WinBugs*).

In 2016, the first empirical results from the *Daphnia* experimental system set up by Professor Sigurd Einum appeared. This system is excellent for parameterizing models describing how resource availability and variability affect population dynamics through changes in fitness-related traits, but are also affected by both temperature and population density. One surprising result here was that population density *per se* did not have a general effect on mass-specific metabolic rate.

One of the great advances at CBD in 2016 was the publication of several papers that linked evolutionary processes with ecological dynamics. A central focus has been to develop theories for phenotypic evolution that include the joint effects density dependence and environmental stochasticity. These models show that density regulation strongly affects the rate of adaptive life history changes to fluctuations in the environment. The concept of *r*- and *K*-selection, as introduced by R.H. MacArthur and E.O. Wilson in the mid 1960s, is therefore important here when trying to understand variation in the rate of phenotypic evolution of life histories. Empirical evidence from a Dutch great tit population demonstrating ongoing *r*- and *K* -selection was the first study to find support for these theoretical predictions (Sæther et al., *Proceedings of the Royal Society of London*).

One approach applied in RA2 has been to use the relatively simple interactions between plants, pollinators and herbivores or seed predators to study how different easily identified selection agents contribute to phenotypic evolution. A study of *Dalechampia scandens* combined phenotypic selection studies with data on genetic and morphological divergence among ca. 20 populations from Costa Rica. This study provided evidence that patterns of natural selection varied from population to population and from year to year, but that selection also tended to remain constant enough to allow genetic tracking of local fitness optima by this species.

Analyses of spatial processes are included in several of the research goals in all RAs. In 2016 Engen and Sæther published significant new theoretical contributions to spatial population dynamics (Mathematical Biosciences), generalizing previous result on spatial scale of population fluctuations to also include local demographic noise, as well as density dependence acting through the density in the whole home-range of individuals rather than only the density at the mean position of the individual. The concept of demographic noise is particularly important by being the major component of random genetic drift. The results on population dynamics have accordingly been extended to include local selection and random genetic drift in spatial models, providing a number of scaling results for the degree of phenotypic differentiation in space (*Theoretical Population Biology*). These results may provide guidelines for empirical analysis of drift and selection over large areas.

In RA3, two different approaches have been applied to the study of temporal and spatial variation in community dynamics. One approach has been to derive characteristics of community structure using variation in the community correlation (the correlation in log abundances of species sampled at two different times or localities), based on theory developed by CBD members Steinar Engen and Russell Lande in the late 1990's. An excellent illustration of the power of this approach was provided in 2016 in a paper by Engen et al. in *Oikos*, which showed how different assumptions concerning the dynamics of species within an ecological community can affect the turnover rate of species. The second approach was developed by Otso Ovaskainen and collaborators, as outlined in two papers in *Methods in Ecology and Evolution*, and involves application of a latent variable model to facilitate the estimation of species interactions in time and space. These two approaches are nicely complementary, because the latent variable model can be used to explore the validity of critical assumptions involved in the use of the community correlation approach.

In 2016, the collaboration between CBD and other Norwegian research institutions was greatly extended. A major reason for this was the project Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems (SUSTAIN), which is a large integrated project funded by the Research Council of Norway. This project is led by Professor Nils Chr. Stenseth at the Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, with Professor Rolf Anker Ims (the Arctic University of Norway in Tromsø) and Professor Bernt-Erik Sæther (CBD) as co-PIs representing the two other nodes of the project. Several other applied research institutions are also involved in SUSTAIN of which CBD has especially extensive collaborations with our partner NINA, as well as with the Norwegian Computing Centre, the Institute of Marine Research, the Norwegian Polar Institute and the University Centre in Svalbard. The collaboration with CEES and the Norwegian University of Life Sciences was further strengthened in 2016, particularly on development of molecular genetic techniques and analyses of eco-evolutionary processes. Finally, we collaborate extensively with researchers at the Norwegian Institute of Bioeconomy Research on statistical analyses of long-term data and water vole demography

As usual, there was considerable international collaboration at CBD also in 2016, with more than 50 visitors from abroad and frequent participation by CBD members at international congresses, conferences and workshops.

The annual report for 2016 also includes some aspects of the activity by members of CBD during the previous years, and this is because it provides one of the basic documents for the midterm evaluation of CBD in 2017. It should therefore be evident from this report that the activity and productivity of the centre have increased tremendously during the last year, indicating the time it takes from establishment to realize the full potential of such an ambitious centre of excellence.


Photo: Henrik Jensen

Release of translocated house sparrows in Mid-Norway. The birds were part of an artificial selection experiment in the wild.


Photo: Henrik Jensen

Master's students Malene Vågen Dimmen and Marlene Wege Stubberud banding house sparrows at Helgeland.


Photos: Endre Grüner Ofstad

Good foraging conditions and favourable climatic conditions makes the moose population at Vega highly productive. Many females produce twins already at first reproduction.

MAJOR HIGHLIGHTS

PRIZES

In 2013, Professor Steinar Engen and Professor Bernt-Erik Sæther received the Research Council of Norway's Award for Outstanding Research (the Møbius Prize) for their cross-disciplinary research collaboration on dynamics of biological systems.

Professor Steinar Engen, Professor Russell Lande and Professor Bernt-Erik Sæther were awarded the Wildlife Society Prize for the best publication in wildlife ecology and conservation in 2014 for the paper *Evolutionary consequences of non-selective harvesting in density-dependent populations* published in American Naturalist 184 (2014): 716-724.

Associate Professor Arild Husby was in 2016 appointed as a member of the Young Academy of Science.

BOOKS

Otso Ovaskainen, Henrik Johan de Knegt and Maria del Mar Delgado. 2016. Quantitative Ecology and Evolutionary Biology. Oxford University Press, Oxford, UK.

CONFERENCES

The Wild Animal Genomics Meeting 2015 on the use of genomics techniques in natural populations was organized by Arild Husby and Henrik Jensen on June 23-25 2015 in Selbu, Norway. The conference was funded by grants from the Research Council of Norway and CBD. 29 researchers from 9 countries in Europe and North-America attended the workshop. Participants ranged from PhD candidates to well-established and internationally leading researchers within the field.

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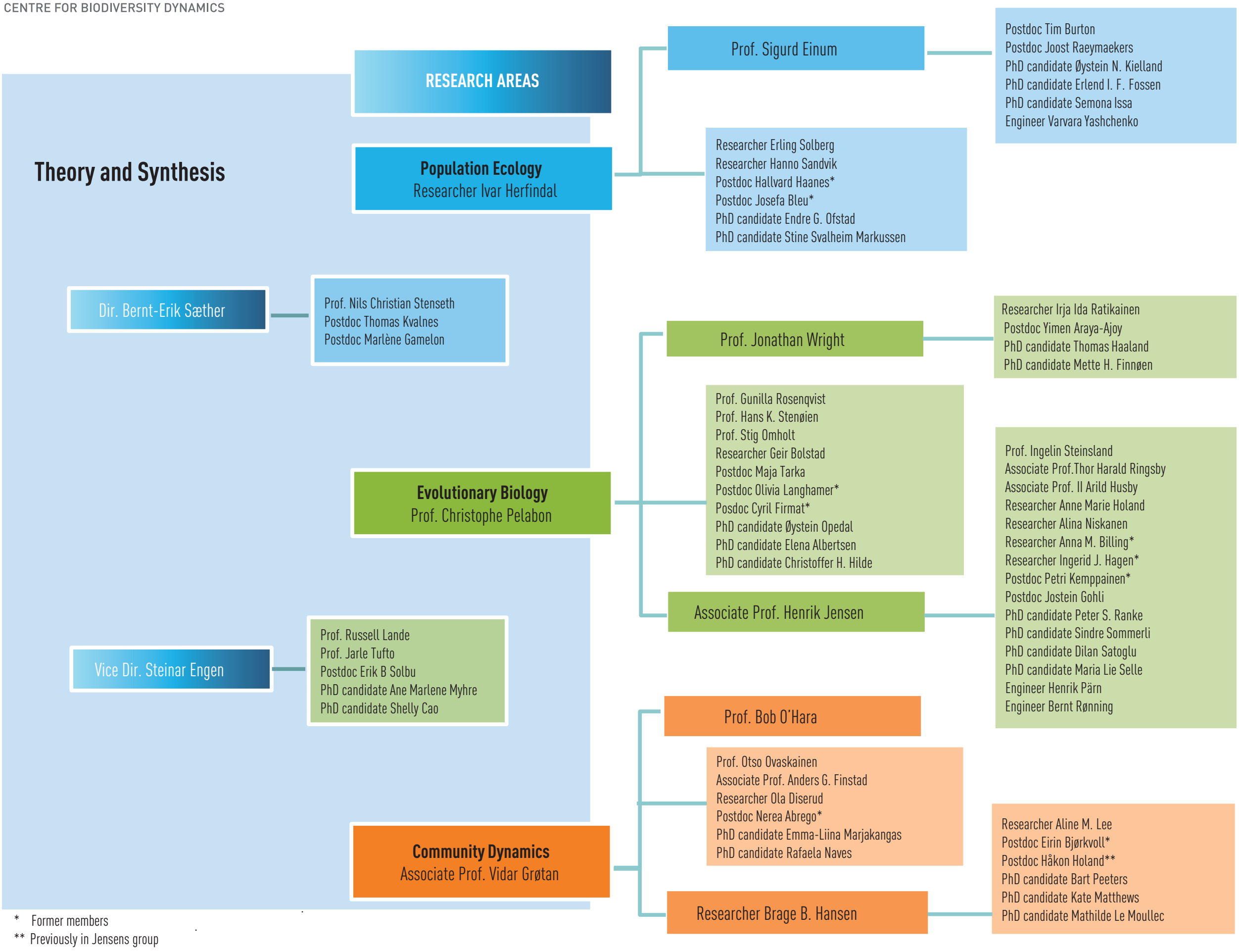
Organization of the research at CBD 2013-2016



RESEARCH AREAS

Theory and Synthesis

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Postdoc Thomas Kvalnes
Postdoc Marlène Gamelon

Vice Dir. Steinar Engen

Prof. Russell Lande
Prof. Jarle Tufto
Postdoc Erik B Solbu
PhD candidate Ane Marlene Myhre
PhD candidate Shelly Cao

Population Ecology
Researcher Ivar Herfindal

Prof. Sigurd Einum

Postdoc Tim Burton
Postdoc Joost Raeymaekers
PhD candidate Øystein N. Kielland
PhD candidate Erlend I. F. Fossen
PhD candidate Semona Issa
Engineer Varvara Yashchenko

Researcher Erling Solberg
Researcher Hanno Sandvik
Postdoc Hallvard Haanes*
Postdoc Josefa Bleu*
PhD candidate Endre G. Ofstad
PhD candidate Stine Svalheim Markussen

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Prof. Jonathan Wright

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PhD candidate Mette H. Finnøen

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PhD candidate Rafaela Naves

Researcher Brage B. Hansen

Researcher Aline M. Lee
Postdoc Eirin Bjørkvoll*
Postdoc Håkon Holand**
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PhD candidate Kate Matthews
PhD candidate Mathilde Le Moullec

* Former members
** Previously in Jensens group

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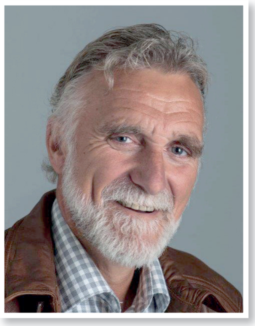
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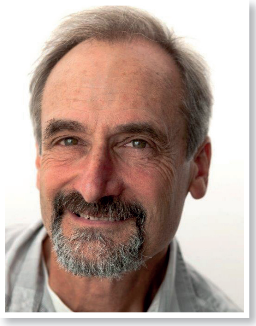
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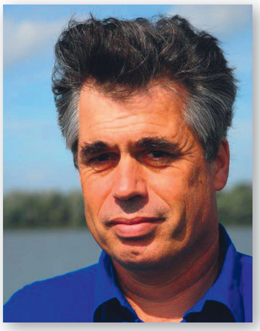
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Professor, Head of Department
Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW),
The Netherlands

ORGANIZATION OF THE RESEARCH AT CBD

The main research activity of CBD is located in two sections in the Natural Sciences Building, at the Department of Biology (IBI), NTNU. In addition, several members are located at the Department of Mathematical Sciences at NTNU. At IBI, CBD also benefits from laboratory facilities, for instance for experiments in the greenhouse and Daphnia lab, as well as access to state-of-the-art equipment for molecular genetic analyses. Important research activity is also going on at the partners, Norwegian Institute for Nature Research (NINA) and NTNU University Museum (VM). These institutions offer infrastructure and expertise in management and sharing of complex ecological and evolutionary data.

The aim of CBD is to improve our ability to predict how changes in the environment (e.g. caused by different forms of human activities) will affect the biological diversity at different organismic levels (genes, species and community). We do this by analysing processes within a common theoretical framework based on stochastic models of dynamics in time and space. The advantage of such a unified approach is that it enables us to include ecologically important processes such as environmental stochasticity and density dependent effects into dynamical models at all organismic level.

In practice, we approach this overall goal by organizing the scientific activity at the centre into three Research Areas (RA). RA1 consists of research in population ecology. The main focus here is mainly to apply various stochastic models to describe population dynamics in time and space, including effects of density-dependence, demographic and environmental stochasticity and fluctuations in age-structure. The aim is to identify parameters that most strongly influence patterns of fluctuations in population size. This requires long time series of population counts, and individual-based demographic data. Unfortunately, such data are available only for a few systems. Some of those (e.g. house sparrows and moose on islands along the Helgeland coast in northern Norway) are operated by CBD. An important task in this RA is therefore to relate variation in parameters affecting the population dynamics to more easily collected variables such as life history characters.

In RA2 the central focus is to understand how rapidly adaptations to changes in environment can evolve. Our approach is to develop models for phenotypic evolution that include ecologically realistic assumptions such as density-dependence and environmental stochasticity. This necessarily involves close theoretical integration between the ecological approaches in RA1 and the evolutionary analyses included in this RA. We apply these models to understand processes which affect the rate of evolutionary responses to changes in the environment, using several natural and experimental study systems (e.g. house sparrow, the plant *Dalechampia*, and the zooplankton *Daphnia*) operated by research groups at CBD. This also requires the application of modern molecular genetic methods to understand the genetic basis of phenotypic response.

The basis for RA3 is that patterns in fluctuations in population size of single species will characterize the form of the distribution of abundances of the species constituting the whole community. A change in the environment will therefore affect the species abundance distribution. In this RA we therefore focus on processes affecting the shape of species abundance distribution. An important topic is also how stochastic fluctuations in the environment will affect the vertical and horizontal trophic interactions among species. These research questions require that the single-species approaches in the other two RAs are extended to include multi-species interactions. An important focus in RA3 is therefore to implement demographic and evolutionary models in the analyses of interspecific interactions.

The different Research Groups (RG) indicated by their Principal Investigator are distributed among the Research Areas (RA) in the following way;

Research Group (RG)	RA1: Population ecology	RA2: Evolutionary biology	RA3: Community dynamics
Einum	X	X	
Engen	X	X	X
Grøtan	X	X	X
Hansen	X		X
Herfindal	X	X	
Jensen	X	X	
Pèlabon		X	X
Sæther	X	X	X
Wright	X	X	


Photo: Bart Peeters

The lack of predation makes the wild Svalbard reindeer particularly suitable for studies of climate effects.

SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

Current group members:
PI: Professor Bernt-Erik Sæther
Postdoc Marlène Gamelon
PhD candidate/postdoc Thomas Kvalnes

Former group member:
Postdoc Eirin Bjørkvoll

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

Bernt-Erik Sæther, Thomas Kvalnes, Marlène Gamelon

One of the central focuses for the research at CBD is to identify predictors that can be used to explain and predict temporal and spatial variation in the dynamics of biological processes. We assume that covariation in basic life history characteristics such as number of offspring produced per reproductive attempt, age of maturity and life expectancy divides species along a 'slow-fast continuum' of life history variation. We expect that position of species along this gradient may characterize the eco-evolutionary dynamics occurring within populations, as well as influence the dynamical consequences of interspecific interactions. An important prerequisite for examining these hypotheses is that age-specific models are available, which have been a central focus for the theoretical work in several of the Research Groups at CBD. An important task in our Research Group has therefore been to parameterize several of these models, using data from suitable model systems either operated by CBD or by our network of collaborating researchers, in order to identify critical parameters that most strongly influence the dynamics. These analyses have provided the foundation for comparative analyses of how interspecific variation in life history characteristics explains differences among species in population dynamics. Another important focus has been to examine how age-specific differences in demography affect the rate of adaptive phenotypic evolution as well as the rate of genetic drift. Our overall aim is to relate evolutionary processes to patterns in population dynamics, which are in turn affected by environmental fluctuations. This enables us to address how environmental changes, often caused by different forms for human actions, may affect the short- and long-term persistence of populations and characteristics of communities.

MAJOR SCIENTIFIC CONTRIBUTIONS

Comparative analyses of population dynamical consequences of life history variation in vertebrates

Several important contributions of this research group to several questions raised in RA1 have been achieved through comparative analyses of how life history variation affects characteristics of the population dynamics. These analyses have been possible through a huge network of international collaborators who have provided long-term studies of individual-based demography in natural populations. For populations of birds and mammals with no density dependence, we approximated population fluctuations with temporal variation in the total reproductive value of the populations. This approach enabled us to cancel out the effects of fluctuations in age-distribution on population size, which could erroneously be interpreted environmental stochasticity. These analyses revealed that variation in age-specific contributions to total reproductive value and to stochastic components of population dynamics was correlated with the position of the species along the slow-fast continuum of life history variation. Younger age-classes (relative to the generation time) accounted for larger contributions to total reproductive value and to demographic stochasticity that declined faster with age in 'slow' than in 'fast' species, where many age-classes contributed more equally. In contrast, fluctuations in population growth rate caused by environmental stochasticity involved a larger proportion of all age-classes independent of life history. Thus, changes in population growth rates can be surprisingly well explained by basic species-specific life history characteristics. However, the long-run growth rate of density-independent populations did not vary with life history neither in birds, mammals nor marine fishes (Bjørkvoll et al. 2014).

Similar comparative analyses of the interrelationship between population dynamics and life history were also performed for bird populations subject to density dependence. Some surprisingly simple patterns emerged: the magnitude of fluctuations in population size are mainly driven by stochastic fluctuations in the environment. Regulation towards an equilibrium population size occurs through density-dependent mortality. At small population sizes, population dynamics are primarily affected by environmental-driven variation in recruitment, whereas close to the carrying capacity *K*, variation in population growth is more strongly influenced by density-dependent mortality of both juveniles and adults. Furthermore, the sensitivity of the population growth rate to variation in population size *N* is more sensitive to variation in adult survival rate when *N* is close to the carrying capacity *K* than at small population size, where the population growth rate is more influenced by variation in fecundity rate. Our results provide evidence for the hypothesis proposed by the English bird ecologist David Lack that population fluctuations in birds arise from temporal variation in the difference between density-independent recruitment and density-dependent mortality during the non-breeding season. These results also show that the population dynamics of species even with quite complex life cycles can be well described by a few processes.

Evolution in age-structured populations

The extension of the classical Robertson-Price equation to age-structured populations derived by Engen and Sæther (see Engen's research group) was applied to analyses of phenotypic evolution in two model systems operated by CBD at the coast off Helgeland in northern Norway. In the house sparrow metapopulation, we analyzed selection on two morphological characters in fledglings: tarsus length and body mass. Although this small passerine species has a relatively simple life history, failure to account for fluctuations in age-distribution resulted in biased estimates of selection on these two characters.

We also applied this approach to analyse selection on body mass of calves and timing of birth of cows in a small harvested population of moose on the island of Vega. This population was probably founded by one male and

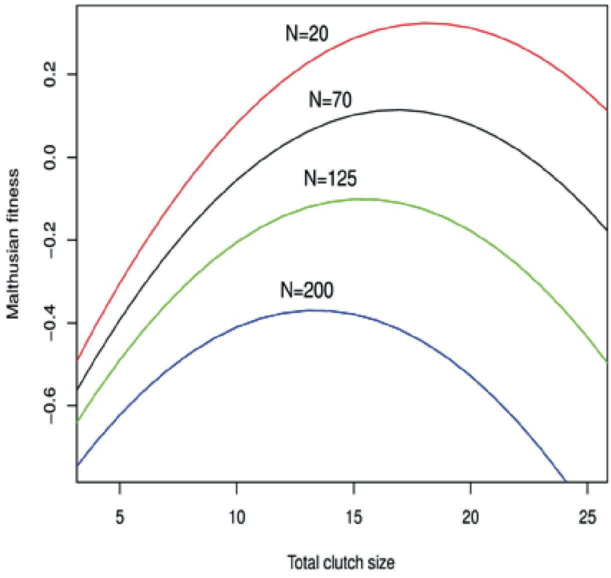


Figure 1. The Malthusian fitness as a function of total clutch size for different population sizes N in a great tit population in Hoge Veluwe, the Netherlands (Sæther et al. 2016b).

2 female yearlings swimming out to this island in 1985. The population grew rapidly and from 1991 hunting was allowed. From 1992 until present almost all individuals have been radio-collared, which has provided detailed long-term individual-based demographic data, as well as construction of genetic pedigrees. Kvalnes et al. (2016) demonstrated harvest-induced directional selection for delayed birth dates in males and reduced body mass as calf in females. During the study period, birth date was delayed by 0.81 days per year for both sexes, while no significant changes occurred in calf body mass. Because there was significant additive genetic variance in both traits, these results show that selective harvesting can induce strong selection which opposes natural selection. This may cause evolution of less favourable phenotypes that become maladaptive once harvesting ceases.

r- and *K*-selection in great tits

Density-dependence plays an important role in regulation of the size of most natural populations. In order to integrate ecological dynamics and evolutionary processes, we have in our research group focused on identifying whether density-dependent effects on the population dynamics affect the rate of phenotypic evolution. According to the theory of *r*- and *K*-selection we would expect that phenotypes with high growth rates at small population sizes would have a disadvantage at population sizes close to the carrying capacity *K*. Using a unique long-term study of temporal variation in the total number of eggs laid per female great tit during a breeding season in a forest population in the Netherlands, we demonstrate strong stabilizing selection.

RECOMMENDED READING:

Kvalnes, T., Sæther, B.-E., Haanes, H., Røed, K.H., Engen, S. and Solberg, E.J. 2016. Harvest-induced phenotypic selection in an island population of moose, Alces alces. *Evolution* 70, 1486–1500.

Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K.B., Barbraud, C., Becker, P.H., Blumstein, D.T., Dobson, F.S., Festa-Bianchet, M., Gaillard, J.-M., Jenkins, A., Jones, C., Nicoll, M.A.C., Norris, K., Oli, M.K., Ozgul, A. and Weimerskirch, H. 2013. How life history influences population dynamics in fluctuating environments. *American Naturalist* 182, 743–759.

Sæther, B.-E., Grøtan, V., Engen, S., Coulson, T., Grant, P.R., Visser, M.E., Brommer, J.E., Grant, B.R., Gustafsson, L., Hatchwell, B.J., Jerstad, K., Karell, P., Pietiainen, H., Roulin, A., Rostad, O.W. and Weimerskirch, H. 2016a. Demographic routes to variability and regulation in bird populations. *Nature Communications* 7, 12001.

Sæther, B.-E., Visser, M.E., Grøtan, V. and Engen, S. 2016b. Evidence for *r*- and *K*-selection in a wild bird population: a reciprocal link between ecology and evolution. *Proceedings of the Royal Society of London* B 283, 20152411.

Photo: Geir Rune Løvstad

Som eof the theories about age-spesific density dependence is currently being tested based on data from a population of white-throated dipper, in collaboration with CEES in Oslo

Research Area 1

RESEARCH GROUP: ECO-EVOLUTIONARY DYNAMICS – AN EXPERIMENTAL APPROACH

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

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

Erlend I. F. Fossen, Joost Raeymaekers, Øystein N. Kielland, Sigurd Einum. Not present: Tim Burton, Semona Issa and Varvara Yashchenko

A fundamental aim in ecology is to understand how organisms respond to changing environmental conditions. Empirical studies typically focus either on the direct and immediate effects on individual characteristics (such as growth rate, longevity, fecundity) and corresponding effects on population abundance changes, or on long-term evolutionary changes. Yet, it is becoming increasingly clear that these two processes occur simultaneously and may influence each other. For example, an environmental change may cause mean reproductive success to decrease, which in turn may cause the population abundance to decline. At the same time, the environmental change may cause certain individual characteristics to be favoured (i.e. having higher fitness) over other previously favoured phenotypes, resulting in evolutionary change. This in turn may cause further change in population abundance. Conversely, change in population abundance may, in itself, cause change in which characteristics have the highest fitness through what is called density-dependent selection. Understanding such feedback mechanisms is challenging, and choice of appropriate model systems is crucial for successful studies. In our research group we use a highly suitable zooplankton model organism (*Daphnia*), which is representative for a wide range of key species in freshwater and marine food webs, and our focus is on one easily controlled environmental factor (temperature). We study target traits that may have strong effects on fitness and that also depend on both temperature and population density, and we determine their potential for evolutionary change (Fig. 1). Our aim is to obtain results that yield a novel understanding of links between ecological (RA1) and evolutionary (RA2) responses to environmental change.

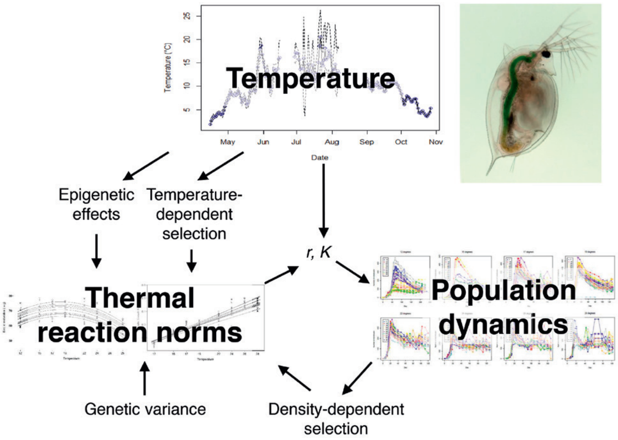


Fig. 1. Our research group focuses on understanding the complex effects of environmental change on the ecology and evolution of organisms through lab experiments using the model organism *Daphnia*.

Major scientific contributions

The important contributions from our group so far involve tests of two hypotheses related to the effect of the environment on phenotypes. By improving experimental designs and developing protocols for accurate measurements of metabolic rates, we have obtained results that cast doubt on a number of previous studies. Our interest in metabolic rate is inspired by its crucial role in how organisms influence their environment (through consumption), and how they are affected by environmental change (e.g. temperature or food abundance, Einum 2014).

Density-dependent metabolic rates?

Population density has recently been suggested to be an important factor influencing metabolic rates, and to represent an important 'third axis' explaining variation beyond that explained by body mass and temperature. In situations where population density influences food consumption, the immediate effect on metabolism acting through specific dynamic action (SDA), and down-regulation due to fasting over longer periods, is well understood. However, according to a recent review, previous studies suggest a more general effect of population density per se, even in the absence of such effects. It has been hypothesized that this results from animals performing anticipatory responses (i.e. reduced activity) to expected declines in food availability. Yashchenko et al. (2016) tested the generality of this finding by measuring density effects on metabolic rates in 10 clones from two different species of *Daphnia*. They also identified additional studies on this topic that were not included in the previous review, compared the results, and evaluated the potential for measurement bias in all previous studies. Significant variation in mass-specific metabolism was found among clones within both species (Fig. 1). However, there was no evidence for a negative relationship between population density and mass-specific metabolism. The previously reported pattern also disappeared when the set of studies analysed was extended. Potential reasons for the discrepancy among studies includes two main sources of bias: microbial respiration and declining oxygen consumption due to reduced oxygen availability. Only one of the previous studies gives sufficient information to conclude an absence of such biases, and in that study no effect of population density on metabolism was found. Yashchenko et al. conclude that population density per se does not have a general effect on mass-specific metabolic rate.


Photo: Christophe Pélabon

Sampling of *Daphnia magna* from Værøy, Lofoten, northern Norway. This is one of the populations that are currently studied in the CBD *daphnia* lab.

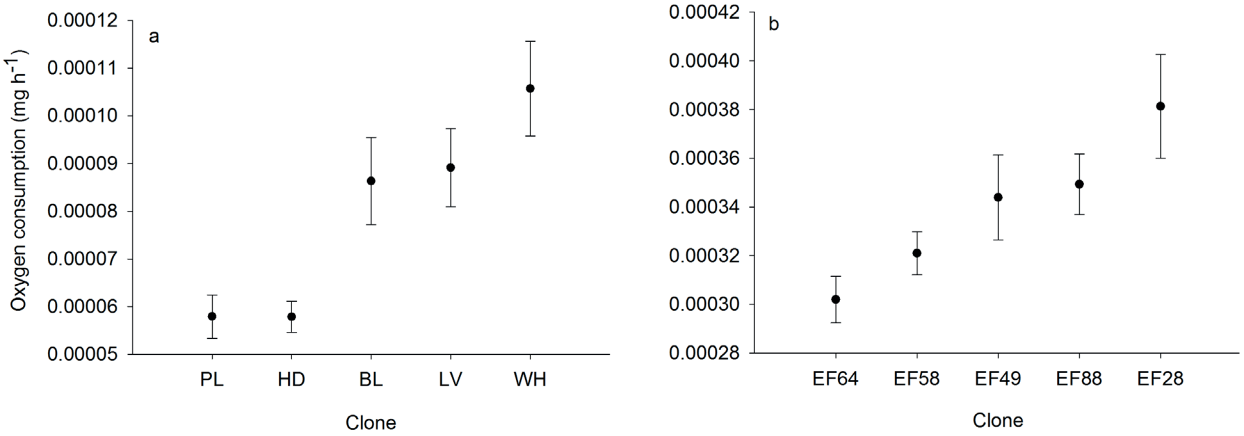


Fig. 2. Individual oxygen consumption rate (mass standardized) of (a) *D. pulex* and (b) *D. magna*, showing significant among-clone variation.

Thermal transgenerational plasticity in metabolism?

Environmental change may cause phenotypic changes that are inherited across generations through transgenerational plasticity (TGP). If TGP is adaptive, offspring fitness increases with an increasing match between parent and offspring environment. Kielland et al. (2016) tested for adaptive TGP in somatic growth and metabolic rate in response to temperature in *Daphnia pulex*. Animals of the first focal generation experienced thermal transgenerational "mismatch" (parental and offspring temperatures differed), whereas conditions of the next two generations matched the (grand)maternal thermal conditions. Adjustments of metabolic rate occurred during the lifetime of the first generation (i.e. within-generation plasticity). However, no further change was observed during the subsequent two generations, as would be expected under TGP. Furthermore, there was no tendency for increased juvenile somatic growth (a trait highly correlated with fitness in *Daphnia*) over the three generations when reared at new temperatures. These results are inconsistent with existing studies of thermal TGP, and Kielland et al. (2016) describe how previous experimental designs may have confounded TGP with within-generation plasticity and selective mortality, and suggest that the current evidence for thermal TGP is weak.

Sampling of *Daphnia magna* from Værøy, Lofoten, northern Norway. This is one of the populations that are currently studied in the CBD *daphnia* lab.

RECOMMENDED READING:

Einum, S. 2014. Ecological modeling of metabolic rates predicts diverging optima across food abundances. *American Naturalist* 183, 410–417.

Yashchenko, V., Fossen, E.I., Kielland, Ø.N. and Einum, S. 2016. Negative relationships between population density and metabolic rates are not general. *Journal of Animal Ecology* 85, 1070–1077.

