CENTRE FOR BIODIVERSITY DYNAMICS

Annual Report 2019

Norwegian Centre of Excellence

NTNU
Norwegian University of Science and Technology

CBD IN SHORT

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

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

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COVER PHOTO:
The water flea *Daphnia magna* is used as an experimental model organism at CBD to study links between ecological and evolutionary responses to environmental change. Photo by Varvara Yashchenko

COMMENTS FROM THE DIRECTOR:

Bernt-Erik Sæther
Director CBD

In 2019 CBD changed. The reason for this change was that all members of the staff were co-located into one common area. Although one may consider the previous situation in which CBD was located in areas two floors apart as a minor obstacle, the extent of interactions among people in different research groups has increased dramatically after the co-location. In my view, this clearly illustrates how important the infra-structure is for the quality of the working environment and the productivity of cross-disciplinary research centres like CBD. A lesson learnt from this is that seemingly small hurdles may easily prove to constitute a door-step mile for daily collegial interactions!

Another important event that occurred in 2019 was that professor Jane M. Reid started as an International Chair professor at NTNU and by this became a member of CBD. Professor Reid is a world-leading evolutionary ecologist. Her major research focus is to apply sophisticated statistical, quantitative genetic and molecular genetic approaches to analyse the relative contribution of genetic and environmental variation to individual differences in life-histories, and then examine how this affects population and evolutionary dynamics. She has addressed these questions using several long-term time series of individual-based data on demography, including island populations of song sparrow in British Columbia, Canada, and choughs on Scotland. Recently, she has been heavily involved in a project on Scottish shags with the long-term aim to study how seasonal variation in space use over large geographical areas affects individual differences in fitness. Professor Reid has also been active in developing actions to implement science into development of management strategies to conserve biological diversity. Thus, professor Reid has a research profile that shows large overlap with central elements of the current research at CBD.

The research at CBD is divided into three areas: population ecology, evolutionary biology and community dynamics. In Research Area 1 (RA1) several papers were published last year that improved our understanding of mechanisms generating age-specific variation in demography. For example, in a paper published in *Science*, Froy et al. showed that late-life declines in resistance to helminth parasites in wild Soay sheep were closely associated with overwinter mortality. This caused reduced adult survival probability, independent of changes in body weight. Similarly, several life history characteristics of great tits (Dingemanse et al., *Journal of Animal Ecology*) were related to whether individuals invested much in reproduction early in life at the expense of a long life-span. Evidence now suggests that such a pace of life syndrome generally explains a large proportion of individual differences in many life history characters and behavioural traits recorded in natural populations and can provide a general framework for analysis of how differences in individual fitness evolve (Wright et al. 2019, *Biological Reviews*). These studies also show how closely integrated research questions in RA1 and RA2: Evolutionary Biology now are.

Another central focus of the research in population ecology (RA1) at CBD is to understand the effects of environmental fluctuations on population dynamics. Such variability can give non-intuitive effects on the population dynamics. In the Svalbard reindeer rain on snow strongly restricts access of the individuals to their food supplies. Hansen et al. (*Nature Communications*) found that increased frequency of such extreme climatic events actually reduces extinction risk and stabilizes population dynamics due to interactions with fluctuations in age structure and effects of density dependence. This occurred because predominantly prime-aged individuals in the best body condition were those who were left after population crashes, which made the population less susceptible to future extreme climate events.

The effects of stochastic fluctuations in the environment were also a major topic for the research in Research Area 2: Evolutionary biology. A series of papers published by Irja I. Ratikainen and colleagues, mainly based on extensive analyses of simulation models, show that evolution of plasticity can be an important mechanism to reduce the impact of environmental variability. For example, plasticity can itself select for longevity. If the environmental fluctuations are highly autocorrelated, this selects for low investment in reversible plasticity and a phenotype that is poorly matched to the environment at older ages as well as has high reproductive effort and short lifespans (Ratikainen and Kokko, *Nature Communications*). Furthermore, in variable environments conservative bet-hedging by which individual variation in fitness is reduced, will often be favoured to reduce temporal variation in fitness due to environmental stochasticity (Haaland et al, *Proceedings of the Royal Society B*). These results demonstrate that not only the mean, but also the variance in environmental conditions strongly affect evolutionary processes.

Evolution of phenotypic plasticity in a variable environment was also modelled by Lande (*Proceedings of the National Academy* *of Sciences USA*), who showed that labile plasticity, in which many quantitative characters undergo continuous reversible development acting on different time scales, can improve tracking of the optimal phenotype to complex environmental cycles. This can contribute to reducing any costs of plasticity.

One central problem in evolutionary biology is to identify characters closely related to individual differences in fitness. In 2019 several papers from the research group lead by Sigurd Einum used metabolic rate as a key trait to analyse phenotypic evolution in ectotherms. One of the key findings appearing from these studies was that in *Daphnia magna* the genetic variance in food consumption and metabolic rate was closely correlated to the genetic variance in age at maturation, creating a direct link between these energy budget components and a life history trait with strong fitness effects (Einum et al., *Evolutionary Biology*). The metabolic rate scales allometrically with body mass following a linear relationship on a logarithmic scale. Fossen et al. *(Journal of Experimental Biology*) then showed that this allometric relationship can evolve due to an interaction between the genotype and the environment, despite little genetic variance present in the slope of this relationship at constant temperatures.

A central focus for the research at CBD in recent years has been to link behavioural ecology and quantitative genetics to understand how changes in behaviour will influence the capacity for evolutionary responses to variation in environmental conditions. Sæther and Engen (*Philosophical Transactions Royal Society B London*) suggested that variation in the strength of sexual selection provides such a link. They presented evidence indicating that variation in mating success affects the demographic variance of the population, which in turn may influence the dynamics, especially at small population sizes, as well as the rate of genetic drift.

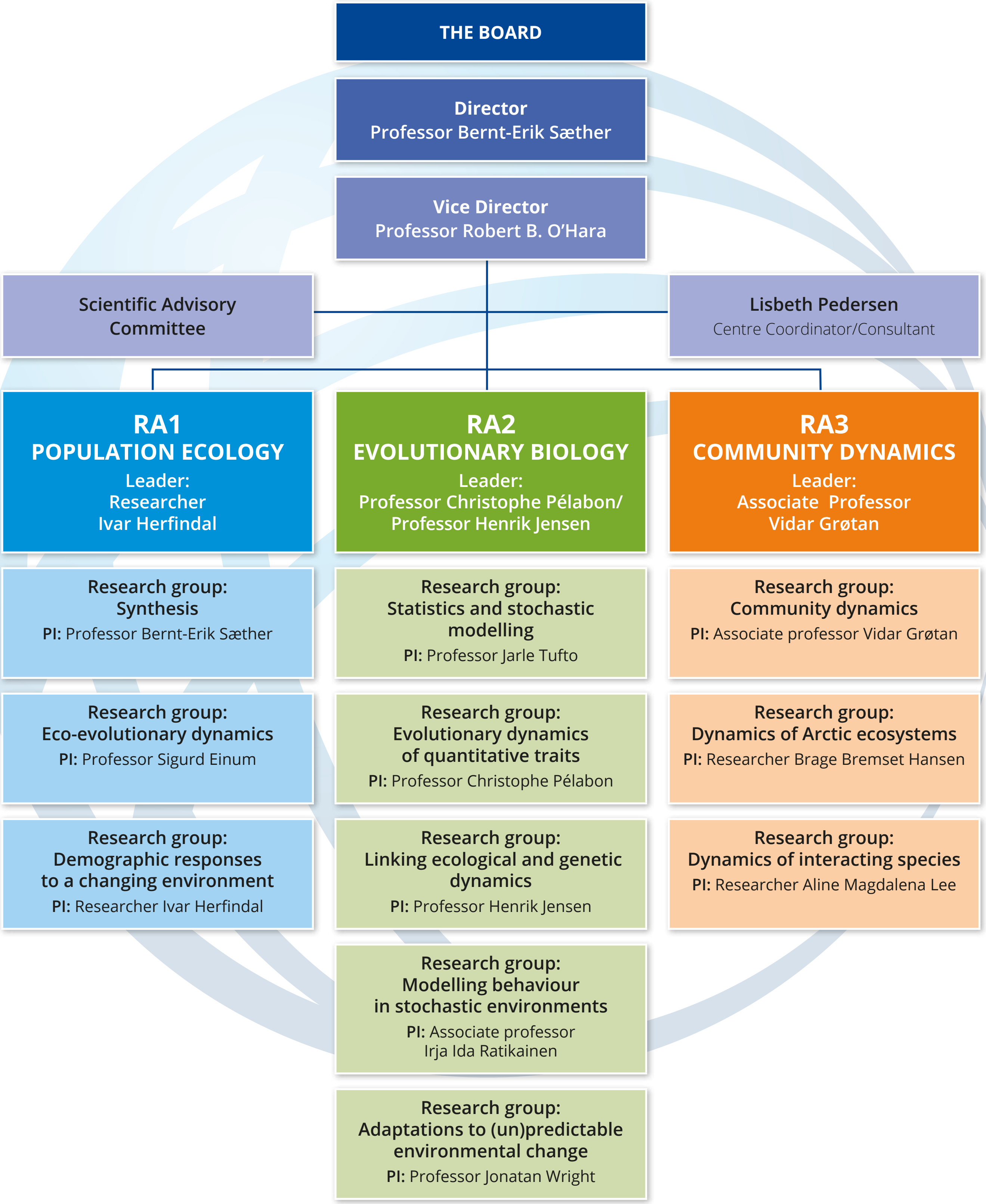
In Research Area 3: Community Dynamics a central question is to understand how different forms of human activity affect fluctuations in species diversity. An important task for facilitating such analyses is the development of statistical methods that are based on ecological realistic assumptions as well as including the effects of sampling. Several important advances have recently been made by researchers at CBD to achieve this goal. An important survey of the current standards with regard to models and procedures for assessment of biodiversity was provided by Araujo et al. in a review of species distribution models published in *Science Advances*. This study strongly recommends including different types of data to broaden the coverage of such biodiversity assessments. This approach should, however, be based on implementation of some agreed-upon standards promoting transparency and repeatability. Similarly, in an evaluation of the predictive power of 33 variants of 15 widely used species distribution models, Norberg et al (*Ecological Monographs*) showed the importance of using strict cross-validation procedures to provide reliable predictions.

A characteristic of the recent developments of the research at CBD has been an increasing focus on questions that combine different research areas. One such example is a study by Gamelon et al. (*Ecology Letters*) of interspecific competition between two tit species in different study areas across Europe. This study is based on models of single-species dynamics from RA1 to study the dynamical consequences of competitive interactions among species, which is an important focus in RA3. This study clearly demonstrated that variation in the numbers of great tits affected the population growth rate of the smaller-sized blue tit. Furthermore, this effect of fluctuations in the density of the competing species (great tits) affected the same demographic traits as variation in the numbers of individuals of the same species (blue tits).

In spring 2019 the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) presented its first global assessment report on biodiversity and ecosystem services. The conclusion of this report received enormous attention all over the world because it was concluded that different kinds of human activities have caused dramatic changes in the global environment, which have resulted in an enormous loss of biodiversity. This represents an important challenge for the international research community to develop methods and models to reliably project future trends in biological diversity, in particular as a response to different types of human activities. A workshop on this topic was organized in collaboration with NTNU Sustainability on February 27 in Trondheim. A major conclusion was that we need better statistical methods and more general models to assess changes in biodiversity and not least to provide reliable projections of future changes.

Classical population models ignore that there may be consistent differences among individuals across years in their fitness contributions, for instance dependent on some unmeasured traits. Such individual heterogeneity in demography causes a huge challenge when predicting population responses to changes in the environment (e.g. caused by climate change) because it potentially introduces time lags in the population dynamics. This makes it difficult to distinguish the dynamical consequences of environmental variation from those caused by individual heterogeneity in demography. A workshop on this topic was organized by Stephanie Jenouvrier, Woods Hole Oceanographic Institution, USA and myself on December 3-5 2019, assembling 17 scientists, including both theoreticians an empiricists. An important conclusion emerging from this workshop was that a common statistical framework can be developed to facilitate comparative analyses of individual heterogeneity in demography across species with different life histories.

ORGANIZATIONAL CHART 2019



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Synthesis
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Research group:
Eco-evolutionary dynamics
PI: Professor Sigurd Einum

Research group:
Demographic responses to a changing environment
PI: Researcher Ivar Herfindal

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EVOLUTIONARY BIOLOGY
Leader:
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Statistics and stochastic modelling
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Research group:
Adaptations to (un)predictable environmental change
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COMMUNITY DYNAMICS
Leader:
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Research group:
Community dynamics
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Research group:
Dynamics of Arctic ecosystems
PI: Researcher Brage Bremset Hansen

Research group:
Dynamics of interacting species
PI: Researcher Aline Magdalena Lee

MANAGEMENT

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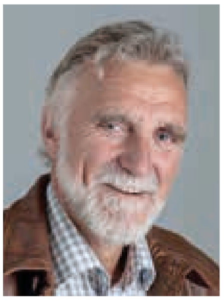

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SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

Current group members:
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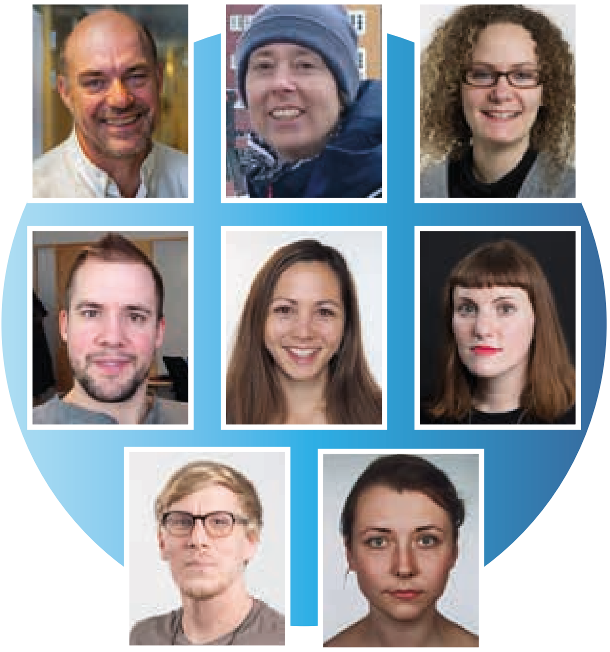
Professor Jane Margaret Reid
Researcher Marlène Gamelon
Postdoc Thomas Kvalnes
Postdoc Hannah Froy
PhD candidate Lara Veylit
PhD candidate Stefan Vriend
PhD candidate Lisa Dickel

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



Bernt-Erik Sæther, Jane Margaret Reid, Marlène Gamelon
Thomas Kvalnes, Hannah Froy, Lara Veylit
Stefan Vriend, Lisa Dickel

MAJOR SCIENTIFIC CONTRIBUTIONS

Modelling interspecific competition in age-structured populations

Fluctuations in population size may be induced by intraspecific density dependence, causing a decrease of population growth rate λ with increasing density N. Classical analyses of density dependence assume that all individuals in the population have an equal competitive effect. In the real world, this assumption is unrealistic and individuals of different ages may have contrasting abilities to compete. Thus, we have developed a modelling framework to analyse how variation in numbers in the different age-classes affect the population growth rate λ by estimating age-specific regression coefficients. In addition, most species live in communities where they interact with other ecologically similar species, often relying on common limiting resources. Thus, in addition to intraspecific density dependence, it is important to account for interspecific density dependence. We therefore estimated competitive coefficients, ωA, where a value of 0 indicates that only intraspecific competition explains variation in λA, and a value of 1 indicates that an individual of species B has the same competitive effect on the population growth rate of species A as an individual of the species itself.

Using this theoretical framework, we tested whether accounting for both interspecific competition and age structure can improve predictions of fluctuations in population size. Great tits and blue tits are two bird species that compete for food resources and nesting cavities. Based on long-term monitoring of these two competing species in Belgium, we found that the classical model of intraspecific density dependence only explains 24% of the observed variation in growth rate of the blue tit population (Figure 1C). Accounting for age structure, our model explains 36% of the observed variation in λ (Figure 1B), whereas accounting for both age structure and interspecific competition with great tits explains 56% of the variation in blue tit´s λ (Figure 1A).

In fact, this blue tit population is not an exception with regards to improved predictions of fluctuations in population size when both age structure and interspecific competition are accounted for. Replicating this analysis for 12 sites across Europe, where the competing great tits and blue tits have been monitored for many years, confirms that accounting for age structure and interspecific competition always improves predictions of fluctuations in population size by up to three times (Figure 2).

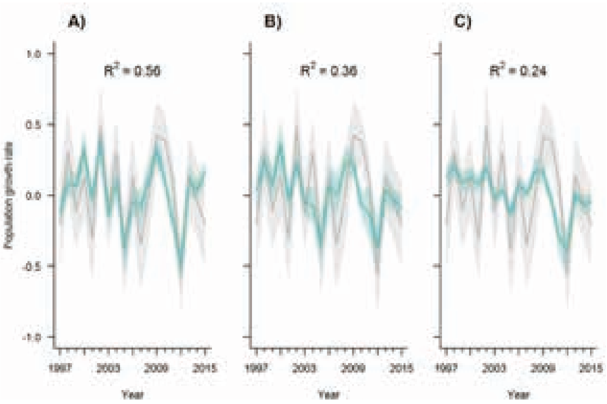


Figure 1. Blue tit population growth rate (log-scale) at Peerdsbos, Belgium, between 1997 and 2016. Grey lines correspond to the observed growth rate and blue lines to growth predicted by a full age-structured model including interspecific interactions (A); an age-structured model without any interactions among species (B); a classical density-dependent single species model without any age-structure (C).

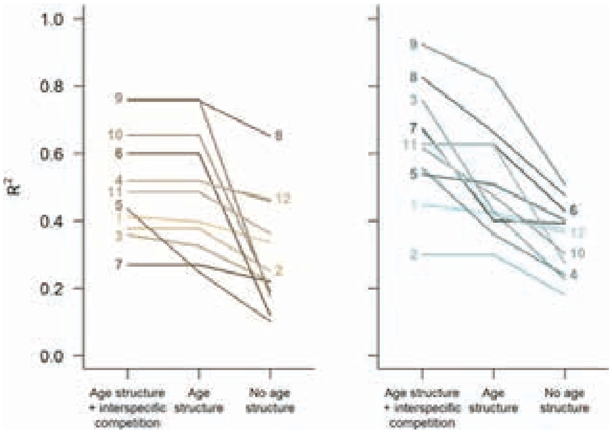


Figure 2. Coefficient of determination (R2) between observed and predicted population growth rates from a fully age-structured model including interspecific interactions, an age-structured model without any interactions among species and a classical density-dependent single species model without any age structure for great tit (in yellow, one number and colour per site) and blue tit populations (in blue, one number and colour per site).

Sexual selection and demographic stochasticity in the population dynamics

An important focus for the research group has been how changes in behaviour can modify the way that fluctuations in the environment affect the population growth rate and especially the stochastic components of the population dynamics. Sæther and Engen (2019) proposed that the structure of the social system affects the strength of sexual selection, which in turn will affect the demographic variance in the population. This indicates that species with certain kinds of social structure will be more vulnerable for extinction than other species with the same population size. Analyses of the population dynamics of the moose at the Island of Vega in northern Norway provide some support for such a link (see the Research Group: Demographic responses to a changing environment).

Spatial scaling of phenotypic variation in fluctuating environments

One of the major objectives of the research at CBD is to provide a common framework for analysing ecological and evolutionary processes. Engen and Sæther (2019) provide such a framework for modelling and analysing phenotypic selection in spatially structured populations. Their approach accounts for density regulation and stochastic variation in the environment (see also description of the theoretical results under the Research Group: Statistics and Stochastic Modelling). Some surprisingly simple results appeared from these analyses. For example, the degree of spatial differentiation of phenotypes is strongly influenced by parameters affecting ecological dynamics. This implies that ignoring density dependence and environmental stochasticity in analyses of geographical variation in phenotypic similarity is likely to produce biased results. Furthermore, the expression for the geographical scale of variation in the mean phenotype has a term corresponding to the classical Moran effect in population dynamics but it is also affected by dispersal and strength of local selection. In fact, the degree of phenotypic differentiation increases with decreasing strength of local density dependence and decreasing strength of local selection. These results imply that the form of the spatial autocorrelation function can reveal important information about ecological and evolutionary processes causing phenotypic differentiation in space.

RECOMMENDED READING:

Engen, S. and Sæther, B.-E. 2019. Ecological dynamics and large scale phenotypic differentiation in density-dependent populations. Theoretical Population Biology 127, 133–143.

Gamelon, M., Vriend, S.J.G., Engen, S., Adriaensen, F., Dhondt, A.A., Evans, S.R., Matthysen, E., Sheldon, B.C. and Sæther, B.-E. 2019. Accounting for interspecific competition and age structure in demographic analyses of density dependence improves predictions of fluctuations in population size. Ecology Letters 22, 797–806.

Sæther, B.-E. and Engen, S. 2019. Towards a predictive conservation biology: The devil is in the behaviour. Philosophical Transactions of the Royal Society of London B 374, 20190013.

RESEARCH GROUP: ECO-EVOLUTIONARY DYNAMICS

Current group members:
PI: Professor Sigurd Einum
Researcher Tim Burton
PhD candidate Semona Issa
PhD candidate Safa Chaabani
Engineer Hanna-Kaisa Lakka

Aim: *To improve understanding of links between ecological and evolutionary responses to environmental change.*

Semona Issa, Tim Burton, Sigurd Einum.
Right: Safa Chaabani, Hanna-Kaisa Lakka

MAJOR SCIENTIFIC CONTRIBUTIONS

One of the major scientific contributions from our group in 2019 was to provide increased understanding of how temperature influences aquatic ectotherms. Aquatic ectotherms face a challenge of obtaining sufficient oxygen, and it is commonly claimed that this challenge increases with increasing environmental temperature, causing concerns about the fate of aquatic ecosystems under climate change. Furthermore, this has been suggested to be a responsible mechanism for the commonly observed decline in maximum body size with increasing temperature, since large individuals have a larger oxygen demand than small ones. However, the oxygen challenge hypothesis often ignores the effect of both evolutionary potential and known phenotypic plastic responses. Evolution of reduced metabolism, and hence oxygen demand, may occur if natural populations harbor genetic variation for this trait. Fossen et al. (2019) demonstrated genetic variance in this trait for a population of the zooplankton *Daphnia magna*, with estimated evolvabilities being similar to those described for other physiological traits. In an accompanying paper, Einum et al. (2019) show that this genetic variation in combination with genetic variation in food consumption can explain a substantial amount of variation in somatic growth rate and age at maturation, and hence fitness. This suggests that populations may evolve a reduced metabolism if they experience selection for this under increased temperature. For phenotypic plasticity, previous studies have identified a number of mechanisms (molecular, behavioural, cell structure, morphological) that may act in concert to increase oxygen supply in response to increased temperature. Kielland et al. (2019) combined a novel modelling approach with empirical measurements that enabled quantification of how both the oxygen supply (maximum oxygen diffusion rate) and demand (metabolic rate) are affected by temperature while allowing for such phenotypic plasticity. This study confirmed that phenotypic plasticity contributes to an increased ability to obtain oxygen on the whole-organism level at high temperatures. However, the observed thermal plasticity in oxygen supply failed to compensate for the increased demand. Thus, we provide empirical evidence that the oxygen challenge in aquatic ectotherms increases with increasing temperature, even in the presence of phenotypic plasticity in oxygen supply. This is highly relevant for understanding population dynamic consequences to rapid heating events (e.g. changes throughout a single season). However, for more gradual changes occurring over longer time periods (e.g. climate change) evolutionary rescue may be an important route through which population persistence is achieved.