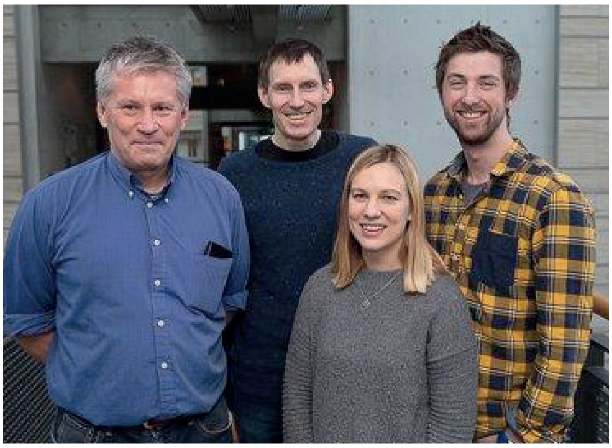
Kielland, Ø.N., Bech, C. and Einum, S. 2016. No evidence for thermal transgenerational plasticity in metabolism when minimizing the potential for confounding effects. *Proceedings of the Royal Society of London B*, In press.

RESEARCH GROUP: DEMOGRAPHIC RESPONSES TO A CHANGING ENVIRONMENT

Current group members:
PI: Researcher Ivar Herfindal
Senior Researcher Erling Johan Solberg
Researcher Hanno Sandvik
PhD candidate Stine Svalheim Markussen
PhD candidate Endre Grüner Ofstad

Former group members:
Postdoc Josefa Bleu
Postdoc Hallvard Haanes

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



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

Individuals and populations are affected by the environmental conditions they experience. Factors such as habitat and resource availability generate spatial patterns in individual traits and population properties. Temporal variation, for example in climatic conditions, can have population dynamical consequences. However, the relationship between climate and populations may depend on the habitat, generating complex links between temporal and spatial variation in environmental conditions and their influence upon individuals, populations and species (Fig. 1). In this research group we aim to understand how individual traits and population properties vary in time and space in relation to variation in factors such as habitat, food availability and quality, weather and climate, but also accounting for species and population properties such as life history and density. We do this by examining carefully selected study systems with a high spatial and/or temporal dimension of the data.

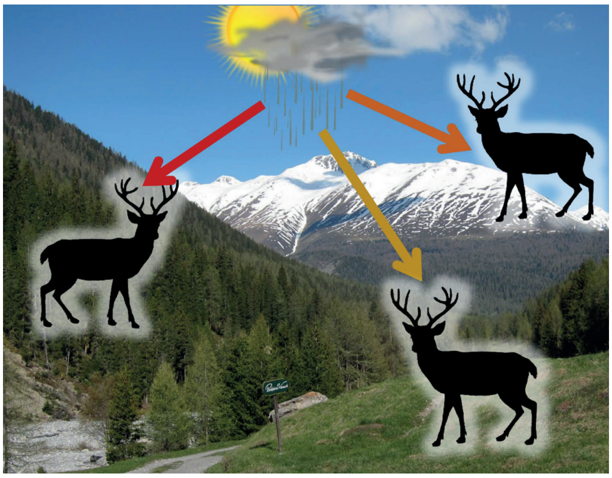


Fig. 1. Properties of individuals and populations are related to the habitat they live in, and by weather and climate. The effect of weather is modified by the habitat, giving complex interactions between temporal and spatial environmental conditions and their influence on individuals, populations and species.

MAJOR SCIENTIFIC CONTRIBUTIONS

Spatial variation in population properties

Factors such as habitat and climate determine the spatio-temporal predictability of food resources, which for example is a key factor explaining the distribution of sea bird colonies along the Norwegian coast (Sandvik et al. 2016). Understanding the relationship between these factors and variation in animal traits and performance is important both from a conservation point of view, and for understanding ecological mechanisms behind variation in nature. For instance, both the life history traits of moose and the demographic rates of two forest grouse species have been shown to be positively related to the diversity of habitat types (Herfindal et al. 2014a, Lande et al. 2014). For forest grouse, the relationship differed between chicks and adults, suggesting that the relationship between environmental conditions and performance may differ between life history stages. A next step that we are currently working on is to explore the spatial scale of these population differences using data from systems with contrasting spatial characteristics in environmental variation, such as comparing terrestrial versus marine species.

However, genetics is also important for spatial variation in population properties. Indeed, for the Norwegian moose, the genetic structure has stronger power in explaining body mass variation than any of the environmental variables. Still, the fact that the genetic structure often is shaped by landscape properties and that habitat has a strong influence on population properties, suggests a spatial structuring of populations corresponding to the geographical structure of landscape characteristics and environmental fluctuations.

Individual heterogeneity in reproductive performance

To fully understand population dynamical responses to environmental variation, one needs to understand the causes of individual variation in demography. One example illustrating this is the study on goshawk by Herfindal et al. (2015, Fig. 2) documenting complex relationships between climatic conditions and short- versus long-term variation in individual reproductive success. The same environmental conditions (April temperature) had contrasting effects on immediate versus long-term reproductive performance. These negative co-variances in environmental effects were further complicated by the fact that offspring hatched under harsh climatic conditions benefitted in terms of relaxed density-dependent effects during early life. Individual differences in reproductive performance may also be related to behavioural differences, such as large-scale movement tactics found in many moose populations (Rolandsen et al. 2016). However, the rapid environmental change in many ecosystems may alter the benefit of long-distance movements between summer and winter ranges, leading to changes in the spatio-temporal distribution of individuals.

These findings highlight the need to assess age- or stage-specific relationships between environmental variation and density dependence in order to understand and predict population response to environmental variation, such as climate change. However, genetics also has a central role here in combination with population structure. In the small and isolated moose population on Vega, lack of mating possibilities due to skewed sex ratios and small population sizes increased the level of inbreeding, with negative effects on fitness (Herfindal et al. 2014b). This provides a direct link between RA1 and RA2.

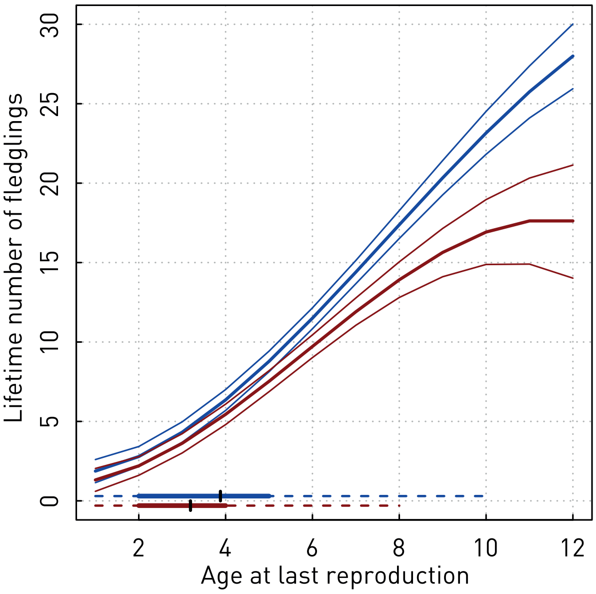


Fig 2. The relationship between lifespan and lifetime number of fledglings in female goshawk hatched in years with cold (blue) and warm (red) April temperature. During warm years a higher proportion of females bred, generating negative covariances between climatic effects on short- and long-term performance.

Comparative analyses of individual variation and population properties

Responses to environmental variation may vary among individuals, and it is vital to understand if such individual heterogeneity in demography affects population dynamical characteristics. A comparative study on two chamois populations documented contrasting age-specific differences in reproductive performance (Bleu et al. 2015). As a result, the age segment that was most sensitive to environmental variation differed between the two populations. This has implications for the possibility to generalise findings from one to many populations, but also for how management strategies can be locally adapted.

Previous and current research form this group revealed how environmental conditions such as habitat can structure populations in space. Greater understanding of these processes is needed, because habitat also affects patterns of space use, which impacts both gene flow and the spatial structuring of population properties. Moreover, changes in the distribution of animals in time and space may be altered following anthropogenic impacts on ecosystems. Based upon the studies in this Research Group, it is evident that it is important to understand how such factors shape individual heterogeneity within a population. At the same time, we need to scale up from one or a few populations, to large-scale (multi-species) analyses in order to understand the processes behind the spatial structuring of populations. This is demanding in terms of the data needed. However, given recent developments in the relevant theoretical frameworks (see e.g. the research groups of Engen and Grøtan), and participation in large-scale ecological research projects, we are confident that significant progress will be made the coming years.

RECOMMENDED READING:

Bleu, J., Herfindal, I., Loison, A., Kwak, A.M.G., Garel, M., Toïgo, C., Rempfler, T., Filli, F. and Sæther, B.-E. 2015. Age-specific survival and annual variation in survival of female chamois differ between populations. *Oecologia* 179, 1091–1098.

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Herfindal, I., Haanes, H., Solberg, E.J., Røed, K.H., Høgda, K.A. and Sæther, B.-E. 2014. Moose body mass variation revisited: disentangling effects of environmental conditions and genetics. *Oecologia* 174, 447–458.

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Lande, U.S., Herfindal, I., Willebrand, T., Moa, P.F. and Storaas, T. 2014. Landscape characteristics explain large-scale variation in demographic traits in forest grouse. *Landscape Ecology* 29, 127–139.

Rolandsen, C.M., Solberg, E.J., Sæther, B.-E., van Moorter, B., Herfindal, I. and Bjørneraas, K. 2016. On fitness and partial migration in a large herbivore – migrant females have higher reproductive performance than resident females. *Oikos*, in press.

Sandvik, H., Barrett, R.T., Erikstad, K.E., Myksvoll, M.S., Vikebø, F., Yoccoz, N.G., Anker-Nilssen, T., Lorentsen, S.-H., Reiertsen, T.K., Skarðhamar, J., Skern-Mauritzen, M. and Systad, G.H. 2016. Modelled drift patterns of fish larvae link coastal morphology to seabird colony distribution. *Nature Communications* 7, 11599.

Sandvik, H., Reiertsen, T.K., Erikstad, K.E., Anker-Nilssen, T., Barrett, R.T., Lorentsen, S.-H., Systad, G.H. and Myksvoll, M.S. 2014. The decline of Norwegian kittiwake populations: modelling the role of ocean warming. *Climate Research* 60, 91–102.

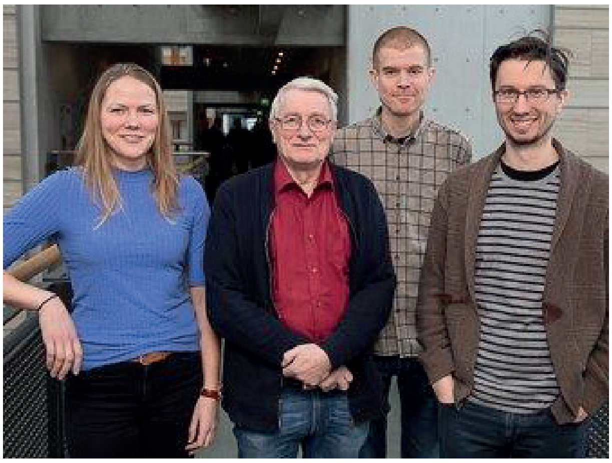
A peak into a breeding colony of kittiwakes in northern Norway.

Photo: Ivar Herfindal

RESEARCH GROUP: STOCHASTIC THEORIES

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

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



Ane Marlene Myhre, Steinar Engen, Jarle Tufto, Erik Blystad Solbu.
Not present: Russel Lande

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, members of this research group actively interact with members of most of the other research groups. Our modelling approach can be divided into two parts. One major approach is to extend stochastic models that describe the dynamics of populations of a single species, which were summarized in the book *Stochastic Population Dynamics in Ecology and Conservation* published by Lande, Engen and Sæther by Oxford University Press. We will do this by developing demographic models that include multi-species interactions as well as dynamic models of whole communities consisting of many species. Another major approach for our modelling effort is to include ecologically realistic assumptions such as density-dependence and environmental stochasticity into population genetic theory and models applied in quantitative genetics. A central focus has been to include age-dependent variation in vital rates in the models because interspecific differences in basic life history characteristics have been generally assumed to be essential for explaining differences in eco-evolutionary dynamics.

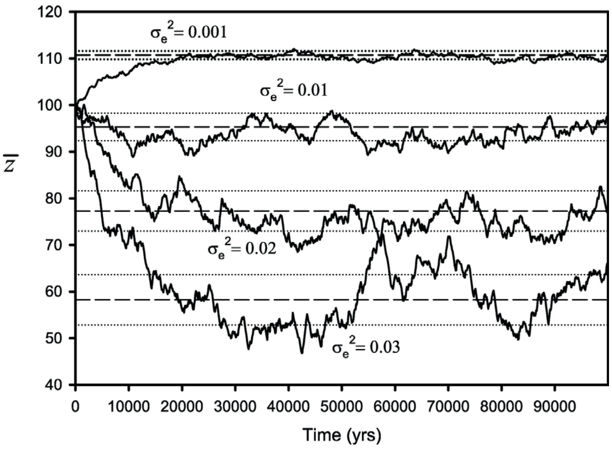


Fig. 1. Variation over time in the mean value across all individuals in the population of a character, $\bar{z}$, subject to r- and K-selection for different degrees of stochastic variation in the environment, σ_e^2. The mean of the character fluctuates around a give value, dashed lines, with a considerable standard deviation (dotted lines), which depends upon the magnitude of the environmental stochasticity.

MAJOR SCIENTIFIC CONTRIBUTIONS

Phenotypic evolution in age-structured populations

The concept of individual fitness provided the foundation for Alan Robertson and George R. Price when they derived exact mathematical expressions for evolutionary change in the mean phenotype during one time step (e.g. a year or generation). This equation simply consists of two terms. The first term is the selection differential, which is the covariance between relative fitness and the trait. The second term is a transmission term generated by the difference in phenotypes between adults and their offspring. Thus, the Robertson-Price equation, originally formulated using fitness across generations, enables statistical analyses of how phenotypes respond to phenotypic selection, and how this response is affected by changes in the environment (e.g. as a consequence of trophic interactions). Our partitioning of the covariance formulation of the selection differential provides a method for separating the effects of selection due to random variation in individual fitness from fluctuating selection caused by environmental variation (Engen and Sæther 2014).

Another advantage of this covariance approach in studies of selection is that it enables us to account for fluctuations in the age-distribution, which can cause temporal changes in the mean phenotype that can mistakenly be interpreted as selection. Engen et al. (2014a) show that these fluctuations in the mean phenotype will disappear if a reproductive value weighting is applied. Changes in any weighted mean phenotype in an age-structured population can then be decomposed into between- versus within- age class components. An advantage of using reproductive value weighting is that the between-age class component then becomes pure noise, generated by previously existing genetic drift or fluctuating selection.

r- and K-selection in fluctuating environments

The concept of r- and K- selection was proposed five decades ago by MacArthur and Wilson in their classic book *The Theory of Island Biogeography* to describe how fitness of different life history phenotypes may depend on population size. An important aspect of this theory is that it assumes that phenotypes with large growth rates at small population sizes have lower fitness at population sizes close to the carrying capacity K, where they are out competed by phenotypes that are better adapted to high densities. Therefore, this process can be studied as fluctuations in Malthusian fitness, due to environmentally driven fluctuations in population density (Engen et al. 2013). This novel theoretical approach is applicable to empirical studies of phenotypic evolution (Sæther and Engen 2015). Engen et al. (2013), show that evolution will move towards the value maximizing a function that expresses the mean population size for a given mean phenotypic value $\bar{z}$. Although the expected evolution of $\bar{z}$ corresponds to an increase of this function, environmental stochasticity will always perturb it back to values slightly below the maximum such that $\bar{z}$ shows temporarily stationary fluctuations over time around the long-term optimal phenotypic value. As environmental variance increases, larger values of r are favoured, producing r-selection. An important advantage of this theory is that it provides a framework for the empirical analyses of the balance between r- and K-selection. A trade-off between r and the strength of density dependence (or between r and K) is necessary for r- and K-selection to occur, because otherwise the evolution of the mean phenotype would always increase $\bar{r}$ and decrease $\bar{\gamma}$, resulting in positively correlated selection for large $\bar{r}$ and K. Some empirical evidence now suggests that such a trade-off may be present in natural populations (see Research Group of Sæther).