RECOMMENDED READING:

Einum, S., Fossen, E.I.F., Parry, V. and Pélabon, C. 2019. Genetic variation in metabolic rate and correlations with other energy budget components and life history in Daphnia magna. Evolutionary Biology 46, 170–178.

Fossen, E.I.F., Pélabon, C. and Einum, S. 2019. Genetic and environmental effects on the scaling of metabolic rate with body size. Journal of Experimental Biology 222, jeb193243.

Kielland, Ø.N., Bech, C. and Einum, S. 2019. Warm and out of breath: Thermal phenotypic plasticity in oxygen supply. Functional Ecology 33, 2142–2149.

Research group:
Demographic responses to a changing environment

Current group members:
PI: Researcher Ivar Herfindal
Research scientist Erling Johan Solberg (NINA)
Research scientist Erlend Birkeland Nilsen (NINA)
Research scientist Brett Sandercock (NINA)
Researcher Hanno Sandvik (NINA)
Postdoc Svenja Kroeger (NIBIO)
PhD candidate Endre Grüner Ofstad
PhD candidate Lars Rød-Eriksen (NINA)

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

Ivar Herfindal, Erling Johan Solberg, Erlend Birkeland Nilsen, Brett Sandercock, Hanno Sandvik, Svenja Kroeger, Endre Grüner Ofstad and Lars Rød-Eriksen.

Our research group focuses on how individuals and populations respond to environmental variation and human factors, such as harvesting. In 2019, much of the research was done within the Vega moose project, which is a collaborative project between NINA and NTNU/CBD. The strong involvement of researchers from NINA makes the research highly relevant for management and conservation.

Major scientific contributions

Demography in harvested populations

Harvesting is a major factor affecting dynamics and demography of animal populations. However, in a recent review Gamelon et al. (2019) shows that we still have surprisingly little knowledge about how harvesting in interaction with environmental variation affects the population dynamics. In fact, most research on the topic is theoretical, and more empirical work is therefore urgently needed to understand how harvesting can amplify or reduce impacts of environmental variation and climate change on population dynamics.

The impact of harvesting on demographic and evolutionary processes depends on the management strategy, but previous studies have focussed mainly on age and sex specific mortality and deliberate harvest selection on specific phenotypes. The Vega moose project represents a unique opportunity to assess demographic contributions to evolutionary processes, for instance by quantifying the effective population size, Ne, which influences genetic drift and rates of evolutionary response. A new study by Lee et al. (in press) showed that Ne was most sensitive to the demographic variance of older males (Figure 1), mainly caused by the high among-individual variation in

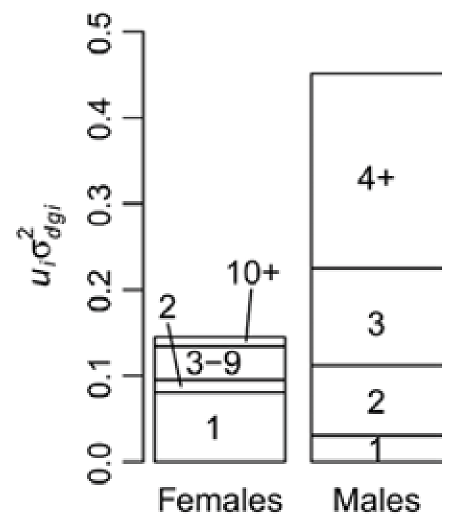


Figure 1. Older males contributed most to the demographic variance. Bars show cumulative sum of the sex-age class specific demographic variances weighted by the proportion of individuals in each sex-age class at stable stage structure. Numbers on bars indicate age classes (years).

reproductive performance in this group. The tendency for the same individuals to be successful several years in a row and the positive covariance between survival and reproduction in both males and females, contributed to decreasing Ne. Our new results demonstrate that harvesting can greatly affect evolutionary processes by affecting the variation in age- and sex-specific vital rates.

Individual use of habitats

Animals can move between different habitat types, and presumably their movements are optimal with respect to trade-offs between factors such as foraging and predation risk or other factors affecting survival. These factors often vary at short and long time scales, which makes habitat use and selection a complex subject to study. Herfindal et al. (2019) showed how ibex habitat use and vertical displacement was strongly influenced by short-term weather variation, as well as interspecific interactions. Indeed, the level of interspecific interactions was more important for annual variation in habitat use than climate and weather.

In a heterogeneous landscape, individuals have access to different resources that often vary in levels of availability, and their habitat use should reflect this. Ofstad et al. (2019) explored such mechanisms by using movement data from the Vega moose population and found that individual variation in habitat selection among adult males was mainly determined by the size and composition of their home range. In contrast, female habitat selection was mainly affected by how individuals utilised resources within their home range.

Management and conservation

Much of our research in 2019 has had a strong conservation focus. Hanno Sandvik has been involved in the development of methodology for assessing ecological impacts of alien species since 2012. In a recent methodological paper, Sandvik et al. (2019) show how parameters related to potential impacts of alien species can be used to assess ecological impact. Recently some work has also been done on the red-listed Peregrine falcon, which has shown remarkable recovery in central Norway (Nygård et al. 2019, Figure 2). In this study, CBD-member B.K. Sandercock was strongly involved in decomposing the contributions of productivity and territory occupancy to habitat-specific changes in population growth during the last four decades (Nygård et al. 2019). Finally, CBD-member E.B. Nilsen was involved in a study on the highly endangered Eld's deer in Myanmar (Bowler et al. 2019). In this study, Nilsen and colleagues showed that by combining data from an extensive camera trap study with long-term line transect distance sampling data, spatial variation in density and total abundance of deer in the reserve could be robustly estimated. According to this study, this population is the world's largest of this highly endangered ungulate species.

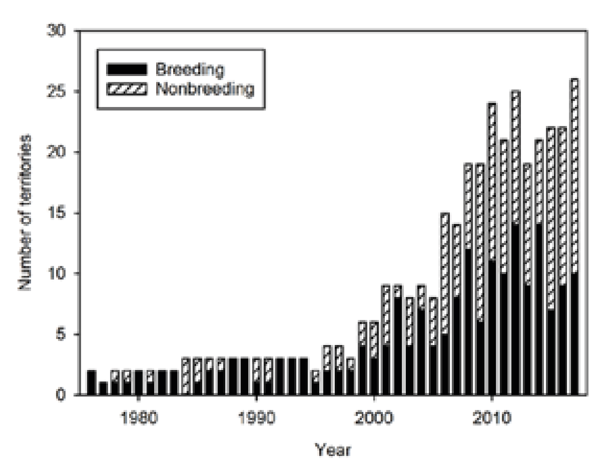


Figure 2. The number of occupied peregrine falcon territories in Nord-Trøndelag has increased dramatically the last 40 years (Nygård et al. 2019).

RECOMMENDED READING:

Bowler, D.E., Nilsen, E.B., Bischof, R., O'Hara, R.B., Yu, T.T., Oo, T., Aung, M. & Linnell, J.D.C. 2019. Integrating data from different survey types for population monitoring of an endangered species: the case of the Eld's deer. Scientific Reports, 9, 7766.

Gamelon, M., Sandercock, B.K. and Sæther, B.-E. 2019. Does harvesting amplify environmentally induced population fluctuations over time in marine and terrestrial species? Journal of Applied Ecology 56, 2186-2194.

Herfindal, I., Anderwald, P., Filli, F., Campell Andri, S. and Rempfler, T. 2019. Climate, competition and weather conditions drive vertical displacement and habitat use of an alpine ungulate in a highly topographic landscape. Landscape Ecology 34, 2523-2539.

Lee, A.M., Myhre, A.M., Markussen, S.S., Engen, S., Solberg, E.J., Haanes, H., Røed, K., Herfindal, I., Heim, M. and Sæther, B.-E. 2019. Decomposing demographic contributions to the effective population size with moose as a case study. Molecular Ecology, in press.

Nygård, T., Sandercock, B.K., Reinsborg, T. and Einvik, K. 2019. Population recovery of peregrine falcons in central Norway in the 4 decades since the DDT-ban. Ecotoxicology 28, 1160–1168.

Ofstad, E.G., Herfindal, I., Solberg, E.J., Heim, M., Rolandsen, C.M. and Sæther, B.-E. 2019. Use, selection, and home range properties: complex patterns of individual habitat utilization. Ecosphere 10, e02695.

Sandvik, H., Hilmo, O., Finstad, A.G., Hegre, H., Moen, T.L., Rafoss, T., Skarpaas, O., Elven, R., Sandmark, H. and Gederaas, L. 2019. Generic ecological impact assessment of alien species (GEIAA): the third generation of assessments in Norway. Biological Invasions 21, 2803–2810.

RESEARCH GROUP: STATISTICS AND STOCHASTIC MODELLING

Current group members:
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Professor emeritus: Steinar Engen
Postdoc: Ane Marlene Myhre
PhD candidate: Yihan Cao

Aim: *To understand the evolutionary responses to temporal and spatial environmental variation as well as the interplay between ecological and evolutionary dynamics*

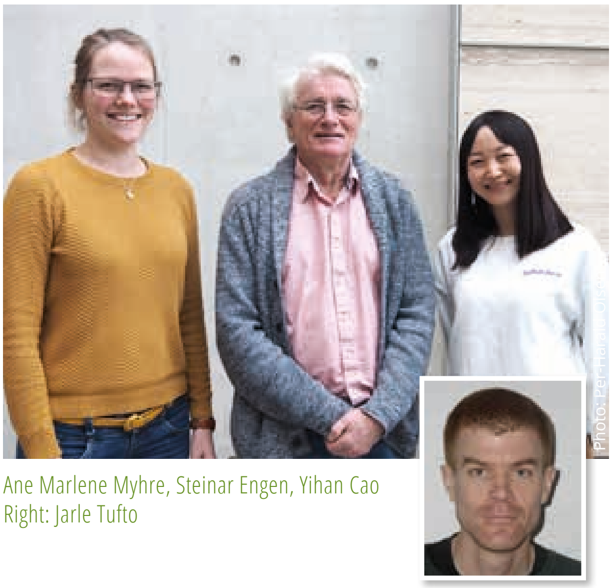


Photo: Per-Harald Olse

Ane Marlene Myhre, Steinar Engen, Yihan Cao
Right: Jarle Tufto

MAJOR SCIENTIFIC CONTRIBUTIONS

In Cao, Visser & Tufto (2019), methods for estimating the pattern of temporal variation in selection are further developed. The model is fitted by maximising the Laplace approximation of the marginal likelihood, computed via automatic differentiation of a function specifying the joint likelihood of observed data and latent random effects. One new feature of the model is estimation of the magnitude of fluctuations in the strength of stabilizing selection on onset of breeding in addition to fluctuations in optimal phenotypes and fitness at the optimum. These three properties of the annual fitness function are assumed to follow a vector first-order autoregressive process. Another novel feature of the model is to treat zero-inflation in number of fledglings produced (the modelled fitness component) as a separate selection episode through which selection acts. Applying the method to a long times series of individual-level data relating fitness to a phenological trait (onset of breeding) in a Dutch Great tit population, we find evidence for directional selection for earlier laying dates, both through the zero-inflation component of the model and through the mean of the non-inflated component of the distribution of number of fledglings. A third improvement over previous methods is the inclusion of multiple broods.

Engen & Sæther (2019) develop an eco-evolutionary model for the spatio-temporal joint evolution of multiple phenotypic traits and the dynamics of population size. Fluctuating selection on the phenotypic traits is generated through fluctuations in population size and density-dependent fitness functions leading to a form of r- and K-selection on the traits. With evolution in a single trait only, the scale of spatial autocorrelation in the trait is shown to depend on the scale of spatial autocorrelation in population size (in turn determined by the spatial scaling of environmental noise, the strength of density dependence and the spatial scale of individual dispersal displacements) but with an additional term involving also the strength of local stabilizing selection on the trait.

RECOMMENDED READING:

Cao, Y., Visser, M.E. and Tufto, J. 2019. A time-series model for estimating temporal variation in phenotypic selection on laying dates in a Dutch great tit population. Methods in Ecology and Evolution 10, 1401–1411.

Engen, S. and Sæther, B.-E. 2019. Ecological dynamics and large scale phenotypic differentiation in density-dependent populations. Theoretical Population Biology 127, 133–143.

RESEARCH GROUP: EVOLUTIONARY DYNAMICS OF QUANTITATIVE TRAITS

Current group members:
PI: Professor Christophe Pélabon
Postdoc Eivind Undheim
Researcher Geir H. Bolstad (NINA)
PhD candidate Elena Albertsen
PhD candidate Christoffer H. Hilde

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


Photo: Per-Harald Olsen

Christophe Pelabon, Geir H. Bolstad, Elena Albertsen and Christoffer Høyvik Hilde.
Right: Eivind Undheim

The group is testing predictive models for the evolutionary dynamics of multivariate quantitative traits, focusing particularly on the evolutionary constraints generated by the genetic architecture of the traits. Using both experimental and comparative approaches, the group aims at operationalizing measures of the evolutionary potential or evolvability. The group, in collaboration with S. Einum and E. Fossen from the Eco-evolutionary dynamics group, has published two papers on the subject in 2019. The project leader, together with Prof. T. Hansen from the university of Oslo has also organized a one-year workshop on Evolvability at the Centre of Advance Studies (CAS) in Oslo (project period August 2019 – June 2020).

MAJOR SCIENTIFIC CONTRIBUTIONS

The project on Evolvability at the Centre of Advance study CAS – Oslo 2019-2020.

Whether organisms are able to adapt to changing environments depends on their evolvability. In the short term, evolvability depends on the standing genetic variation on which selection can act. On longer time scales, it depends on the ability of organisms to produce potentially beneficial variation through mutations, and thus on the structure of the genotype-phenotype map that determines how genomic variation is converted to phenotypic variation. For even longer time frames, evolvability may be linked to the ability of organisms to break developmental constraints and evolve new character identities or evolutionary modes that can produce qualitatively new forms of variation. Examples can be seen when the bones in a fin became individualized to allow the evolution of a hand with specialized fingers, which in turn evolved into the diversity of limbs seen among vertebrates today, or when the evolution of multicellularity or sexual reproduction allowed new modes of organization, specialization or information transfer. What makes such transitions possible? The answer to this question is central for understanding the evolution of complex organisms and unifying across biological disciplines and time scales.

Some evolutionary biologists consider evolvability as a key concept in an extended synthesis of evolutionary theory that allows disciplines such as developmental biology, molecular and systems biology to communicate with mainstream evolutionary biology, while others simply consider evolvability as a replacement of the older concept of developmental constraints. Still, the interest of different fields in the same topic marks it as a "trading zone" where researchers can exchange ideas and develop a common language.

T.F. Hansen (UiO) and C. Pélabon (NTNU, CBD) have organized a one-year meeting (2019-2020), at the CAS in Oslo where they have gathered a distinguished group of scholars who have been influential in the development and study of evolvability across different disciplines. Together they evaluate what has been learned from the various approaches over the last 25 years, aiming at unifying the understanding of evolvability across disciplines.
The two organizers have been able to invite to CAS most of the people that were instrumental in the development of the concept (e.g. GP Wagner; D Houle; A Wagner; J. Cheverud; M. Pigliucci among others) to reflect on the socio-historical circumstances of its emergence and to discuss the validity and applicability of a more unified concept of evolvability across the different fields.

A larvae of the common green lacewing *Chrysoperla carnea*, the new model organism to understand the evolution of animal venom. (NFR project from Eivind A. Undheim)

RECOMMENDED READING:

Fossen, E.I.F., Pélabon, C. and Einum, S. 2019. Genetic and environmental effects on the scaling of metabolic rate with body size. Journal of Experimental Biology 222, jeb193243.

Einum, S., Fossen, E.I.F., Parry, V. and Pélabon, C. 2019. Genetic variation in metabolic rate and correlations with other energy budget components and life history in Daphnia magna. Evolutionary Biology 46, 170–178.

Hildesheim, L.S., Opedal, Ø.H., Armbruster, W.S. and Pélabon, C. 2019. Fitness costs of delayed pollination in a mixed-mating plant. Annals of Botany 124, 869–881..

RESEARCH GROUP: LINKING ECOLOGICAL AND GENETIC DYNAMICS

Current group members:
PI: Professor Henrik Jensen
Associate Professor Thor Harald Ringsby
Associate Professor Stefanie Muff
Associate Professor Michael D. Martin
Associate Professor Arild Husby
Professor Stig W. Omholt
Professor Ingelin Steinsland
Researcher Ingerid J. Hagen (NINA)
Researcher Alina Niskanen (University of Oulu)
Researcher Peter S. Ranke
Postdoc Laurène Lecaudey
Postdoc Hannu Mäkinen (Uppsala University)
PhD candidate Sindre L. Sommerli
PhD candidate Dilan Saatoglu
PhD candidate Maria L. Selle
PhD candidate Michael P. Pedersen
PhD candidate Sarah Lundregan
PhD candidate Vanessa Bieker
PhD candidate Ådne M. Nafstad
PhD candidate Isabelle Russell
PhD candidate Fabian Kellner
PhD candidate Gabriel David (Uppsala University)
PhD candidate John McAuley (University of Edinburgh)
Engineer Henrik Pärn
Engineer Bernt Rønning

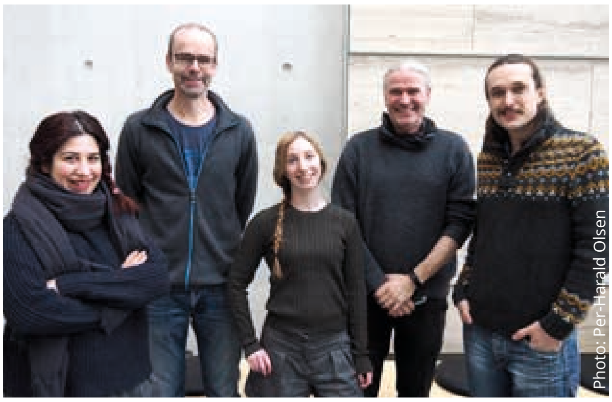


Photo: Per-Harald Olsen

Dilan Saatoglu, Henrik Jensen, Sarah Lundregan, Thor Harald Ringsby, Michael P. Pedersen

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

Our research group produces knowledge targeting key questions at the interface between RA1 and RA2. In particular, our goals are to examine how spatiotemporal variation in population dynamics (including the effects of density dependence, environmental stochasticity and dispersal) interact with phenotypic variation and evolutionary dynamics, and the role of genetic variation in these interactions. Furthermore, our group seeks to understand the genetic basis of the evolution of diversity within and across species, which may be very rapid on geological time-scales. To achieve our goals, we combine state-of-the-art genomic tools with the development and application of novel statistical methods. Using such interdisciplinary approaches, we analyze individual-based data on fitness-related phenotypic traits, life history traits, and fitness components, as well as genome-level genetic variation across populations and species. Our main study systems are several intensively studied natural vertebrate metapopulations, including house sparrows, water voles, arctic foxes and Atlantic salmon, as well as various groups of plants such as Daisy trees and ragweed. 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, not only needed to parameterize and test models developed by other RGs at CBD, but also particularly 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.

MAJOR SCIENTIFIC CONTRIBUTIONS

Effects of a changing climate on host-parasite dynamics in natural populations

Climate and weather conditions may have substantial effects on the ecology of both parasites and hosts in natural populations. The strength and shape of the effects of weather on parasites and hosts are likely to change as global warming affects local climate. These changes may in turn alter fundamental elements of parasite–host dynamics. In Holand et al. (2019) we explored the influence of temperature and precipitation on the prevalence of a nematode parasite in a metapopulation of house sparrow hosts in northern Norway. We also investigated if annual change in parasite prevalence was related to winter climate, as described by the North Atlantic Oscillation (NAO). We found that parasite prevalence increased with temperature within years and decreased slightly with increasing precipitation. We also found that a mild winter (positive winter NAO index) was associated with higher mean parasite prevalence the following year. Our results indicate that both local and large-scale weather conditions may affect the proportion of hosts that become infected by parasites in natural populations. From previous studies in the same metapopulation we know that parasite infection has negative effects on fitness components of individual hosts. Consequently, it is possible that parasite prevalence may affect host population growth rates negatively. Some climate models have predicted that frequencies of positive winter NAO indices may increase in the future.
This could lead to significant changes in the parasite–host relationship in the future. For instance, as global warming is predicted to result in wetter and milder winter temperatures in northern Europe, the current study suggests that parasite species that are limited by low temperatures during the winter season may extend their geographical distribution to higher altitudes and latitudes. Understanding how climate impacts parasites and hosts may be vital in accurately predicting the changes in natural communities due to climate change. Such knowledge may prove crucial in conservation and management efforts of threatened species and ecosystems.

Development of methods to identify dispersers and effects of spatial population structure on the distribution of adaptive genetic variation

Baseline oriented network estimation

Dispersal, the movement of individuals between populations, is a fundamental process in ecology, evolution and conservation. However, direct identification of dispersing individuals is difficult or impossible in most natural populations. To solve this problem, we developed a novel genetic assignment method that can be used to assign individuals with unknown genetic origin to source populations (Kuismin et al. 2020). Our approach, BONE (Baseline Oriented Network Estimation), is a network-based tool, which borrows concepts from undirected graph inference. By comparing BONE with three genetic assignment methods implemented in R packages radmixture, assignPOP and RUBIAS using both simulated and real data (high-density SNP-genotype data from an insular house sparrow metapopulation and Chinook salmon populations) we show that BONE is competitive or superior compared to the other assignment methods. In contrast to other methods, our approach also identifies outlying mixture individuals that could originate outside of the baseline populations. BONE is a freely available R package.

Animal models

The animal model is a key tool in quantitative genetics that has been used extensively to estimate fundamental parameters, such as additive genetic variance or heritability. An implicit assumption of animal models is that all founder individuals derive from a single population. This assumption is commonly violated, for instance in geographically structured (fragmented) populations. Ignoring that base populations are genetically heterogeneous and thus split into different 'genetic groups' may lead to biased parameter estimates, especially for additive genetic variance. In Muff et al. (2019) we developed an extension of the animal model that allows groups to differ in their mean breeding values and permits estimation of group-specific additive genetic variances. This was achieved by employing group-specific relatedness matrices for the breeding value components to different genetic groups, and by developing computationally favorable approximations for these matrix components, which were shown to be uncritical. Simulations and an example from an insular meta-population of house sparrows in Norway with three distinct genetic groups (where dispersers between groups had been identified using the BONE genetic assignment method) illustrate that our method is successful in estimating group-specific additive genetic variances. Quantifying differences in additive genetic variance within and among populations is of major biological interest in ecology, evolution, and animal and plant breeding because it directly predicts the populations' adaptive potential. The proposed method provides a major development in this field because it allows estimating such differences for subpopulations that are connected through dispersal. This means it will be useful to study temporal or spatial variation of additive genetic variances.

Using genetic data to understand drivers of species extinction

The great auk was once abundant and distributed across the North Atlantic. It is now extinct, having been heavily exploited for its eggs, meat, and feathers. In Thomas et al. (2019) we investigated the impact of human hunting on its demise by integrating genetic data, GPS-based ocean current data, and analyses of population viability. We sequenced complete mitochondrial genomes of 41 individuals from across the species' geographic range and reconstructed population structure and population dynamics throughout the Holocene. Taken together, our data do not provide any evidence that great auks were at risk of extinction prior to the onset of intensive human hunting in the early 16th century. In addition, our population viability analyses reveal that even if the great auk had not been under threat by environmental change, human hunting alone could have been sufficient to cause its extinction. Our results emphasise the vulnerability of even abundant and widespread species to intense and localised exploitation, and emphasise the need for thorough monitoring of commercially harvested species, particularly in poorly researched environments such as our oceans. This will lay the platform for sustainable ecosystems and ensure the evidence-based conservation management of biodiversity.