The major advantage of using this approach is that it enables us to include important processes known to affect fluctuations in population size, such as density dependence and stochastic variation caused by demographic and environmental stochasticity in models of phenotypic evolution. We can also apply this theory to analyse how different human activities, such as harvesting, can affect the population's ability to adapt to a changing environment (Engen et al. 2014b).

Effective size of density regulated populations

The effective population size is a central concept in evolutionary biology, because it determines the rate of genetic drift. For populations that fluctuate in size, the harmonic mean across generations is commonly used as a proxy for the effective size. However, this assumes no density-dependence, which makes it difficult to assess how density regulation will affect evolutionary processes. A study of Myhre et al. (2015) shows that density regulation and environmental stochasticity must be included in order to obtain meaningful estimates of effective sizes of natural populations.

Evolution in spatially auto-correlated environments

A phenomenon that is poorly understood is how spatial auto-correlation in the environment affects the synchrony in fluctuations in the size of populations separated in space. An important theoretical foundation for the empirical analysis of such spatial processes was provided in a model developed by Engen and Sæther (2016a). This enabled us to assess how demographic stochasticity affects the spatial scaling of synchrony in population fluctuations. An important finding here was that the effects of demographic stochasticity are closely dependent upon the interactions of other parameters, such as the strength of density dependence. Engen and Sæther (2016b) were also able to derive expressions for how ecological dynamics at single locations and spatial auto-correlations in the environment will affect how the rate of phenotypic evolution changes as a function of the distance between the populations. Both of these models illustrate how important it is to consider any assumptions about demographic stochasticity in analyses of dynamical processes in space.

Evolution of plastic responses

Plasticity is an individual's ability to adapt to the present state of the environment by non-genetic phenotypic changes. The ability to perform such adaptions, however, may be genetically determined. Tufto (2015) made a significant contribution to understanding the evolution of this ability in a stochastic environment, also considering diversification bet-hedging as an adaptive response.

RECOMMENDED READING:

Engen, S. and Sæther, B.-E. 2014. Evolution in fluctuating environments: decomposing selection into additive components of the Robertson-Price equation. *Evolution* 68, 854–865.

Engen, S., Kvalnes, T. and Sæther, B.-E. 2014a. Estimating phenotypic selection in age-structured populations by removing transient fluctuations. *Evolution* 68, 2509–2523.

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Engen, S., Lande, R. and Sæther, B.-E. 2013. A quantitative genetic model of r- and K-selection in a fluctuating population. *American Naturalist* 181, 725–736

Engen, S. and Sæther, B.-E. 2016a. Spatial synchrony in population dynamics: The effects of demographic stochasticity and density regulation with a spatial scale. *Mathematical Biosciences* 274, 17–24.

Engen, S. and Sæther, B.-E. 2016b. Phenotypic evolution by distance in fluctuating environments: The contribution of dispersal, selection and random genetic drift. *Theoretical Population Biology* 109, 16–27.

Myhre, A.M., Engen, S. and Sæther, B.-E. 2016. Effective size of density-dependent populations in fluctuating environments. *Evolution* 70, 2431–2446.

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Photo: Ivar Herfindal

Small passerines such as the blue tit are used to apply the theoretical models developed at CBD in natural systems.

RESEARCH GROUP: EVOLUTIONARY DYNAMICS OF QUANTITATIVE CHARACTERS IN FLUCTUATING ENVIRONMENTS

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

Former group member:
Postdoc Cyril Firmat

Aim: To develop and test models on the effects of the genetic architecture of complex characters on their evolutionary dynamics in fluctuating environments

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

The activity of this research group is directly linked to the RA2 which aims at developing predictive models for the evolutionary dynamics of quantitative traits in fluctuating environment. By focusing on the role of the genetic architecture on phenotypic evolution, this group is testing the generality of the Lande equation which represents the foundation of the theory developed by other groups in RA2.

The ability of populations to adapt to new environments (i.e. their evolvability) depends on their level of genetic variation as described by the Lande equation $\Delta z = G\beta$, where z is the mean phenotype, β is the selection gradient vector and G is the additive genetic variance of the trait. However, the presence of genetic variation in a particular trait does not guarantee its evolvability, because genetic correlation with other traits may strongly diminish evolvability in particular directions (Fig. 1). Because complex characters are inherently multivariate, their genetic architecture (i.e. patterns of covariation among components) may constrain the direction and the magnitude of their response to selection. Predicting the ability of such complex characters to evolve therefore requires understanding how different genetic architectures affect evolutionary trajectories. Combining artificial selection experiments, field studies and meta-analyses, the group is studying the constraining effect of different types of genetic architecture on the evolution of multivariate characters.

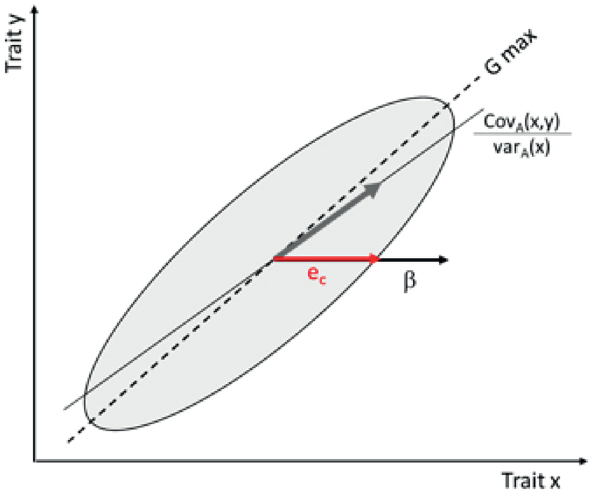

Fig. 1 Effects of the genetic correlation between two traits X and Y on the response to selection. If selection is acting on X only (β), the response to selection (grey arrow) will be aligned with the slope of the genetic regression between X and Y (solid black line). The response to selection is expected to be maximal if β is aligned with Gmax and minimum when β is perpendicular to g_{max}. Furthermore, if Y is under stabilizing selection, the evolvability of X will be strongly diminished as represented by the conditional evolvability e_c (red arrow).

MAJOR SCIENTIFIC CONTRIBUTIONS

Based upon a framework developed by Hansen and collaborators to measure the constraining effects of genetic correlations on evolutionary potential, Bolstad et al. (2014) developed a series of predictions concerning the different relationships expected between evolvability of complex characters and the patterns of phenotypic divergence among populations, under drift or different types of selection. Testing these predictions on high quality data, they demonstrated that directions of preferential evolution (i.e. directions in the multivariate phenotypic space showing the highest variation among populations) were often congruent with the directions of highest multivariate genetic variance.

In collaboration with D. Houle (Florida State University), the group performed a series of artificial selection experiments on the allometric relationship between morphological traits of the *Drosophila* wing (Bolstad et al. 2015). This study was the first to test how much covariance (i.e. the direction of the relationship) between strongly correlated traits could be changed by selection. This study revealed that not only the covariance between traits was very difficult to alter, but that the changes obtained by artificial selection rapidly disappeared when selection stopped, most likely due to internal developmental constraints.

Using *D. scandens,* for which we had particularly good quantitative genetic data on large number of floral traits (Bolstad et al. 2014), the group also tested the evolvability of complex characters in a natural environment. Opedal et al. (2016) combined phenotypic selection studies with population genetics data (Fst) and morphological divergence among ca. 20 populations of *Dalechampia scandens* from Costa Rica. They first showed that, due to variation in the pollinator fauna, patterns of selection changed from population to population. Furthermore, herkogamy (the physical separation between male and female organs in hermaphroditic flowers), a multivariate character influencing plant mating system, was able to genetically track selective optima defined by the pollinator reliability at a small geographical scale (Opedal et al. 2016, see Fig. 2). This result confirmed the high evolutionary potential of herkogamy found earlier in this plant species.

RECOMMENDED READING:

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Bolstad, G.H., Hansen, T.F., Pèlabon, C., Falahati-Anbaran, M., Perez-Barrales, R. and Armbruster, W.S. 2014. Genetic constraints predict evolutionary divergence in Dalechampia blossoms. *Philosophical Transactions of the Royal Society of London B* 369, 20130255.

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.

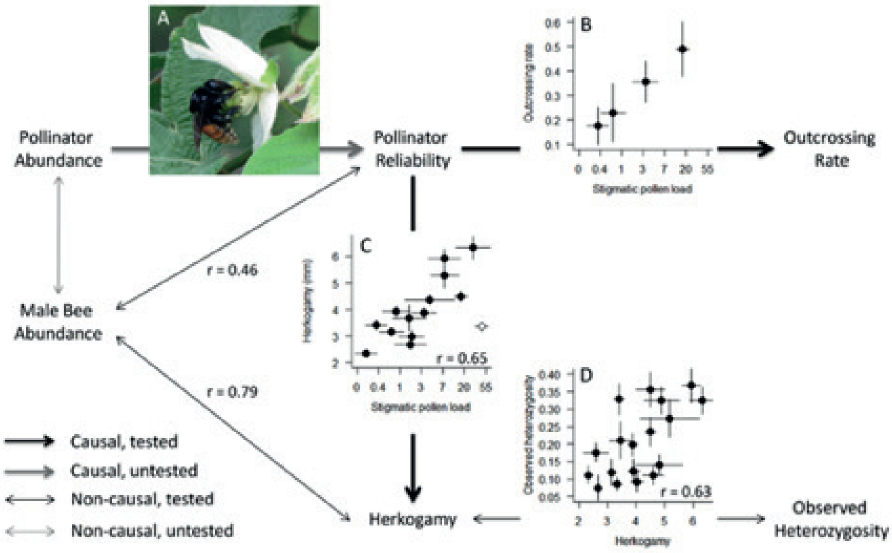
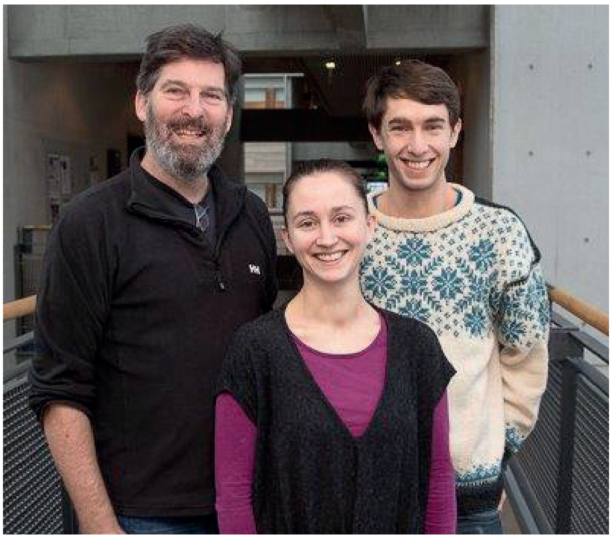


Fig. 2 Relationships between pollinator reliability (selection), herkogamy (quantitative traits affecting the level of self-pollination), outcrossing rate (the short term consequence of selfing) and observed heterozygosity (long term consequences of selfing) in populations of *D. scandens* from Costa Rica (From Opedal et al 2016).

RESEARCH GROUP: ADAPTATIONS TO PREDICTABLE AND UNPREDICTABLE ENVIRONMENTAL CHANGE

Current group members:
PI: Professor Jonathan Wright
Researcher Irja Ida Ratikainen
Postdoc Yimen Araya-Ajoy
PhD candidate Thomas Haaland
PhD candidate Mette H. Finnøen

Aim: To explore adaptive evolution in fluctuating environments



Jonathan Wright, Irja Ida Ratikainen, Thomas Haaland. Not present: Yimen Araya-Ajoy and Mette H. Finnøen.

This research group is in practice run by Wright and Ratikainen as joint PIs, 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 life history, morphological, physiological and behavioural traits, and to testing them on model organisms, such as house sparrows and zebrafish.

Quantifying individual differences in plastic traits such as behaviours is crucial for understanding their evolution. As an extension of work on animal personality and behavioural syndromes, we have been borrowing statistical approaches to trait (co-)variation from quantitative genetics and applying them to various problems in evolutionary behavioural ecology. For example, social reaction norms conceptualize the various genetic and environmental sources of individual phenotypic variation we expect to see in adaptively flexible social strategies that mediate all cooperative and competitive interactions within populations.

Phenotypic plasticity is obviously an adaptation to predictable environmental variation, but we have been investigating how it evolves in unpredictable environments alongside specific responses to environmental uncertainty, such insurance, risk-sensitivity and bet-hedging. In this way, we seek to understand the eco-evolutionary dynamics of fast versus slow paces-of-life (POL), and how these contrasting life histories generate phenotypic (co-)variation (or pace-of-life syndromes, POLS) with other morphological, physiological and behavioural traits at the levels of the individual, the social group, the population and species.

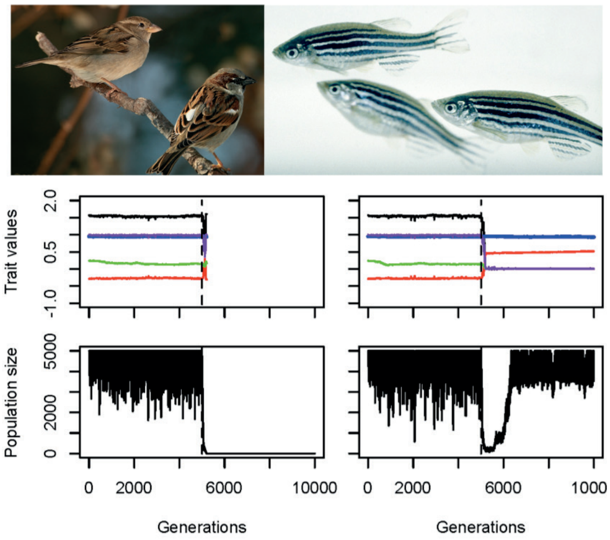


Fig. 1 Examples of study species (house sparrows and zebrafish) and an evolutionary simulation model in the Wright/Ratikainen research group Adaptations to predictable and unpredictable environmental change.

Major scientific contributions

Adaptations to environmental variation – a conceptual framework

Environmental variation is becoming more frequent and unpredictable as a consequence of anthropogenic change, yet we currently lack the tools to evaluate the extent to which organisms can adapt to this phenomenon. Botero et al. (2015) involves a conceptually unifying individual-based simulation model concerning a variety of evolutionary responses to environmental change. The model assumes a very simple genetic architecture. The main result is that different combinations of environmental predictability and the timescale of environmental variation produce distinct regions where a single class of response (reversible phenotypic plasticity, irreversible phenotypic plasticity, bet-hedging, or adaptive tracking) has a clear selective advantage over all others (Fig. 2). Our model also indicates that although populations can often cope with fairly large changes in these environmental parameters within each region, on occasions when they are forced across the boundaries between regions populations will collapse abruptly and go extinct. We characterize the conditions as 'evolutionary tipping points' and discuss how vulnerability to such cryptic threats may depend upon the specific genetic architecture and life history of the organisms involved. These insights are aimed at helping to identify and address some of the threats to natural populations from natural or human-induced changes in environmental conditions. They also demonstrate the value of evolutionary thinking in the study of effects such as global climate change.

The evolution of phenotypic plasticity in changing environments

Phenotypes vary hierarchically among taxa and populations, among genotypes within populations, among individuals within genotypes, and also within individuals for repeatedly expressed labile phenotypic traits. This hierarchy produces some fundamental challenges to clearly defining biological phenomena and constructing a consistent explanatory framework. To address this challenge, as part of a wider group of collaborative partners, we are combining approaches from behavioural ecology and quantitative genetics to better understand the evolution of phenotypic plasticity. Using heuristic statistical models and the concept of the reaction norm, Westneat et al. (2015) explore phenotypic variation among individuals alongside within-individual plasticity variance in labile phenotypes (behaviour, physiology, and sometimes morphology). A statistical partitioning of phenotypic variance using the phenotypic equation (see Fig. 3) allows us to explore an array of additional processes that may influence within- and between-individual phenotypic variance, including interactions between environmental factors, uncertainty regarding the exact environmental conditions, and various types of adaptive phenotypic variance (e.g. risk sensitivity, diversification bet-hedging). Our framework for investigating phenotypic plasticity in the context of predictable and unpredictable environmental variation reveals that interactions between levels of the hierarchy form the preconditions for the evolution of all types of plasticity, and this idea can be usefully extended to the

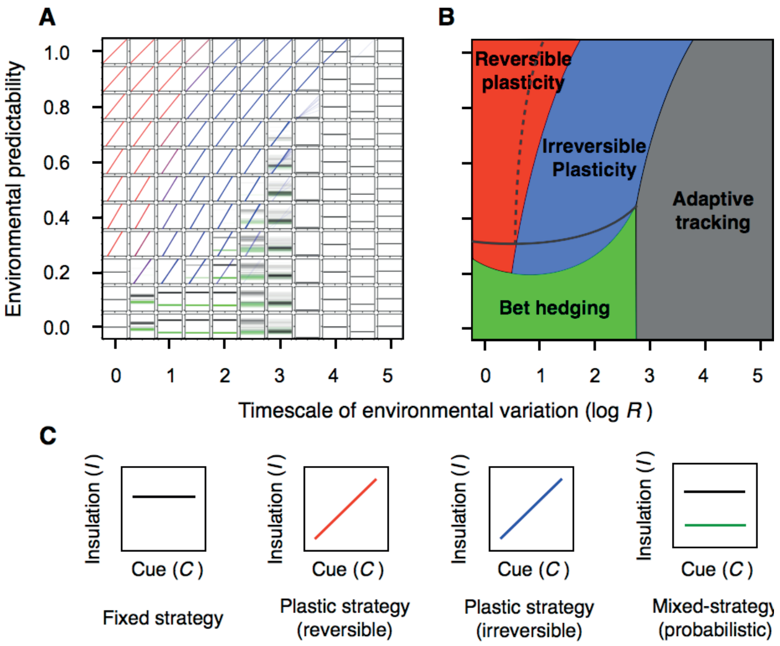


Fig.2. The four different classes of adaptive strategies (reversible phenotypic plasticity, irreversible phenotypic plasticity, bet-hedging, or adaptive tracking) that evolve in response to different timescales of environmental change (R=1= one generation) and predictability (P= 0 = completely unpredictable; P= 1 = completely predictable). The norm of reaction plots for each part of parameter space depict the mean strategies of 5,000 individuals (at generation 50,000) from over 100 different simulations each. These reaction norms are colour-coded according to the type of strategy.

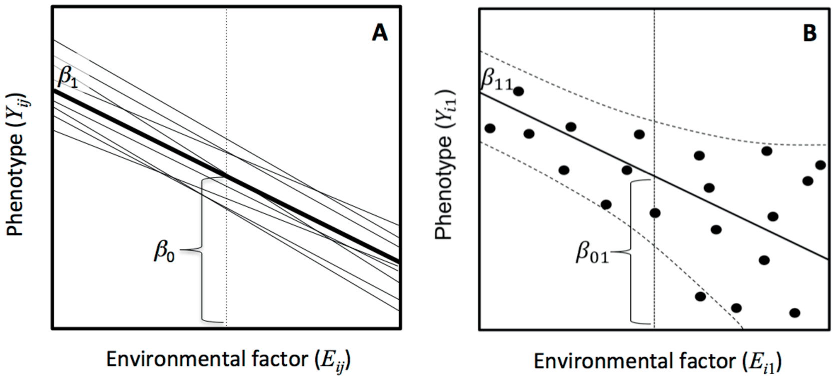


Fig. 2. Plots of phenotypic measures (Y_{i1}) from an individual (j=1) across an environmental gradient (E_{i1}). The mean phenotype (E_{01}) is the elevation and taken at the mean-centred environment, and the slope (β_{11}) describes the individual's plasticity, with elevation and slope together producing a norm of reaction (thin black lines). In this case there is heterogeneous residual variance, with confidence limits indicated by the dashed lines that 'fan out' over the gradient. These heterogeneous residuals could be the result on non-linear reaction norms, an interaction between the slope-intercept of different reaction norms, interactions between more than one environmental factor in a multi-dimensional reaction norm. Biases in sampling or measurement error, or more interestingly biases in organismal error (e.g. misinformation), along the environmental gradient could also be a cause.

residual level within individuals, where both adaptive plasticity in residuals and canalization-like processes (stability) can evolve. With the statistical tools now available to examine heterogeneous residual variance, an array of novel questions linking phenotype to environment can be usefully addressed.

RECOMMENDED READING:

Botero, C.A., Weissing, F.J., Wright, J. and Rubenstein, D.R. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences of the United States of America* 112, 184–189.

Ratikainen, I.I. and Wright, J. 2013. Adaptive management of body mass by Siberian jays. *Animal Behaviour* 85, 427–434.

Westneat, D.F., Schofield, M. and Wright, J. 2013. Parental behavior exhibits among-individual variance, plasticity, and heterogeneous residual variance. *Behavioral Ecology* 24, 598–604.

Westneat, D.F., Wright, J. and Dingemanse, N.J. 2015. The biology hidden inside residual within-individual phenotypic variation. *Biological Reviews* 90, 729–743.

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 %)
PhD candidate/Postdoc Anna Marie Holand
Researcher Ingerid J. Hagen
Postdoc Alina Niskanen
Postdoc Jostein Gohli
PhD candidate Peter S. Ranke
PhD candidate Sindre L. Sommerli
PhD candidate Dilan Saatoglu
PhD candidate Maria L. Selle
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, Anna Marie Holand, Jostein Gohli, Dilan Saatoglu and Maria Selle.

Former group members:
Researcher Petri Kemppainen
Postdoc Anna M. Billing
PhD candidate Håkon Holand

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 spatio-temporal variation in population dynamics (e.g. 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 meta-populations, 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, along with results from our studies: 1) needed to parameterize and test models developed by other RGs at CBD; 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.

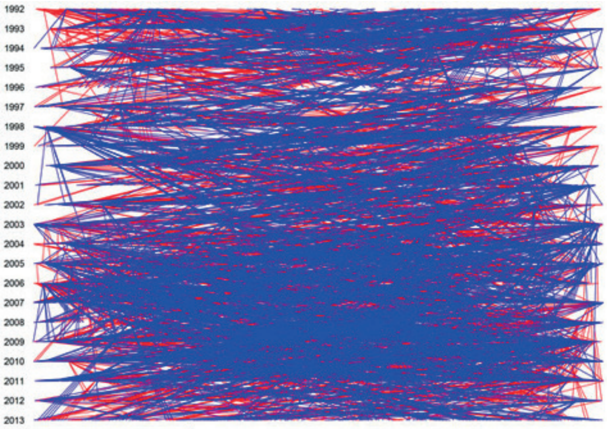


Fig. 1. The pedigree for one island in CBD's house sparrow metapopulation study system. The pedigree includes 4060 individuals born on the island during a 22 year period. Each row represents individuals born to the indicated cohort (from 1992 to 2013). Red lines show links between mothers and their offspring, and blue lines show links between fathers and their offspring. A colour ringed male house sparrow is shown to the left.

MAJOR SCIENTIFIC CONTRIBUTIONS

Identification of mechanisms that link ecological and evolutionary processes

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 one of CBD's long-term model systems, the house sparrow metapopulation at the coast of Helgeland, we have identified a number of phenotypic traits related to fitness (i.e. survival and/or reproduction) and which are involved in important life history trade-offs.

For example, we used recent advances in disease modeling to show that severe infection by the nematode parasite (*Syngamus trachea*) can have a negative effect on survival probability and lifetime reproductive success (Holand et al. 2014). Furthermore, prevalence of the parasite varied both between populations and over time, as well as between sexes and age classes. These results provide important contributions to both RA1 and RA2 by identifying host-parasite relationships as one important mechanism through which age-structure may interact with spatio-temporal variation in selection to affect both population dynamics and evolutionary dynamics of populations in a fragmented landscape.

A central life history trade-off is between body size and life span: larger body size is generally associated with faster ageing within species. Using data from an artificial selection experiment for larger body size in house sparrows, we showed that the negative relationship found between body size and telomere length at the start of the experiment was strengthened and extended when body size increased during the experiment (Ringsby et al. 2015). These results suggest that telomere dynamics could play an important role in the evolution of optimal body size through its effect on the trade-off between life span and body size. Because lifespan is a key component of lifetime reproductive success, the link between body size and telomere length could have important fitness consequences. Consequently, telomere dynamics is likely to be important in the senescence process, and thus provides a potential mechanism linking ecological (RA1) and evolutionary (RA2) dynamics in natural populations.

Effects of dispersal and population characteristics on genetic variation

Knowing what factors affect the distribution of genetic variation within and between populations is important to understand evolutionary processes and the viability of endangered populations. The effective population size (N_e) is a key parameter linking RA1 and RA2 because it depends on e.g. fluctuations in population size and demographic variance, and it determines the rate of loss of genetic variation due to genetic drift and inbreeding.

Using data from CBD's long-term metapopulation study on house sparrows, we estimated contemporary N_e, compared this to population size (N), and examined how Ne and N_e/N ratios varied across time and space (Baalsrud et al. 2014). An important result was that N_e/N ratios within populations increased with immigration rates. Furthermore, genetic estimates of N_e were generally larger than demographic estimates, probably due to a greater effect of immigration on genetic than demographic processes in local populations. Our results suggest that loss of genetic variation by genetic drift and inbreeding in fragmented populations that fluctuate in size depends critically on rates of dispersal, which is also one of the main factors affecting the ecological dynamics of spatially distributed populations.

The relative importance of genes and environment for phenotypic variation

Estimates of the relative importance of genes and environment are crucial to predict the rate of evolutionary change, and obtaining such estimates therefore constitutes a key component of RA2. To meet this challenge we have developed a non-sampling-based Bayesian inference methodology for animal model estimation of additive genetic (co)variances, which is based on Integrated Nested Laplace Approximation, INLA. Our methodology, which is available in the R packages INLA and Animal INLA, provides a flexible framework especially useful in analyses of complex pedigrees common in natural populations, while it also has major advantages with respect to e.g. computation time. This allows efficient use of simulation studies to examine and compare different models even for very large pedigrees and data sets, such as those used in animal breeding. We have also made important extensions to our basic methodology. For example, we can model and account for nonrandom missing data (Steinsland et al. 2014). Using simulations and empirical data from a long-term study of Swiss Barn owls (*Tyto alba*), we demonstrated that these issues may be important because wrong conclusions can be drawn regarding evolutionary change if ignored. Hence, our INLA animal model framework represents a powerful tool to estimate both the magnitude of natural selection (inherent in the missing data process) and additive genetic (co)variances with high accuracy and good precision.

Genetic basis of ecologically important characters

To understand the interaction between ecological (RA1) and evolutionary (RA2) processes 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 such as a high-quality reference genome assembly, and/or a high-density genome-wide panel of genetic markers exist for the species under study. We have developed such resources in house sparrows, and contributed to this in e.g. collared flycatchers (*Ficedula albicollis*) and Atlantic salmon (*Salmo salar*). Furthermore, we have developed several statistical methods to map genes for important phenotypic characters, such as a Genome Wide Association Study (GWAS) method that can correct for population structure and model repeated measures, often important in natural populations. This method was used on data from collared flycatcher in Sweden to identify multiple candidate gene regions for clutch size, a key life history trait in birds (Husby et al. 2015).

During the last decade it has been suggested that epigenetic mechanisms may play an important role for rapid evolutionary change. To understand if and how organisms can adapt to environmental changes we must therefore quantify the relative importance of genetic and epigenetic mechanisms for evolution. We have developed a theoretical-experimental and individual-based population model, which was used on an experimental evolution study where clonal populations of yeast were exposed to a range of stressors (Gjuvsland et al. 2016). Our results showed that even ultrafast adaptation can be achieved by purely genetic de novo solutions, without invoking either direct or indirect action of epigenetics. Moreover, in experimental evolution studies, loci that display larger allele frequency change than expected by genetic drift are assumed associated with traits under selection. In Kemppainen et al. (2016) we suggest a new method for analyzing such data which is based on GWAS methods to account for relatedness. Using this method on data from an artificial selection experiment on body size in house sparrows we show that allele frequencies in large parts of the genome may change when selection acts on a heritable trait. The results from these two studies are very important because they: 1) provide evidence that traditional genetic mechanisms may be important for evolution on ecological time-scales; 2) show that selection is likely to have considerable consequences for eco-evolutionary dynamics because selection will affect many genes (not only the ones directly causing variation in the phenotypic trait under selection). The statistical frameworks we have developed therefore provide tools to study links between ecological (RA1) and evolutionary (RA2) dynamics.

RECOMMENDED READING:

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Gjuvsland, A.B., Zörgö, E., Samy, J.K., Stenberg, S., Demirsoy, I.H., Roque, F., Maciaszczyk-Dziubinska, E., Migocka, M., Alonso-Perez, E., Zackrisson, M., Wysocki, R., Tamás, M.J., Jonassen, I., Omholt, S.W. and Warringer, J. 2016. Disentangling genetic and epigenetic determinants of ultrafast adaptation. *Molecular Systems Biology* 12, 892.

Holand, H., Jensen, H., Tufto, J., Soliman, M., Pärn, H., Sæther, B.-E. and Ringsby, T.H. 2014. Lower survival probability of house sparrows severely infected by the gapeworm parasite. *Journal of Avian Biology* 45, 365–373.

Husby, A., Kawakami, T., Rönnegård, L., Smeds, L., Ellegren, H. and Qvarnström, A. 2015. Genome-wide association mapping in a wild avian population identifies a link between genetic and phenotypic variation in a life-history trait. *Proceedings of the Royal Society B:* 282, 20150156.

Kemppainen, P., Rønning, B., Kvalnes, T., Hagen, I.J., Ringsby, T.H., Billing, A.M., Pärn, H., Lien, S., Husby, A., Sæther, B.-E. and Jensen, H. 2016. Controlling for p-value inflation in allele frequency change in experimental evolution and artificial selection experiments. *Molecular Ecology Resources*, in press.

Ringsby, T.H., Jensen, H., Pärn, H., Kvalnes, T., Boner, W., Gillespie, R., Holand, H., Hagen, I.J., Rønning, B., Sæther, B.-E. and Monaghan, P. 2015. On being the right size: increased body size is associated with reduced telomere length under natural conditions. *Proceedings of the Royal Society of London:* 282, 20152331.

Steinsland, I., Thorrud Larsen, C., Roulin, A. and Jensen, H. 2014. Quantitative genetic modeling and inference in the presence of non-ignorable missing data. *Evolution* 68, 1735-1747.

RESEARCH GROUP: COMMUNITY DYNAMICS

Current group members:
PI: Associate professor Vidar Grøtan
Professor Otso Ovaskainen
Senior researcher Ola Diserud
Postdoc Nerea Abrego
Postdoc Erik Blystad Solbu
PhD candidate Emma-Liina Marjakangas

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, Nerea Abrego.

In this research group we study the joint temporal and spatial dynamics of multiple species. The species we find in a community and their relative abundance, depends on several factors; for instance how such species respond to environmental conditions and their interactions. Species may for example interact through competition for a limited resource varying temporally and spatially. Studying how the species composition change through both time and space allows us to gain a better understanding of the relative importance of the different mechanisms shaping patterns of species composition. This will contribute towards providing better predictions of how communities may respond to a changing environment.

The statistical analysis of multi-species data in time and space is challenging due to the curse of dimensionality involved in estimating parameters of the ecological processes from the data. The research group focus on development of improved estimation techniques of parameters of fundamental interest within community dynamics as well as applying these techniques for analyzing data from communities across several taxa.