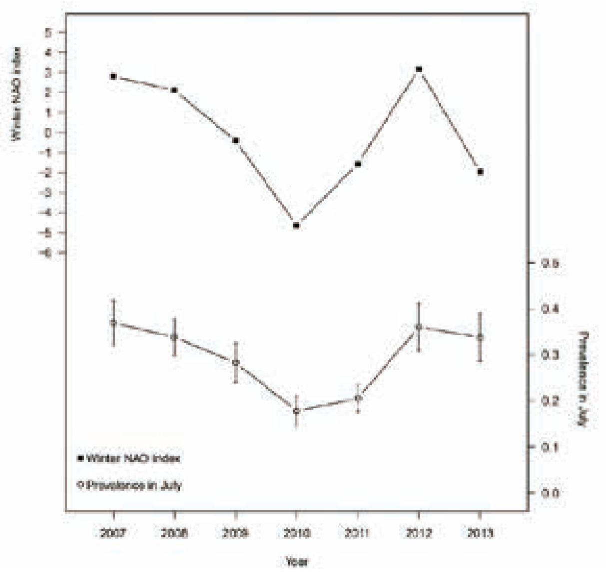


Figure 1: The relationship between the winter NAO index and observed mean prevalence of the parasite S. trachea in a metapopulation of house sparrows at the coast of Helgeland, Norway, in July (Holand et al. 2019). Estimates of mean July prevalence are shown with ±1 S.E.

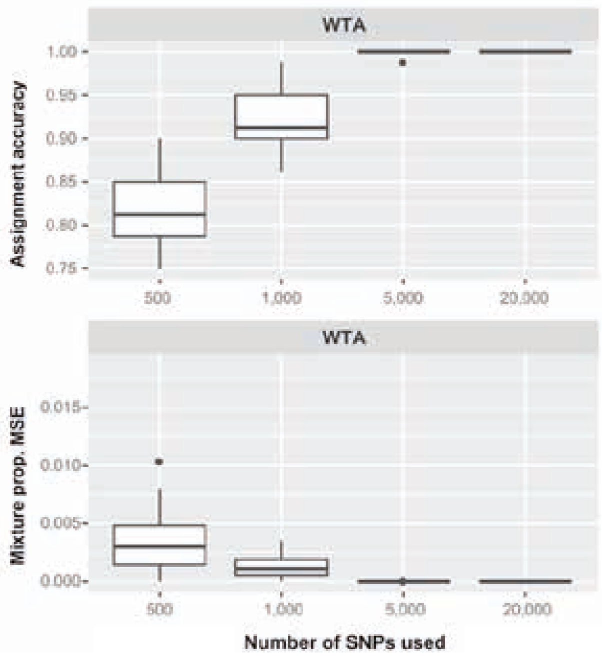


Figure 2: The assignment accuracy and the mean squared errors (MSE) of mixture proportions recovery based on 50 simulation replications (house sparrow data SNP genotype frequencies as the starting point) show the effect of number of SNP markers in the BONE method ('WTA' is short for the 'Winner Takes it All' procedure). Assignment accuracy represents the proportion of correctly assigned mixture individuals.

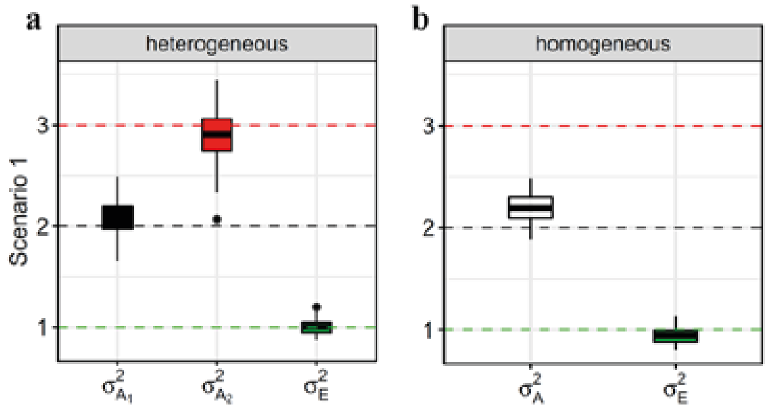


Figure 3: Results from simulation scenarios to illustrate the performance of the genetic group animal model with heterogeneous additive genetic variances. The boxplots represent the distributions of estimated variances (posterior modes) from a model with genetic groups and heterogeneous additive genetic variances $\sigma^2_{A_1}$ and $\sigma^2_{A_2}$ (left panel, a), compared to the results from a model that only allowed for a single homogeneous variance σ^2_A (right panel, b). Dashed lines indicate the refe rence values that were used to generate the data (black: $\sigma^2_{A_1}$, red: $\sigma^2_{A_2}$, green: σ^2_E).

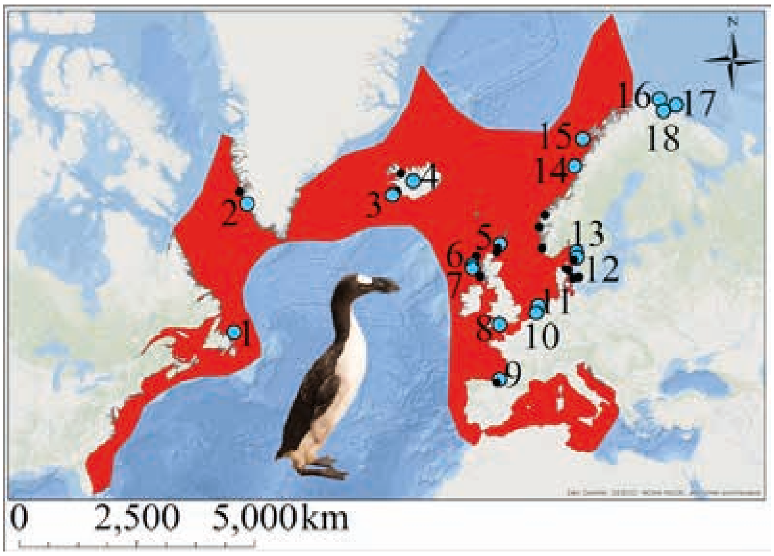


Figure 4: The great auk and its former distribution in the North Atlantic. Red shading indicates the geographic distribution of the great auk, as defined by BirdLife International/IUCN (BirdLife International). Sites marked with blue dots represent samples used in our analyses (n = 41 individuals).

RECOMMENDED READING:

Holand, H., Jensen, H., Kvalnes, T., Tufto, J., Pärn, H., Sæther, B.-E. and Ringsby, T.H. 2019. Parasite prevalence increases with temperature in an avian metapopulation in northern Norway. Parasitology 146, 1030–1035.

Kuismin, M., Saatoglu, D., Niskanen, A.K., Jensen, H. and Sillanpää, M.J. 2019. Genetic assignment of individuals to source populations using network estimation tools. Methods in Ecology and Evolution 11, 333-344.

Muff, S., Niskanen, A.K., Saatoglu, D., Keller, L.F. and Jensen, H. 2019. Animal models with group-specific additive genetic variances: extending genetic group models. Genetics Selection Evolution 51, 7.

Thomas, J.E., Carvalho, G.R., Haile, J., Rawlence, N.J., Martin, M.D., et al. 2019. Demographic reconstruction from ancient DNA supports rapid extinction of the great auk. ELife 8, e47509.

Research group: Modelling behaviour in stochastic environments

Current group members:
PI: Associate professor Irja Ida Ratikainen
Assistant professor Martin Lind
PhD candidate Thomas Haaland

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

We are a small research group with strong collaborations both within CBD, but also internationally. Our main project is "Evolutionary responses to variable and unpredictable environments", a "Young talented researchers" project from the Norwegian Research Council. We combine several different modelling techniques to investigate evolution of epigenetic information use, plasticity and learning, insurance and bet-hedging of both behaviour and life history strategies, all in variable and unpredictable environments. Martin Lind is a visiting researcher from Uppsala University, interested in life history evolution in general, focusing particularly on 1) evolution of inheritance systems (phenotypic plasticity, parental and epigenetic inheritance) during adaptation to heterogeneous environments, and 2) the role of life-history trade-offs during the evolution of long lifespan. Together with Dr. Ratikainen, his lab is testing novel theory in the powerful *Caenorhabditis remanei* and *C. elegans* empirical model systems.

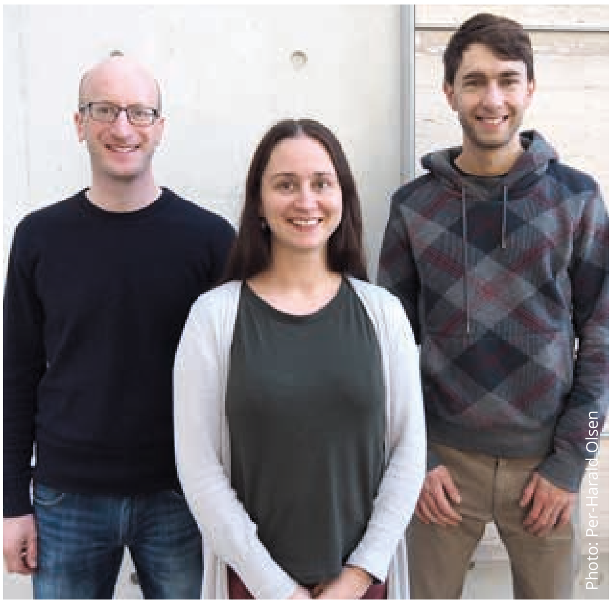
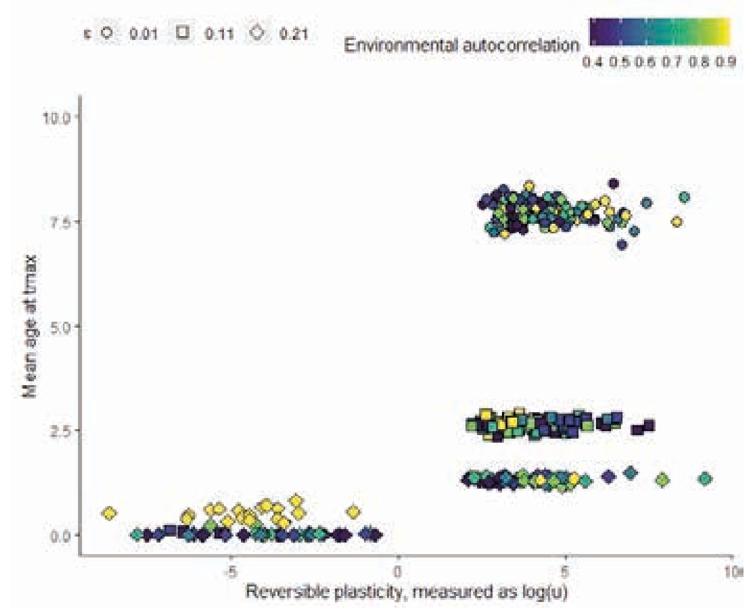


Photo: Per-Harald Olsen

Martin Lind, Irja Ida Ratikainen, Thomas Haaland

Simulation results show strong support for the idea that reversible plasticity and lifespan can coevolve.

We (Ratikainen and Kokko 2019) found that stable environments generally lead to less plasticity (yellow squares and diamonds), and this is associated with short lifespans. If these conditions combine with low updating error, reproductive effort evolves to be lower, yielding relatively long lifespans (yellow circles), while plasticity stabilizes at intermediate values (yellow circles). Low updating error is clearly associated with 'slow' life histories (circles). The longest lifespans require both that updating error is low and that lifelong plasticity has evolved (in the form of frequent updating, i.e. high u). The effect of low updating error leading to a 'slow' life history is far clearer than low error conditions selecting for high updating frequency per se. Conversely, we find the fastest life histories when updates are error-prone (diamonds).



MAJOR SCIENTIFIC CONTRIBUTIONS

In order to understand how organisms cope with ongoing changes in environmental variability, it is necessary to consider multiple adaptations to environmental fluctuations and how they co-evolve. In this group we have taken several steps towards this goal in the last year. Firstly, we have shown that reversible phenotypic plasticity, the ability to change one's phenotype repeatedly throughout life, will co-evolve with the balance in the trade-off between investment in reproduction and survival. To understand why reversible plasticity may covary with lifespan, studies have tended to assume unidirectional causality: plasticity evolves under suitable rates of environmental variation with respect to life history. We have shown that if lifespan also evolves in response to plasticity, then long life is not merely a context that sets the stage for lifelong plasticity but plasticity itself can select for longevity.