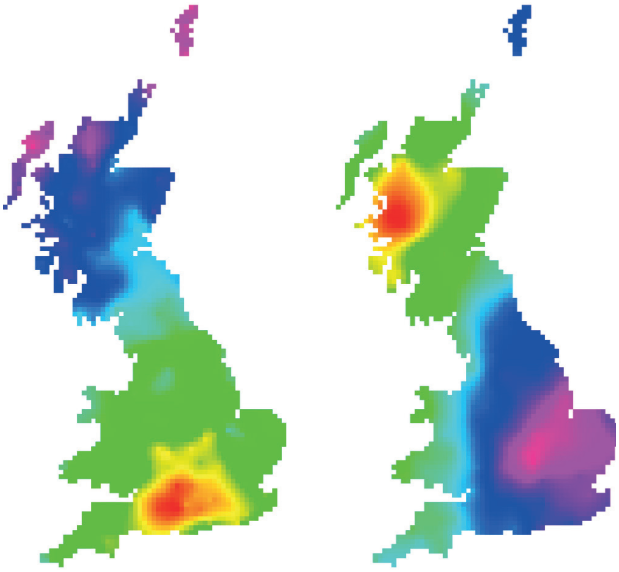

Fig. 1. Latent environmental variables influencing the spatial community structure of butterflies in UK (Ovaskainen et al. 2016b)

Photo Otso Ovaskainen

Photo Otso Ovaskainen

The hyacinth macaw (*Anodorhynchus hyacinthinus*) nesting in the Pantanal Conservation Area in Brazil.

MAJOR SCIENTIFIC CONTRIBUTIONS

Spatial and temporal fluctuations in community structure may be due to dispersal, variation in environmental conditions, ecological heterogeneity among species and demographic stochasticity. The relative contribution from these factors in shaping species abundance distributions and in causing spatio-temporal variation in community composition has been debated. Two major approaches are followed: analyses of spatial and temporal variation in the community correlation (summarized in Sæther et al. 2013) and the latent variable model approach developed by Ovaskainen et al. (2016a, b).

A hot topic of debate is the role of heterogeneity among species. Solbu et al. (2016) showed that differences in intrinsic growth rate and strength of density regulation among species lead to species abundance distributions resembling those found in empirical data. Homogenous models lead to species abundance distribution with far too small variance except for cases when density regulation was extremely weak or environmental variance was very large.

Our group has estimated the effects of spatio-temporal environmental variation on community dynamics have been estimated using the community correlation approach in several systems:

Bellier et al. (2014) analyzed the spatiotemporal community dynamics of freshwater zooplankton. They partitioned the variance of the distribution of log abundance for a random species at a random time and location into components of demographic stochasticity, ecological heterogeneity among species, and independent environmental noise components for the different species. Non-neutral mechanisms such as ecological heterogeneity among species (20%) and spatiotemporal variation in the environment (75%) explained the majority of the variance in log abundances, and spatiotemporal variation in lake acidity was identified as the environmental variable contributing the most to decay of similarity in space and time.

Grøtan et al. (2014) showed that seasonal influences of environmental conditions cause cycles in temporal similarity of butterfly communities in Ecuador and Costa Rica. Although environmental conditions had a large short-term influence, the communities tended to return to the same relative species abundance distribution with a 12-month lag, and the community similarity did not decrease in the long term because of heterogeneity among species in their density dependent dynamics.

These studies have shown that both species heterogeneity and environmental stochasticity contribute to the structure of communities. A study of a vertebrate community at Spitsbergen by Hansen et al. (2013) (also reported by the Research Group of Hansen) also points to the importance of considering the role of interspecific interactions. Most communities are however more species rich and more complex than the community of overwintering terrestrial vertebrates at Svalbard. Estimating interaction effects among species in species rich communities have been difficult due to the curse of dimensionality involved in estimating large covariance matrices of interaction effects among species and large covariance matrices of random effects (e.g. spatial autocorrelation in abundance of species).

In two papers Ovaskainen et al. (2016a, b) presented a statistical approach that through an ingenious and statistically efficient sparse representation of covariance structures allows estimating environmental responses and species interactions from data on species-rich communities at multiple spatial scales. The approach also allows for estimating latent (unobserved) environmental variables influencing community structure. The authors demonstrated that estimated species-to-species associations doubled the predictive power of the model compared to accounting for environmental covariates only.

RECOMMENDED READING:

Bellier, E., Grøtan, V., Engen, S., Schartau, A.K., Herfindal, I. and Finstad, A.G. 2014. Distance decay of similarity, effects of environmental noise and ecological heterogeneity among species in the spatio-temporal dynamics of a dispersal-limited community. *Ecography* 37, 172–182.

Grøtan, V., Lande, R., Chacon, I.A. and DeVries, P.J. 2014. Seasonal cycles of diversity and similarity in a Central American rainforest butterfly community. *Ecography* 37, 509–516.

Hansen, B.B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., Ims, R.A., Yoccoz, N.G. and Pedersen, Å.Ø. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. *Science* 339, 313–315.

Ovaskainen, O., Abrego, N., Halme, P. and Dunson, D. 2016. Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods in Ecology and Evolution* 7, 549–555.

Ovaskainen, O., Roy, D.B., Fox, R. and Anderson, B.J. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. *Methods in Ecology and Evolution* 7, 428–436.

Solbu, E.B., Engen, S. and Diserud, O.H. 2016. Characteristics of temporal changes in communities where dynamics differ between species. *Theoretical Population Biology* 111, 65–74.

Sæther, B.-E., Engen, S. and Grøtan, V. 2013. Species diversity and community similarity in fluctuating environments: parametric approaches using species abundance distributions. *Journal of Animal Ecology* 82, 721–738.

RESEARCH GROUP: DYNAMICS OF ARCTIC ECOSYSTEMS

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

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

Bart Peeters, Mathilde Le Moullec, Brage Bremset Hansen, Kate L. Matthews, Håkon Holand, Aline M. Lee.

The goal of CBD is to understand the role of environmental stochasticity in shaping patterns of biodiversity in time and space. Accordingly, by taking advantage of the simple trophic system and unique availability of long-term monitoring data in high Arctic Svalbard, this research group seeks to achieve a general understanding of how climate change and harvest impact spatiotemporal dynamics of wildlife communities (RA3). Since late 2016, we also focus on studies of semi-domesticated reindeer and fish community dynamics in the Barents Sea. Our main approach involves implementing stochastic demographic models of single key species into analyses of dynamics of communities in time and space, in order to predict how interspecific interactions will affect the structure of ecosystems facing changes in climate and harvest (Fig. 1).

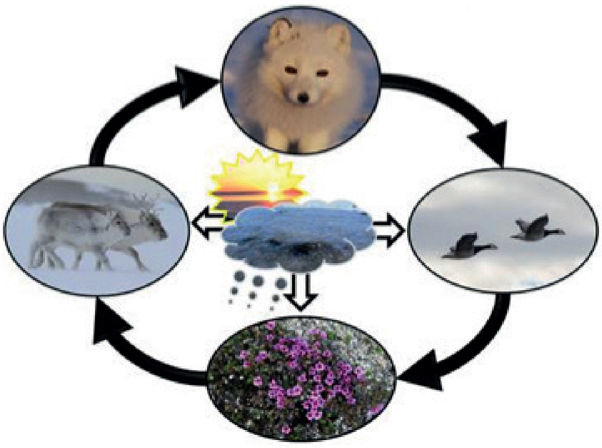

Fig. 1. Climate may drive the temporal and spatial dynamics of communities through common (i.e. shared) environmental noise, which may influence the different species and trophic levels directly or indirectly (i.e. through interactions with other species).

MAJOR SCIENTIFIC CONTRIBUTIONS

One important contribution towards an understanding of community dynamics was made through analyses of the synchronizing role of weather fluctuations among overwintering vertebrate species in Svalbard (Hansen et al. 2013), demonstrating for the first time that climate may generate synchronized population dynamics across an entire animal community. In this tundra environment characterized by huge weather fluctuations around a marked warming trend, two climate drivers stand out as particularly important: summer warming and winter rain events. The recent focus of the research group has therefore been on developing a mechanistic understanding of how key components of the ecosystem respond to these climate drivers. Remote sensing studies have revealed that summer warming leads to increased productivity and, over time, a high Arctic "greening" trend (Vickers et al. 2016). Recently, this trend has diminished in spite of continued warming, possibly for reasons related to winter climate change. Accordingly, the first results from a long-term field experiment suggest that extreme winter rain events, which encapsulate the tundra vegetation in solid ground-ice (Hansen et al. 2014), may have a dramatic impact on the growth, mortality and reproduction of plants (Milner et al. 2016) (Fig. 2).

For the overwintering herbivores, climate change effects may operate indirectly (e.g. through food plant productivity) or directly through changing food plant accessibility during winter (Fig. 1). A recent study based on two decades of mark-recapture data on wild Svalbard reindeer showed that while the summer warming increases body mass gain during the snow-

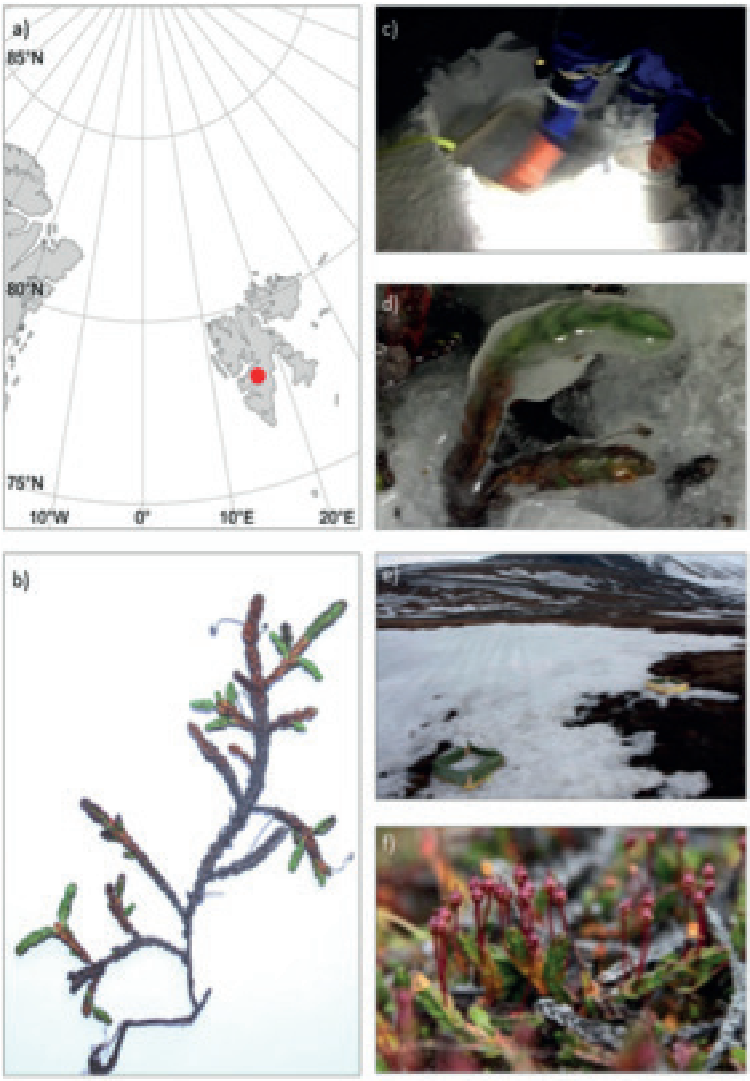

Fig. 2. The Svalbard research group combines time-series and field experiments to assess climate effects on tundra vegetation (Milner et al. 2016).

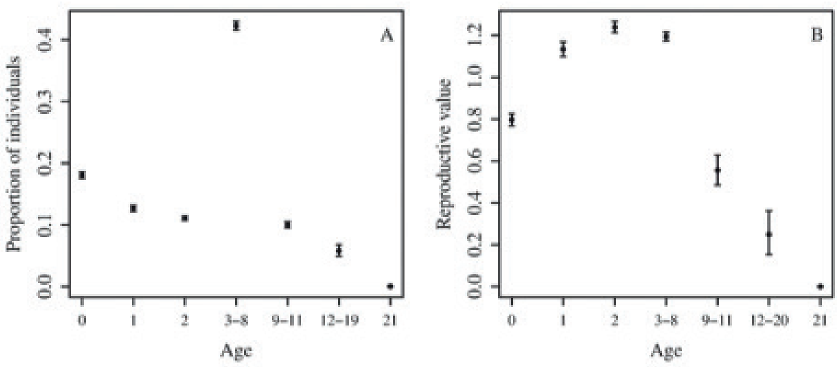

Fig. 3. The stable age structure and reproductive values for wild female Svalbard reindeer (Bjørkvoll et al. 2016) estimated from an integrated population model (Lee et al. 2015).

free season, winter rain events and associated icing block food accessibility and determine late winter body mass, which in turn explains annual variation in age-specific survival and fecundity (Albon et al. 2016). Thus, while the "greening effect" due to summer warming increases the reindeer carrying capacity, the annual fluctuations in population size are more likely driven by winter weather fluctuations. In this long-lived species, the annual fluctuations in age-specific vital rates and population sizes are large (Lee et al. 2015). However, the vital rates of certain age classes (i.e. prime-aged) vary less and contribute more to population growth than others (Bjørkvoll et al. 2016) (Fig. 3). One should therefore expect that the bottom-up processes, such as climate effects and extreme events, acting on the long-term population dynamics may interact with fluctuations in age-distribution and density-dependence, which may erroneously be interpreted as environmental stochasticity. These interactions are currently being disentangled in demographic models in order to, model and predict how environmental perturbations (e.g. extreme icing events) operating on key species may cascade through the food-web, indirectly affecting other resident as well as migratory species via population densities of the Arctic fox, their shared predator/scavenger (Hansen et al. 2013) (Fig. 1). Since late 2016, the research group has extended these stochastic demographic modelling approaches including trophic interactions and harvest to studies of fish community dynamics in the Barents Sea.

RECOMMENDED READING:

Albon, S.D., Irvine, R.J., Halvorsen, O., Langvatn, R., Loe, L.E., Ropstad, E., Veiberg, V., van der Wal, R., Bjørkvoll, E.M., Duff, E.I., Hansen, B.B., Lee, A.M., Tveraa, T. and Stien, A. 2016. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, in press.

Bjørkvoll, E.M., Lee, A.M., Grøtan, V., Sæther, B.-E., Stien, A., Engen, S., Albon, S.D., Loe, L.E. and Hansen, B.B. 2016. Demographic buffering of life histories? Implications of the choice of measurement scale. *Ecology* 97, 40–47.

Hansen, B.B., Grøtan, V., Aanes, R., Sæther, B.-E., Stien, A., Fuglei, E., Ims, R.A., Yoccoz, N.G. and Pedersen, Å.Ø. 2013. Climate events synchronize the dynamics of a resident vertebrate community in the High Arctic. *Science* 339, 313–315.

Hansen, B.B., Isaksen, K., Benestad, R.E., Kohler, J., Pedersen, Å.Ø., Loe, L.E., Coulson, S.J., Larsen, J.O. and Varpe, Ø. 2014. Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters* 9, 114021.

Lee, A.M., Bjørkvoll, E.M., Hansen, B.B., Albon, S.D., Stien, A., Sæther, B.-E., Engen, S., Veiberg, V., Loe, L.E. and Grøtan, V. 2015. An integrated population model for a long-lived ungulate: more efficient data use with Bayesian methods. *Oikos* 124, 806–816.

Milner, J.M., Varpe, Ø., van der Wal, R. and Hansen, B.B. 2016. Experimental icing affects growth, mortality, and flowering in a high Arctic dwarf shrub. *Ecology and Evolution* 6, 2139–2148.

Vickers, H., Høgda, K.A., Solbø, S., Karlsen, S.R., Tømmervik, H., Aanes, R. and Hansen, B.B. 2016. Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters* 11, 105004.