In a second theoretical development we have looked into how variance sensitivity co-evolves with bet-hedging, when there is environmental uncertainty on different time scales. Variance-prone strategies increase the expected arithmetic mean fitness if the relationship between payoffs and fitness is accelerating. However, such strategies also produce greater variance in short term payoffs. We investigated whether selection for such variance-prone strategies is counteracted by selection for bet-hedging that works to adaptively reduce fitness variance, and find that this depends on how fitness accumulates within lifetimes and across generations. Specifically, variance proneness is favoured only when environmental effects on individuals are uncorrelated or individuals can use many time steps to accumulate resources prior to selection. Conversely, multiplicative fitness accumulation, caused by high correlations between individuals and fewer decision events before selection, favours variance aversion. These results can improve our understanding of variance-sensitive strategies in optimal foraging, migration, life histories and cooperative breeding.

While the existence of life-history trade-offs is well supported, their nature has remained elusive. The emerging *Developmental Theory of Ageing* provides a conceptually novel framework by proposing that ageing is a direct consequence of physiological processes optimized for early-life function. Contrary to the classic view based on energy allocation trade-offs, this theory predicts that survival and fitness can be simultaneously improved by optimising gene expression in late life. Using age-specific down-regulation of gene expression for the evolutionarily conserved insulin/IGF-1 nutrient-sensing signaling via *daf*-2 RNA interference (RNAi) in *Caenorhabditis elegans* nematodes, we found that long-lived *daf*-2 RNAi parents showed normal fecundity. Remarkably, the offspring of *daf*-2 RNAi parents also had higher fitness. We demonstrated that hyper-function of diverse physiological processes after maturity is detrimental for survival and fitness. Therefore, optimisation of gene expression in adults can ameliorate ageing and increase fitness.

Caenorhabditis elegans nematode worm

RECOMMENDED READING:

Ratikainen, I.I. and Kokko, H. 2019. The coevolution of lifespan and reversible plasticity. Nature Communications 10, 538.

Haaland, T.R., Wright, J. and Ratikainen, I.I. 2019. Bet-hedging across generations can affect the evolution of variance-sensitive strategies within generations. Proceedings of the Royal Society B: Biological Sciences 286, 20192070.

Lind, M.I., Ravindran, S., Sekajova, Z., Carlsson, H., Hinas, A. and Maklakov, A.A. 2019. Experimentally reduced insulin/IGF-1 signaling in adulthood extends lifespan of parents and improves Darwinian fitness of their offspring. Evolution Letters 3, 207–216.

RESEARCH GROUP: ADAPTATIONS TO (UN)PREDICTABLE ENVIRONMENTAL CHANGE

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

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


Jonatan Wright, Mette Helene Finnøen, Yimen Araya-Ajoy

This research group contributes to the research program of CBD primarily in Research Area 2. A variety of approaches is applied: from the development of mathematical models and wider conceptual frameworks to detailed life history and behavioural studies on vertebrates in the field and laboratory. 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. Adaptations to predictable short-term environmental variation should favour reversible or irreversible (developmental) plasticity, whilst unpredictable long-term environmental variation will favour bet-hedging and adaptive tracking. A fundamental challenge here is in defining such adaptive phenomena for phenotypes that vary hierarchically among species, populations, genotypes and individuals, and also within individuals for repeatedly expressed labile phenotypic traits (behaviour, physiology and morphology). To address this challenge, we combine approaches from behavioural ecology and quantitative genetics, using statistical models and the concept of the reaction norm to explore phenotypic variation among individuals alongside within-individual plasticity in labile phenotypes. Working at the interface between theoretical and empirical research, we are involved in a wide range of activities from the development of mathematical models and wider conceptual frameworks to detailed life history and behavioural studies on vertebrates in the field and laboratory.

MAJOR SCIENTIFIC CONTRIBUTIONS

Community stability in invertebrate communities in Swedish lakes

Research on ecosystem stability has had a strong focus on local systems. However, environmental change often occurs slowly and at broad spatial scales. This requires regional-level assessments of long-term stability, so in this study we assessed the stability of macroinvertebrate communities across 105 lakes in the Swedish lakescape. Using a hierarchical mixed-model approach, we first evaluated the environmental pressures affecting invertebrate communities in two ecoregions (north versus south) using a 23-year time series (1995–2017), and then examined how a set of environmental and physical variables affected the stability of these communities.

Lake latitude, size, total phosphorus and alkalinity affected community composition in both northern and southern lakes. We found that lake stability was affected by species richness and lake size in both ecoregions and alkalinity and total phosphorus in northern lakes. There was considerable heterogeneity in the patterns of community stability across individual lakes, but clear relationships between that stability and environmental drivers began to emerge when regions composed of many discrete lakes were the focal unit of study. The results of this study highlight that broad-scale comparisons in combination with long time series are essential to understand the effects of environmental change on the stability of lake communities in space and time.

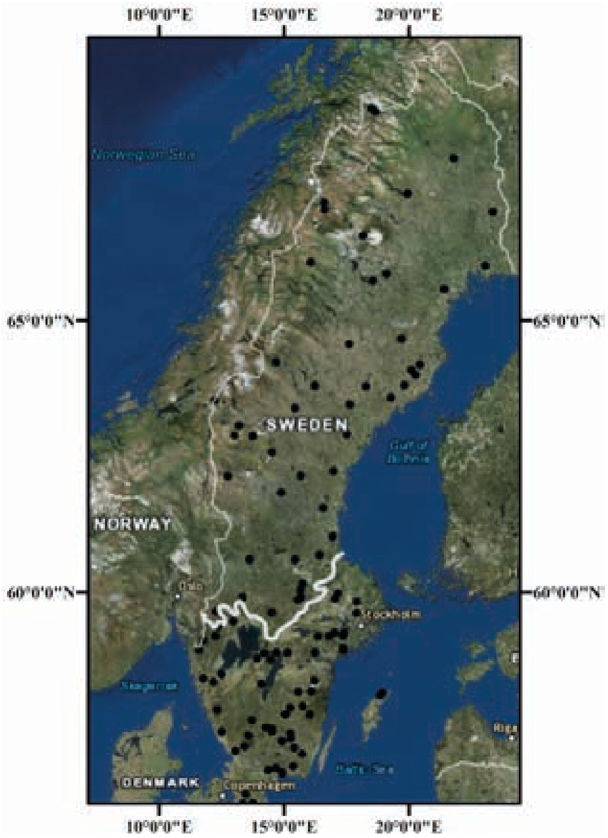


Figure 1a. Map showing lake locations across Sweden below (N=57) and above (N=48) the Limes Norrlandicus.

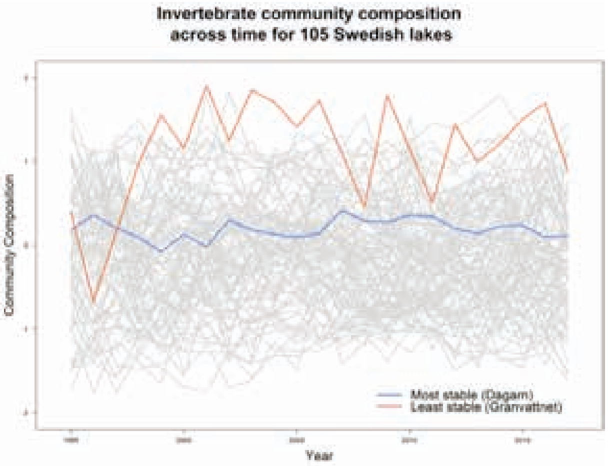


Figure 1b. Community composition fluctuations across time for 105 Swedish lakes. Highlighted a very variable and a very stable lake.

Parental provisioning in response to nestling begging and predation threat

Parental provisioning behavior is a major determinant of offspring growth and survival, but high provisioning rates might come at the cost of increased predation threat. Parents should thus adjust provisioning activity according to current predation threat levels. Moreover, life-history theory predicts that response to predation threat should be correlated with investment in current reproduction. We experimentally manipulated perceived predation threat in free-living great tits (*Parus major*) by presenting parents with a nest predator model while monitoring different aspects of provisioning behavior and nestling begging. Experiments were conducted in 2 years differing greatly in ecological conditions, including food availability. We further quantified male territorial aggressiveness and male and female exploratory tendency.

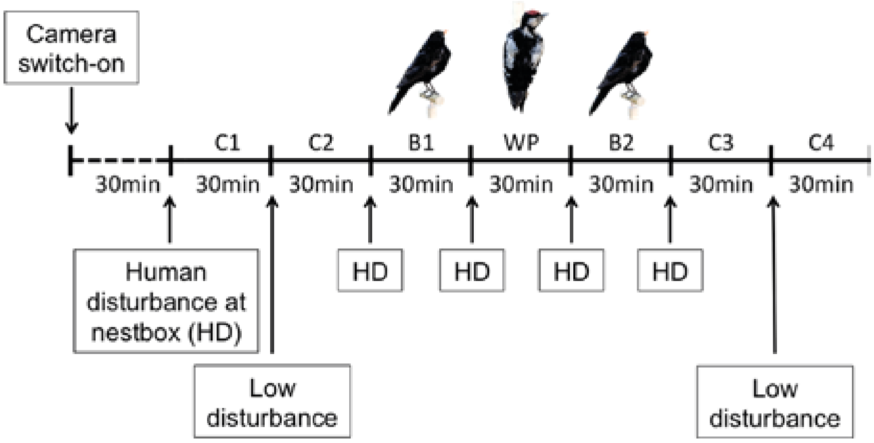


Figure 2a. Setup of the perceived predation threat experiment (C = control, B = blackbird, and WP = woodpecker presentation at the nestbox). HD refers to high levels of disturbance at the nestbox at the beginning of those treatments.

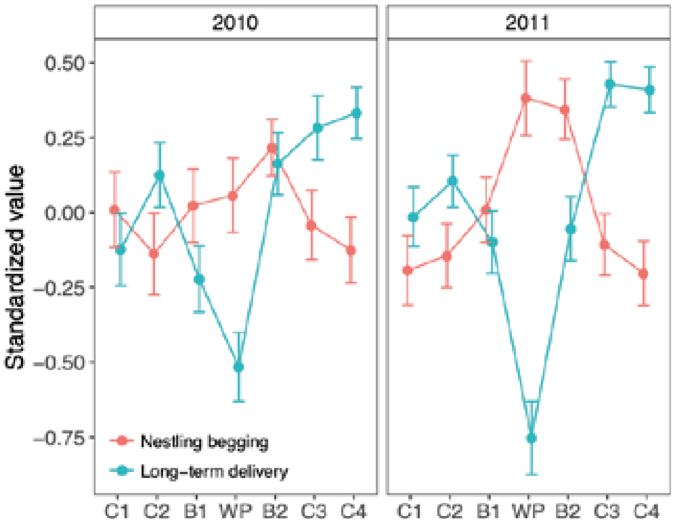


Figure 2b. Effect of experimental treatment on long-term delivery and average nestling begging for 2010 and 2011 (C = control, B = blackbird, and WP = woodpecker presentation at the nestbox). The graph depicts standardized values of both variables (to a mean of 0 and standard deviation of 1 within year) to allow direct comparison of the strength of the treatment effect across behavioral variables with different units. Dots show mean values and whiskers give standard errors.

Parents adjusted provisioning according to current levels of threat in an apparently adaptive way. They delayed nest visits during periods of elevated perceived predation threat and subsequently compensated for lost feeding opportunities by increasing provisioning once the immediate threat had diminished. Nestling begging increased after elevated levels of predation threat, but returned to baseline levels by the end of the experiment, suggesting that parents had fully compensated for lost feeding opportunities. There was no evidence for a link between male exploration behavior or aggressiveness and provisioning behavior. In contrast, fast-exploring females provisioned at higher rates, but only in the year with poor environmental conditions, which might indicate a greater willingness to invest in current reproduction in general. Future work should assess whether these personality related differences in delivery rates under harsher conditions came at a cost of reduced residual reproductive value.