RESEARCHER TRAINING

CBD has 18 active PhD candidates and 9 postdocs. During the first half of the project period, 5 PhD-dissertations (including 2 by female students) were completed:

Holand, Anna Maria (Female) Statistical methods for estimating intra- and inter-population variation in genetic diversity, September 2013.

Bjørkvoll, Eirin Marie (Female) Life-history variation and stochastic population dynamics in vertebrates, May 2014.

Holand, Håkon (Male) The parasite *Syngamus trachea* in a metapopulation of house sparrows, June 2014.

Solbu, Erik Blystad (Male) Modelling and statistical analyses of demographic and environmental changes in populations and communities, November 2015.

Kvalnes, Thomas (Male) Evolution by natural selection in age-structured populations in fluctuating environments, January 2016.

In addition, 4 more PhD candidates have now accepted positions opened in 2016, and they will start in the beginning of 2017.

Workshops and Courses:

PhD level courses run by CBD staff at Department of Biology, NTNU, include:

BI8082	Evolution and Ecological Genetics (H. Jensen, C. Pelabon)
BI8091	Advanced Conservation Biology (V. Grøtan, G. Rosenqvist)
BI8091	Advanced Evolutionary Biology (C. Pelabon, J. Wright)

PhD training workshops organized by CBD:

CBD/IMPRS *"Statistical Approaches to Multivariate Phenotypes"*, internationally taught 5-day residential course, Seewisen, January 2015.

CBD *"Modelling ecology and evolution"*, two-week course, spring 2015, by Otso Ovaskainen.

CBD/SQuID *"Study design & sampling decisions in mixed-effect model analyses"*, internationally taught 5-day residential course, Sletvik, October 2016.

Other courses:

Swiss Ornithological Institute, Sempach, Switzerland, August 12-16 2013. "Bayesian Population Analysis using WinBUGS". Organized by Michael Schaub and Marc Kéry, 3 participants from CBD.

Schweizerische Vogelwarte, Sempach, Switzerland, December 12-16 2016. "Bayesian integrated population modeling (IPM) using BUGS and JAGS". Organized by Michael Schaub and Marc Kéry, 5 participants from CBD.

In August 2017 CBD will organize a similar course in IPM in Trondheim, extending it with one week during which CBD-members will introduce the participants to basic stochastic population modelling

PhD training at IBI:

Teaching assistantships on IBI bachelor & master courses as part of paid 4th year on IBI PhD program. It is also a policy at CBD that PhD candidates as far as possible should be included as co-supervisors of MSc-students.

Two PhD candidates at CBD are part of the SUSTAIN-project, which means that they will spend a period at one of the other nodes in the project. They also have a scientific mentor there.

International co-supervision of PhD students:

Several PhD candidates have co-supervisors at other research institutions. Elena Albertson and Øystein Opedal are co-supervised by Prof. W.S. Armbruster, University of Portmouth, UK; Thomas Haaland by Ass. Prof C. Botero, Washington University in St. Louis, USA; Christoffer Hilde by Prof. J.M. Gaillard, LBBE and Claude Bernard Université Lyon, France, and Kate Matthews by Prof. M. Luunen, University of Groningen, The Netherlands.

PhD visits to collaborator labs abroad:

Aurora grant *"Genetic architecture"* was awarded to C. Pèlabon and A. Lerouzic 2015. This grant allowed Elena Albertsen from CBD to visit Lerouzic CNRS lab in Gif-sur-Yvette, France, during spring 2015, and to host Clementine Renneville from Gif-sur-Yvette in the spring 2015.

Kate l. Matthews spent one week in October 2016 at the Loonen lab, University of Groningen.

In spring and autumn 2016, Emma-Liina Marjakangas visited collaborators Milton Ribeiro, Mauro Galetti, Danilo Boscol in Rio Claro and Sao Paulo, Brazil.

Mathilde Le Moullec spent three weeks in November-December 2016 in a collaborating lab (Prof. Jeffrey Welker) at the University of Anchorage, Alaska, USA.

Peder Sæter grant *"Disentangling the evolutionary relationships in a tropical plant species complex: From systematics to character evolution and speciation"* to C. Pelabon (CBD) and B. Baldwin Dept. of Integrative Biology, UCB, USA, in collaboration with W.S. Armbruster (Portsmouth University UK). This grant allowed Ø.H. Opedal to travel for 2 months to UCB during his PhD to learn molecular techniques necessary for the description of sister species of *Dalechampia scandens*.

Teaching experience for postdocs/researchers:

Irja Ida Ratikainen (currently employed as Associate Professor II by IBI) is part of a career developing scheme at NTNU entitled *"NTNU Outstanding Academic Fellows programme"*. This programme aims to provide potential faculty members feedback on their career development through individual follow-up by senior faculty members and meetings at regular intervals, including all the members in plenum as well as through mentoring by an internationally leading scientist.

RESEARCH COLLABORATION ACROSS RESEARCH GROUPS

At CBD, there is considerable collaboration across research groups. This is illustrated by a large extent of co-authorship of papers among researchers belonging to different research groups (Fig. 1). Such collaboration is mainly facilitated by establishing informal arenas for dialogue, the mandatory weekly CBD-lunches and active involvement by the leadership of the centre in identifying questions suitable of inter-group collaboration.

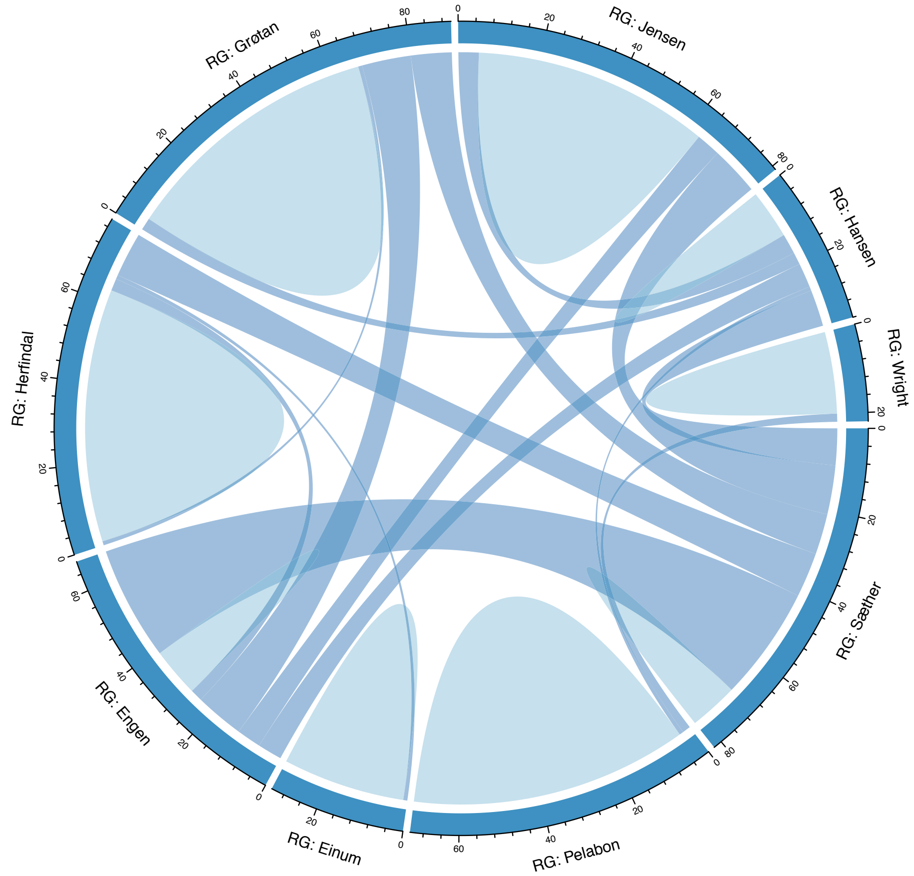

Figure 1. Collaboration in CBD expressed as number of co-authorships among members of the different research groups. The numbers refer to the number of times members of a research group appear as authors on scientific publications. Lines between research groups indicate shared authorship on publications, where the width of the line represents the number of times this occurred. The width of the light blue ellipses represents authorships on publications not involving other research groups.

This interdisciplinary interaction among researchers at CBD is also evident through a large extent of joint supervising PhD-students and postdocs (Fig. 2). In general, PhD candidates and postdocs have supervisors from several research groups involving at least 2 research areas.

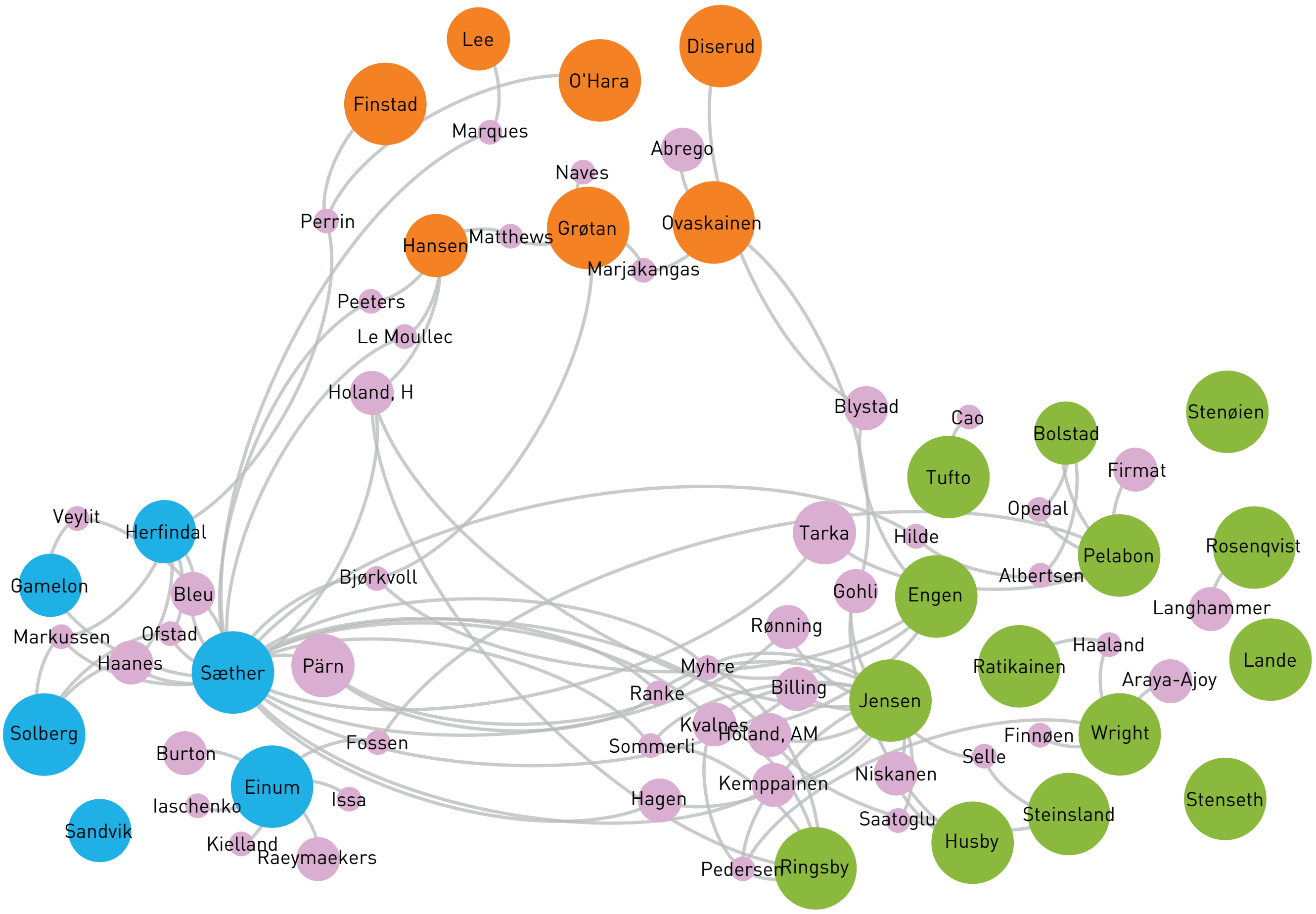

Fig. 2. Collaboration between CBD-members as visualised by supervision of PhD candidates and postdocs. Colours represent research area of the supervisor (**blue** = RA1, **green** = RA2, **orange** = RA3, **pink** = PhD and postdocs). The size of the circle represents the position (from large to small: Permanent scientific staff, researcher, postdoc, and PhD candidate or engineer). The figure includes both current and former supervision at CBD. Some people have changed position during the centre period, and are here shown with the highest academic position during the period. Engineers are shown similar as PhD candidates.

INTERNATIONAL COLLABORATION

CBD is a very internationally orientated centre with collaborators almost all over the world. In addition to regular visits by international scientists almost on a weekly basis during the term, many researchers at CBD are involved in analysing data from field studies in a wide range of biomes ranging from the tropical environments in Brazil up to the high Arctic. CBD has also financially supported some of these long-term field studies. Consequently, a characteristic of many CBD papers is their comparative approaches involving a large number of co-authors from many different countries (Fig. 3). Some of those collaborators are among the world-leading scientists within central research fields for CBD.

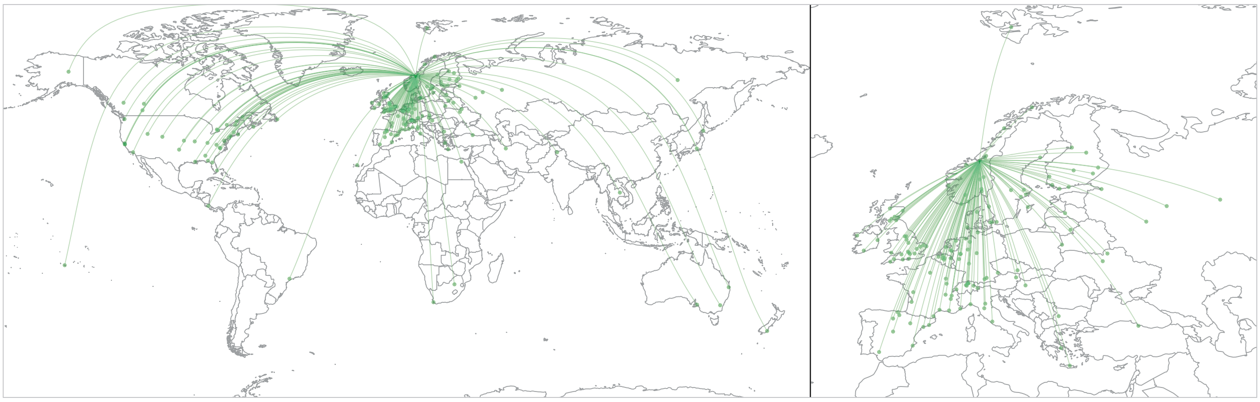

Fig. 3. Localisation of institutions where co-authors of CBD-papers were affiliated, or institutions with extensive collaborations with CBD.

DISSEMINATION AND COMMUNICATION

Many of the projects at CBD have received attention by different kinds of Norwegian media. In particular, CBD's research on climate change impacts on the Svalbard ecosystem dynamics has drawn considerable media attention. A paper published in Science in 2013 was thoroughly covered on national television (NRK) and in scientific magazines (e.g. Editor's highlights in Nature, Science Daily, Cosmos Magazine), national and international newspapers (e.g. Die Welt, Berliner Zeitung), international radio (Deutchlandradio), as well as hundreds of online media across the world. CBD members have hosted field visits by several scientific writers, e.g. from Smithsonian Magazine, resulting in even greater media coverage. A cross-disciplinary study on the impact of an extreme weather event was also broadly covered in Scientific American, Science Daily and The Independent, as well as several Norwegian newspapers. The latest results from this research group have been disseminated on national (P4 news) and international radio (Yale Climate Connections, podcast for 200 US radio channels) and science magazines (News Deeply, US). The major research findings now also represent a significant part of the curriculum at the Arctic Biology studies (BSc, MSc, PhD) at the University Centre in Svalbard and have been extensively communicated to local and national end-users through reports (e.g. MET report no. 20/2015. Norwegian Meteorological Institute), conferences, public talks, popular science articles and newspaper chronicles.