Individual variation in risky behaviour, body mass and age-dependent reproduction

There has been mixed evidence for adaptive integration of life history and behaviour as pace-of-life variation. We posit that 'risky' phenotypes that live-fast-and-die-young may in fact invest heavily in early-life reproduction and consequently suffer greater reproductive senescence. Using a 7 year dataset with >1,200 breeding records of >800 female great tits (Parus major) assayed annually for exploratory behaviour, we tested whether within-individual age dependency of reproduction varied with exploratory behaviour. We controlled for biasing effects of selective (dis)appearance and within-individual behavioural plasticity. Slower and faster explorers produced moderate-sized clutches when young; faster explorers subsequently showed an increase in clutch size that diminished with age (with moderate support for declines when old), whereas slower explorers produced moderate-sized clutches throughout their lives. There was some evidence that the same pattern characterized annual fledgling success, if so, unpredictable environmental effects diluted personality-related differences in this downstream reproductive trait. Support for age-related selective appearance was apparent, but only when failing to appreciate within-individual plasticity in reproduction and behaviour. Our study identifies within-individual age-dependent reproduction, and reproductive senescence, as key components of life-history strategies that vary between individuals differing in risky behaviour. Future research should thus incorporate age-dependent reproduction in pace-of-life studies.

Natural selection often favours particular combinations of functionally related traits, resulting in adaptive phenotypic integration. Phenotypic integration has been proposed as a potential mechanism explaining the existence of repeatable among-individual differences in behavior (i.e., animal personality). In this study, we investigated patterns of covariation between morphology and behaviour in a population of free-living great tits monitored for 7 years. In particular, we aimed to disentangle the effect of structural size versus body condition on risk-taking behavior. To do so, we repeatedly quantified multiple morphological (body mass, wing, tarsus, and bill length) and behavioural traits (aggressiveness and exploration) in 742 individual males. Structural equation modelling (SEM) allowed us to test causal a priori hypothesized relationships between the different morphological and behavioural traits. Our best-fitting SEM model supported the existence of a behavioural character, "risk-taking behaviour" that covaried simultaneously with the latent variable "body size," and "body condition." Our findings thus demonstrate that an individual's morphological and behavioural traits represent expressions of an integrated phenotype, suggesting a role for phenotypic integration in generating animal personality in a wild bird population.

RECOMMENDED READING:

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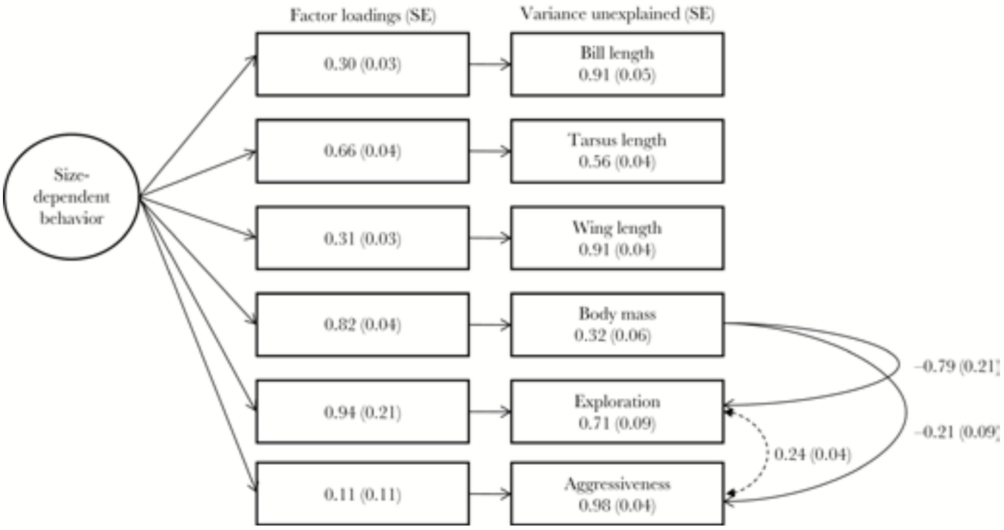

Figure 3. Parameter estimates of the structural equation model that best fitted our data (Model 10) based on male great tits (n = 742). For each trait, we report the variance unexplained by the SEM structure and factor loadings with the corresponding standard error extracted from the SEM model (SE) in parentheses. Solid lines represent causal relationships, and dashed lines are linking the behavioral traits between them (i.e., constituting "risk-taking behavior").

RESEARCH GROUP: COMMUNITY DYNAMICS

Current group members:
PI: Associate professor Vidar Grøtan
Professor Bob O'Hara
Professor Otso Ovaskainen
Professor Anders Gravbrøt Finstad
Senior researcher Ola Diserud
Postdoc Emily Grace Simmonds
Postdoc Christophe Coste
PhD candidate Emma-Liina Marjakangas
PhD candidate Sam Perrin
PhD candidate Lisa Sandal
PhD candidate Tanja Petersen
PhD candidate Bert van der Veen (NIBIO)
PhD candidate Kwaku Adjei
PhD candidate Caitlin Mandeville
PhD candidate Wouter Koch
(Norwegian Biodiversity Information Centre)
Researcher Knut Anders Hovstad

Tanja Petersen, Lisa Sandal, Anders Gravbrøt Finstad, Bob O'Hara, Emily Grace Simmonds, Vidar Grøtan, Emma-Liina Marjakangas, Sam Perrin, Christophe Coste

Aim: *To examine how community dynamics in time and space of different taxa along ecological gradients are affected by environmental stochasticity.*

MAJOR SCIENTIFIC CONTRIBUTIONS

In addition to effects of environmental stochasticity, a central question within Community Dynamics is to understand how different forms of human activity affect species diversity. Tropical forests are rightfully considered as biodiversity conservation hotspots as they host a large proportion of the global biodiversity and are under an imminent threat due to multiple anthropogenic pressures. In the tropics, habitat loss and degradation as well as overexploitation are major drivers of biodiversity loss. As species in local communities are organized into interconnected ecological networks, also the (local) extinctions caused by anthropogenic pressures are potentially cascading through the networks via species interactions. Ecological networks consist of interactive relationships, i.e. pairwise interaction links, between species within one trophic level or between species at different trophic levels. Emma-Liina Marjakangas defended her PhD-thesis entitled "Understanding species interactions in the tropics: dynamics within and between trophic levels" in October 2019. The thesis focused on linking within-trophic level assembly processes and between-trophic level interaction dynamics in a general context, evaluating assembly of species' co-occurrences within trophic levels, evaluating the effects of environmental drivers on interactions between trophic levels, and using predicted interactions between trophic levels for conservation and management prioritization.

Marjakangas et al. (2019) studied how seed dispersal interactions were affected by increasing forest fragmentation in the Atlantic forest biome in Brazil. The results showed that forest fragmentation lead to loss of interactions. Both the total seed disperser availability for the local tree communities and the proportion of interactions provided by keystone seed dispersers declined with increasing degree of fragmentation.

A main component of this work was based on using a model-based approach named Hierarchical Modelling of Species Communities (HMSC) developed by Otso Ovaskainen and coworkers. A major milestone was reached in 2019 by the implementation and publication of an R-package (Tikhonov et al. 2020). The HMSC-approach will in 2020 be presented in a separate book (Ovaskainen, O. and Abrego, N. 2020. Joint Species Distribution Modelling – With Applications in R. Cambridge University Press, in press.), and several workshops on HMSC are planned this year.

Statistical methods for species distribution modelling, and joint species distribution modelling (such as HMSC), have seen a rapid development in recent years. Such analyses have earlier been limited by lack of efficient algorithms and methods for handling the inevitably large matrices involved when modelling

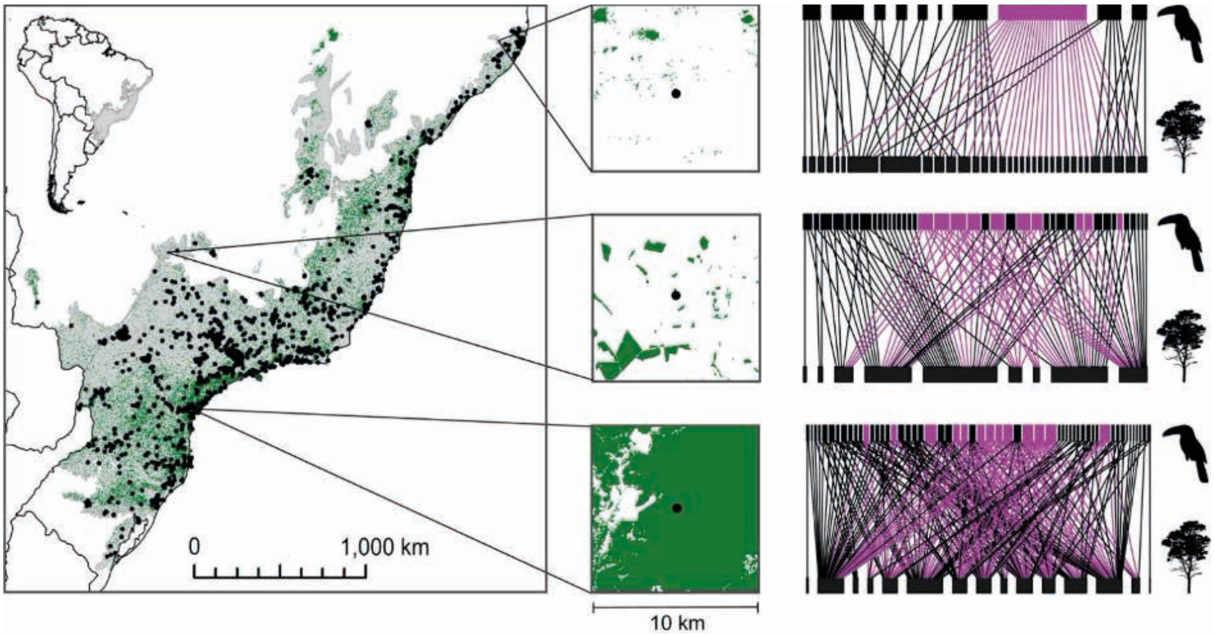

Figure 1. The study design of Marjakangas et al. (2019) and schematic illustration of the key results. In the left-most panel, the black dots represent the sampling from which occurrence data on seed dispersers and trees were acquired. The grey colour delineates the original extent of the Atlantic Forest biome, and green colour shows remaining forest fragments. The three locations highlighted in the middle panel have been selected to represent a gradient in forest fragmentation, with decreasing degree of fragmentation from top to bottom. The right-most panel shows predicted interaction networks as bipartite graphs, where the upper and lower boxes correspond, respectively, to the seed dispersers and trees, and purple color indicates keystone seed dispersers and their respective interactions.

associations among species. The research focus has now moved more in the direction of e.g. how to best combine different kinds of data of vastly different quantity and quality (e.g. data collected by scientists versus citizen science data), which methods work best for which data, and what kind of mechanisms can we reliable infer from results of such analyses. Another important question is of course related to the reliability of predictions. Although these questions are interrelated, the different questions put emphasis on different aspects and properties of models as well as data. A method may give reliable predictions without detailed modelling of ecological mechanisms, and detailed modelling of mechanisms may (at least in the short term) reduce the predictive reliability of the approach because of well-known effects of increased uncertainty of parameter estimates in more complex models. Gaining more understanding of which mechanisms need to be included in models, both for ecological understanding and predictive reliability is an active area of research at CBD and is also likely to be a key component in immediate future.

Norberg et al (*Ecological Monographs*) tested the predictive power of 33 variants of 15 widely used species distribution models. The results show that relative model performance may vary a lot. Although a group of models often do well and may be regarded as obvious starting points for such analyses, the study shows that different data sets often changed the ranking of the best-performing models. Moreover, the study was not able to explain this variation based on structural model assumptions, and relatively small differences in amount, quality and spatial structure of data lead could be highly influential for relative model performance. The authors recommend testing a suite of different models for a given data set and test relative predictive reliability by cross-validation procedures.