Other CBD projects have also received media attention. In particular, field projects off the coast of Helgeland involving the house sparrows, moose and water voles have been closely followed by the regional office of the Norwegian Broadcasting Corporation (NRK) in Bodø, which has resulted in several presentations in national as well as regional radio and television. Junior staff at CBD have also served as scientific experts in a national television science show for youth (NRK Newton).

The Norwegian Broadcasting Corporation (NRK) has also broadcast an extended interview with the centre leader concerning the issues related to the consequences of climate change and subsequent loss of biodiversity. Parts of this interview have since been used in several radio programmes. In addition, together with several other leading biologists in Norway, the centre leader was in April 2016 interviewed by the national media in an attempt to increase public focus on the unfortunate consequences of losses of biodiversity in Norway. Another attempt to raise the public awareness of that issue has been the Director's participation in the Environmental and Climate Committee of the Norwegian Academy of Science and Letters in Oslo, which aims to organize high-profile open meetings and conferences of interest to especially high-level decision makers, as well as the general public.

An important arena for dissemination of results from the research at CBD has been the project SUSTAIN, which is an integrated project lead by the Centre for Ecological and Evolutionary Synthesis (CEES - a Centre of Excellence (SFF-II) at the University of Oslo) with CBD and University of Tromsø as the other two major nodes. This project includes close interactions with various kinds of end-users, representing local, regional and national management authorities, as well as several NGOs.

Researchers at CBD have been actively involved in applied research projects funded by the Norwegian Environment Agency. This means that results obtained at CBD are often quite rapidly disseminated among environmental managers, both at the national, regional and local levels, and therefore have the potential to be rapidly implemented as part of practical management actions. For example, Professor S. Einum will from January 1 2017 be member of the Scientific Board for Salmon Management in Norway. Furthermore, the results from the moose project on the island of Vega in northern Norway have been presented at several meetings with environmental mangers and NGOs. Together with the analyses of long-term data collected through the Norwegian Monitoring Programme of Cervids, we believe that results obtained at CBD have provided an important foundation for science-based management of the large populations of cervids in Norway.

CBD's research on alien species (RA1) has been carried out in close cooperation with the relevant governmental bodies (The Norwegian Biodiversity Information Centre, NBIC, and The Norwegian Environment Agency). The set of criteria that is used in black listing alien species in Norway, has been developed by CBD (Sandvik et al. 2013). Under the guidance of NBIC, several expert teams have used CBD's set of criteria to risk-assess almost 1400 alien species. Since 2015, CBD has been responsible for revising the set of criteria, refining the screening methodology and developing modelling tools for risk assessment. The methodology devised by CBD consists of criteria that are quantitative (i.e. numerically defined) and generic (i.e. taxon- and habitat-independent). This makes the risk-assessments testable, repeatable and comparable. Swedish authorities (The Swedish Environmental Protection Agency, and The Swedish Agency for Marine and Water Management) have also recently decided to adopt CBD's and NBIC's methodology in risk-assessing alien species in Sweden.

The Director is a member of the Steering Board for the Division for research in energy, resources and environment in the Research Council of Norway. This division operates research programmes on petroleum, energy and marine resources, which includes a large part of the total budget spent on thematic research in Norway. The experience gained as a leader for a centre of excellence has on several occasions been communicated in discussions about organization of this type of applied research in Norway.

PUBLICATIONS

During the first period of CBD (2013-2016), researchers at CBD published one book, 4 reviewed book chapters and 245 papers in journals. The largest output occurred in 2016 when 97 papers were published, printed or available online on journals website, which corresponds to 40% of the total number of articles.

A summary of publications in the most relevant journals for the scientific goals of CBD:

Journal	2013	2014	2015	2016	Sum
American Naturalist	3	4		1	8
Animal Behaviour	2			1	3
Behavioral Ecology	2	1		3	6
Biological Reviews			1		1
Biology Letters		1	1		2
Ecography	1	2	1		4
Ecology				2	2
Ecology Letters				1	1
Evolution	2	5	3	5	15
Evolutionary Applications		1			1
Functional Ecology			1	1	2
Journal of Animal Ecology	2	2	1	6	11
Journal of Ecology				1	1
Journal of Evolutionary Biology		2	3	1	6
Journal of Theoretical Biology	1				1
Methods in Ecology and Evolution	1	2		6	9
Molecular Ecology	1	1	1	2	5
Nature			1	2	3
Nature Communications		1		2	3
Oecologia	2	1	1	1	5
Oikos	2	1	1	5	9
Philosophical Trans Royal Society B		3			3
Proceedings Royal Society B	1		2	4	7
PNAS			2		2
Quarterly Reviews in Biology	1				1
Science	2			1	3
Theoretical Population Biology				2	2
Trends in Ecology & Evolution			2	1	3
Others	29	20	28	49	131
Book Chapters		1		3	4
Total	52	48	49	100	249

The Norwegian university system categorizes journals into two levels. Category 2 journals represent internationally leading journals in respective research fields, whereas category 1 are other peer-reviewed journals with a peer review system. CBD researchers have published 104 papers in category 2 journals.

The publication strategy of CBD is to aim for high-impact journals rather than focusing on numbers. Web of Sciences has a system that classifies the journals according to their impact on their respective research fields. It is evident that researchers at CBD have shown an increasing tendency for publication in the most influential journals, with more than 60 % of all papers published in 2016 in the upper quartile of the journals with highest impact factor in the different fields of research (Fig. 4).

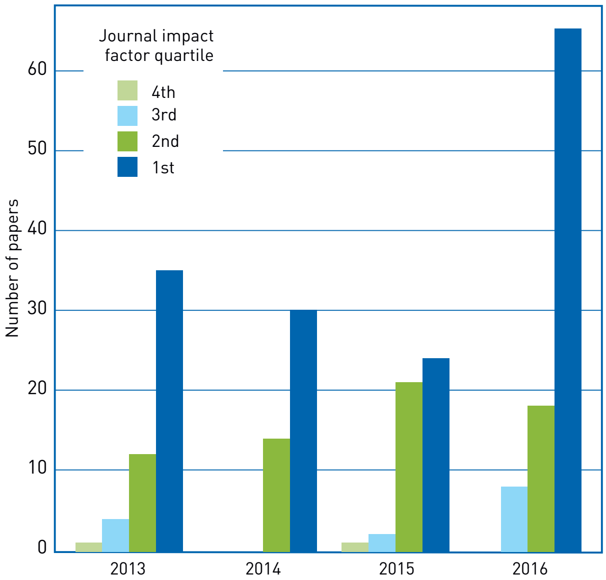

Fig. 4. Distribution of papers in quartile of journal impact factor. Journals in the 1st quartile belongs to the 25% most cited journals in the category it belongs to, as defined by Web of Science Journal Citation Reports.

CBD is involved in mark-recapture programs on several species in Svalbard, including the wild reindeer.

Adult male Svalbard reindeer ready to fight for his harem.

KEY PUBLICATIONS IN 2016

Book

Ovaskainen, O., de Knegt, H. J. and del Mar Delgado, M. 2016. Quantitative Ecology and Evolutionary Biology. Oxford University Press, Oxford, UK.

Papers and book chapters

Albon, S.D., Irvine, R.J., Halvorsen, O., Langvatn, R., Loe, L.E., Ropstad, E., Veiberg, V., van der Wal, R., Bjørkvoll, E.M., Duff, E.I., Hansen, B.B., Lee, A.M., Tveraa, T. and Stien, A. 2016. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, in press.

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. 2016. 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*, in press

Beumer, L.T., Varpe, Ø. and Hansen, B.B. 2016. Cratering behaviour and faecal C:N ratio in relation to seasonal snow-pack characteristics in a high-Arctic ungulate. *Polar Research*, in press

Bjørkvoll, E.M., Lee, A.M., Grøtan, V., Sæther, B.-E., Stien, A., Engen, S., Albon, S.D., Loe, L.E. and Hansen, B.B. 2016. Demographic buffering of life histories? Implications of the choice of measurement scale. *Ecology* **97**, 40–47.

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Engen, S., Solbu, E.B. and Sæther, B.-E. 2016. Neutral or non-neutral communities: temporal dynamics provide the answer. *Oikos*, in press.

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Engen, S. and Sæther, B.-E. 2016. Spatial synchrony in population dynamics: The effects of demographic stochasticity and density regulation with a spatial scale. *Mathematical Biosciences* **274**, 17–24.

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Gamelon, M., Grøtan, V., Engen, S., Bjørkvoll, E.M., Visser, M.E. and Sæther, B.-E. 2016. Density dependence in an age-structured population of great tits: identifying the critical age classes. *Ecology* **97**, 2479–2490.

Gohli, J. and Voje, K.L. 2016. An interspecific assessment of Bergmann's rule in 22 mammalian families. *BMC Evolutionary Biology* **16**, 222.

Holand, H., Kvalnes, T., Gamelon, M., Tufto, J., Jensen, H., Pärn, H., Ringsby, T.H. and Sæther, B.-E. 2016. Spatial variation in senescence rates in a bird metapopulation. *Oecologia* **181**, 865–871.

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Lien, S., Koop, B.F., Sandve, S.R., Miller, J.R., Kent, M.P., Nome, T., Hvidsten, T.R., Leong, J.S., Minkley, D.R., Zimin, A., Grammes, F., Grove, H., Gjuvsland, A., Walenz, B., Hermansen, R.A., von Schalburg, K., Rondeau, E.B., Di Genova, A., Samy, J.K.A., Vik, J.O., Vigeland, M.D., Caler, L., Grimholt, U., Jentoft, S., Våge, D.I., de Jong, P., Moen, T., Baranski, M., Palti, Y., Smith, D.R., Yorke, J.A., Nederbragt, A.J., Tooming-Klunderud, A., Jakobsen, K.S., Jiang, X., Fan, D., Hu, Y., Liberles, D.A., Vidal, R., Iturra, P., Jones, Steven J M, Jonassen, I., Maass, A., Omholt, S.W. and Davidson, W.S. 2016. The Atlantic salmon genome provides insights into rediploidization. *Nature* **533**, 200–205.

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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.

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Pelabon, C., Hennet, L., Bolstad, G.H., Albertsen, E., Opedal, Ø.H., Ekrem, R.K. and Armbruster, W.S. 2016. Does stronger pollen competition improve off spring fitness when pollen load does not vary? *American Journal of Botany* **103**, 522–531.

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Sandvik, H., Barrett, R.T., Erikstad, K.E., Myksvoll, M.S., Vikebø, F., Yoccoz, N.G., Anker-Nilssen, T., Lorentsen, S.-H., Reiertsen, T.K., Skarðhamar, J., Skern-Mauritzen, M. and Systad, G.H. 2016. Modelled drift patterns of fish larvae link coastal morphology to seabird colony distribution. *Nature Communications* **7**, 11599.

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Vickers, H., Høgda, K.A., Solbø, S., Karlsen, S.R., Tømmervik, H., Aanes, R. and Hansen, B.B. 2016. Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. *Environmental Research Letters* **11**, 105004.

Yashchenko, V., Fossen, E.I., Kielland, Ø.N. and Einum, S. 2016. Negative relationships between population density and metabolic rates are not general. *Journal of Animal Ecology* **85**, 1070–1077.

PhD student Sindre Sommerli on one of the water vole study islands in the Helgeland archipelago.

A juvenile water vole, captured in the study area in the Helgeland archipelago.

Photos: Henrik Pärn

EMPLOYEES 2013 - 2016

Professors and Associate professors

Name, position	Institution*	Note
Anders Gravbrøt Finstad, Ass. Prof	VM	From Septemeber 2014
Arild Husby, Ass. Prof	NV University of Helsinki	20% From July 2015
Bernt-Erik Sæther, Prof	NV	
Bob O'Hara, Prof	IE	From December 2016
Christophe Pélabon, Prof	NV	
Gunilla Rosenqvist	NV	
Hans K. Stenøien, Prof	VM	
Henrik Jensen, Ass. Prof	NV	
Ingelin Steinsland, Prof	IE	
Irja Ida Ratikainen, Researcher/Ass Prof 10%	NV	From July 2015
Jarle Tufto, Prof	IE	
Jonatan Wright, Prof	NV	
Nils Christian Stenseth, Prof II	NV	From May 2016
Ola Diserud, Prof	IE	
Otso Ovaskainen, Prof II	IE	From September 2014
Russell Lande, Prof II	NV	20% Prof II until September 2016 100% Prof September 2016 to December 2016 Currently 40% Prof II
Sigurd Einum, Prof	NV	
Steinar Engen, Prof	IE	
Stig Omholt, Prof	NV	
Thor Harald Ringsby, Ass. Prof	NV	
Vidar Grøtan, Ass. Prof	NV	

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IE: Faculty for Information Technology and Electrical Engineering, NTNU
VM: NTNU University Museum
NINA: Norwegian Institute for Nature Research

Researchers

Name	Institution*	Note
Alina Niskanen	NV	From February 2016
Aline Magdalena Lee	NV	From August 2016
Anna Maria Billing	NV	Until May 2014
Brage Bremset Hansen	NV	
Erling Johan Solberg	NINA	
Geir Hysing Bolstad	NINA	Postdoc at NV until May 2015 Researcher at NINA from May 2015
Hanno Sandvik	NV	
Ingerid Julie Hagen	NV	Until June 2016
Ivar Herfindal	NV	

Postdocs

Name	Institution*	Note
Cyril Firmat	NV	Until August 2014
Eirin Bjørkvoll	NV	Until March 2015
Erik Blystad Solbu	NV	PhD candidate at IE until November 2016
Hallvard Haanes	NV	Until December 2013
Holand, Anna Maria	IE	PhD candidate at NV until June 2013 Postdoc at IE from June 2013 to November 2016
Holand, Håkon	NV	PhD candidate at NV until April 2014 Researcher at NV from May 2014 to March 2016 Postdoc at NV from April 2016
Joost Raeymaekers	NV	From February 2016
Josefa Bleu	NV	From October 2013 to June 2014
Jostein Gohli	NV	From September 2016
Maja Tarka	NV	From November 2014
Marlene Gamelon	NV	From February 2014
Nerea Abrego	NV	From January 2015 to December 2016
Olivia Langhamer	NV	Until April 2016
Petri Kemppainen	NV	From January 2015 to May 2016
Thomas Kvalnes	NV	PhD candidate at NV until December 2015
Tim Burton	NV	From September 2015
Yimen Araya-Ajoy	NV	From April 2016

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PhD candidates

Name	Institution*	Note
Ane Marlene Myhre	NV	From June 2013
Bart Peeters	NV	From March 2015
Christopher H. Hilde	NV	From August 2016
Dilan Saatoglu	NV	From February 2016
Elena Albertsen	NV	From November 2013
Emma-Liina Marjakangas	NV	From December 2015
Endre Grüner Ofstad	NV	From August 2013
Erling I. F. Fossen	NV	From September 2014
Kate L. Matthews	NV	From May 2016
Maria Lie Selle	IE	From August 2016
Mathilde Le Moullec	NV	From August 2014
Øystein H. Opedal	NV	From June 2013
Øystein N. Kielland	NV	From Novmeber 2013
Peter Sjolte Ranke	NV	From October 2013
Rafaela Naves	NV	Guest visit from May to September 2016
Semona Issa	NV	From September 2016
Shelly Cao	IE	From November,ber 2016
Sindre L. Sommerli	NV	From February 2016
Stine Svalheim Markussen	NV	From June 2013
Thomas R. Haaland	NV	From October 2015

Administrative and technical staff

Name/position	Institution*	Note
Bernt Rønning, Engineer	NV	Postdoc at NV until December 2014 Researcher at NV until December 2015 Engineer at NV from Dececember 2015
Henrik Pärn, Engineer	NV	Researcher at NV until Apr 2015 Engineer at NV from Apr 2015
Solveig Johnsen, Coordinator	NV	
Varvara Yaschenko, Engineer	NV	

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