Araujo et al. reviewed species distribution models and their use in biodiversity assessment and proposed a set of best-practise standards and guidelines for their use in biodiversity assessments. Evaluation of 400 studies during the past 20 years suggested low model adequacy, but there was however a marked tendency of improvement of time in model building. This study strongly recommends including different types of data to broaden the coverage of such biodiversity assessments. With the expansion in the quantity and types of biodiversity data being collected, there is a need to find ways to combine these different sources to improve estimates of to provide species' realized and potential distributions in space and time. Model-based data integration may achieve this by combining datasets in ways that retain the strengths of each. Integrated population models

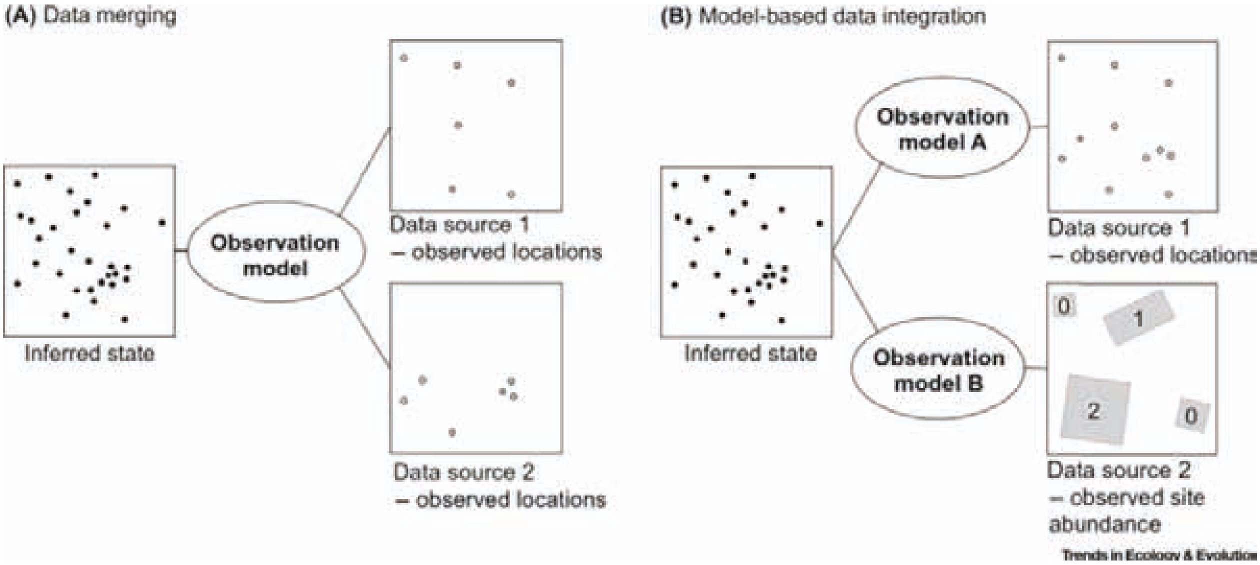

Figure 2. Data pooling (A) brings together observations from different sources that could be modeled with a single observation model, ignoring their disparities or reducing the data to a common denominator. In contrast, data integration (B) uses distinct observation sub models for each data source.

(IPM) in population ecology have become very popular during the past 15 years because of the benefits of using multiple data sources representing different aspects of an ecological process. Sharing parameters across submodels has allowed demographic parameters to be estimated more precisely than through independent models.

Application of similar models in species distribution modelling has been less common. Isaac et al. (2019) described an approach to data integration for species distribution models using point process models and showed that framework may be used to translate across spatial ecological data obtained by different forms of observations.

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RESEARCH GROUP: DYNAMICS OF ARCTIC ECOSYSTEMS

Current group members:
PI: Researcher Brage Bremset Hansen
Senior researcher Vebjørn Veiberg (NINA)
PhD candidate/Postdoc Mathilde Le Moullec
PhD candidate Bart Peeters
PhD candidate Kate Layton-Matthews

Aim: *To understand how climate change and harvesting influence spatiotemporal population and community dynamics, through a combination of direct and indirect effects (i.e. trophic interactions).*

Photo: Per-Harald Olsen

Bart Peetes, Mathilde Le Moullec, Brage Bremset Hansen, Kate L. Matthews
Right: Vebjørn Veiberg

MAJOR SCIENTIFIC CONTRIBUTIONS

2019 was a year characterized by high publication activity, two successful PhD dissertations (Mathilde Le Moullec and Bart Peeters), and four MSc theses (on snow bunting, barnacle geese, and field vegetation experiments). In Le Moullec et al. (2019, *Journal of Wildlife Management*) and Peeters et al. (online 2019, *Global Change Biology*), we demonstrated important consequences of past overharvesting, reintroduction programs, and recent sea-ice loss for the current distribution, abundance, and population genetics of Svalbard reindeer (figure 1). Interestingly, the effects of these two anthropogenic drivers (harvest and climate change) appear to interact. Because of the rapid warming and strong ecological signals of climate change in this study system, this potentially has large implications for management.

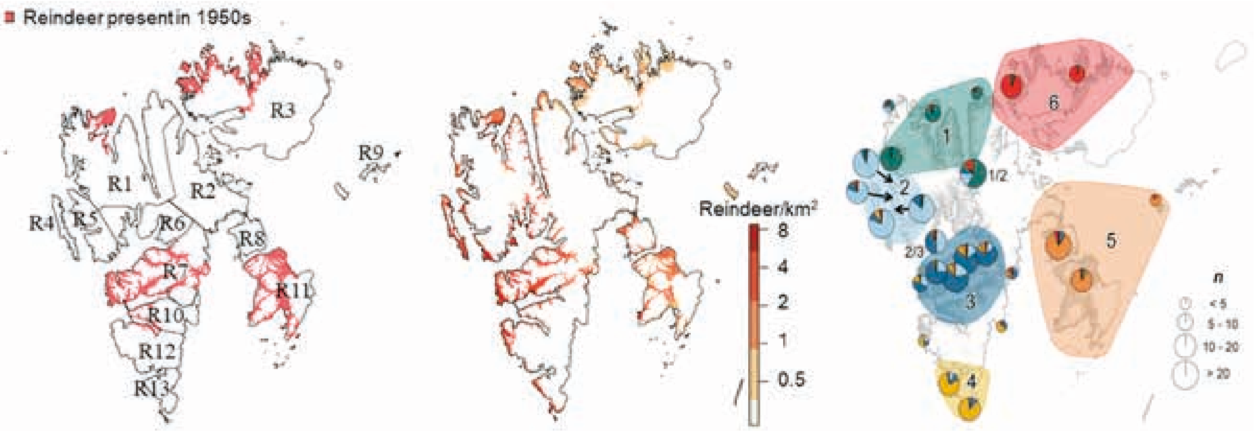

Figure 1. Distribution of Svalbard reindeer three decades after they were protected from harvest (left map) versus today (middle map), and their current spatial population-genetic structure (right map) obtained from cluster analysis of microsatellite data (n = 411 individuals). This strong genetic differentiation in space is largely explained by the past extirpations due to overharvest, reintroduction programs, and recent lack of sea-ice, an important dispersal corridor. From Le Moullec et al. (2019, *Journal of Wildlife Management*) and Peeters et al. (2019, *Global Change Biology*).

Research Area 3 COMMUNITY DYNAMICS

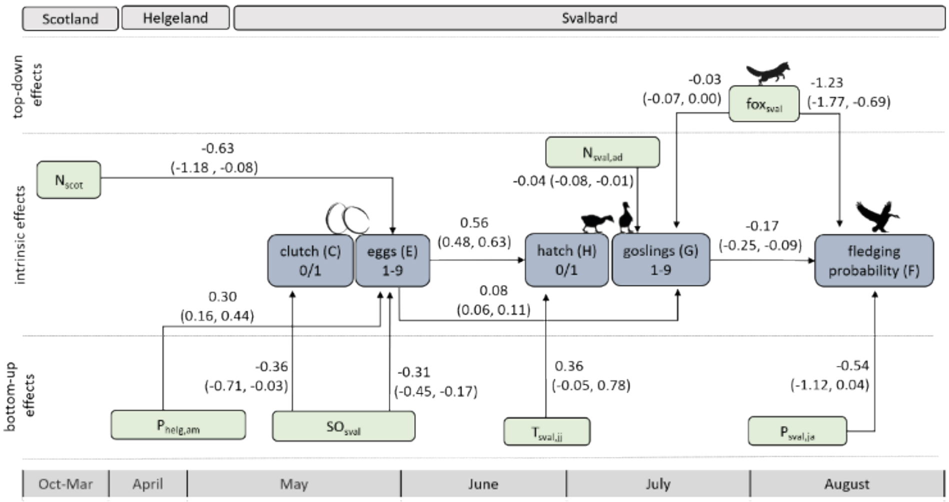

Figure 2. Best fitting path model diagram for top-down effects, intrinsic (density-dependent) effects, and bottom-up effects on Svalbard barnacle goose reproduction, with standardised slope coefficients and associated 95% confidence intervals (from Layton-Matthews et al. 2019, *Global Change Biology*).


Photo: Brage B. Hansen

Figure 3. From the 2019 reindeer capture-mark-recapture (Ny-Ålesund, Svalbard), a collaboration project with the Norwegian Polar Institute.

In papers by Hansen et al. published in Global Change Biology and Nature Communications, we provided novel empirical insights into the importance of spatial heterogeneity and intrinsic regulation (reindeer density dependence and age structure effects, and their interactions with weather effects) for the long-term and large-scale outcome of changes in climate and extreme weather events. Density dependence also appears to play an important role in the population dynamics of migratory species, such as our barnacle goose study population in Ny-Ålesund (Layton-Matthews et al. 2019, *Journal of Animal Ecology*). Importantly, the long-term dynamics of barnacle geese may also be indirectly linked to fluctuations in reindeer abundance, due to the strong impact of gosling predation by the Arctic fox (figure 2; Layton-Matthews et al. 2019, *Global Change Biology*), whose dynamics are shaped by reindeer carcass availability. In project INSYNC we are now investigating whether these strong trophic links may lead to cascading climate effects across the tundra community, and how this may impact community dynamics under different scenarios of climate change and harvest. To achieve such understanding, we will rely on continued collection of longitudinal individual-based data (figure 3) combined with state-of-the-art demographic modelling, across species and trophic levels.

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RESEARCH GROUP: DYNAMICS OF INTERACTING SPECIES

Current group members:
PI: Associate Professor Aline Magdalena Lee
Postdoc Marie Vestergaard Henriksen (NIBIO)
PhD candidate Jonatan Fredricson Marquez

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

Jonatan Fredricson Marquez, Aline Magdalena Lee
Right: Marie Vestergaard Henriksen

We work in the gap between classical single-species population ecology and community ecology, studying the dynamics of interacting species in fluctuating environments. We are interested in how interacting species covary in space and time, and how their dynamics are driven by combinations of factors, such as life history, spatial movement, characteristics of their interactions, and different types of environmental stochasticity. Our work involves a combination of theoretical modeling and empirical data analysis.

MAJOR SCIENTIFIC CONTRIBUTIONS

SPATIAL DYNAMICS OF INTERACTING SPECIES IN FLUCTUATING ENVIRONMENTS

Environmental fluctuations and spatial processes can both have strong impacts on the dynamics and distribution of natural populations. Understanding how stochastic fluctuations in the environment influence populations in a spatial setting is therefore essential for successful management and sustainable harvesting. For example, the spatial scaling of environmental fluctuations influences the synchrony of population fluctuations, thus affecting population extinction risk. One important factor that is often overlooked in this context is that species do not live in isolation. We lack knowledge of how species interactions and characteristics of each of the competing species together influence responses to environmental fluctuations.

In Lee et al. (2020a) we developed a new analytical model for understanding patterns of covariation in space between interacting species. We showed that the correlation between two species in how they experience the same environmental conditions determines how correlated fluctuations in their densities would be in the absence of competition. In other words, without competition, synchrony between the species is driven by the environment. Competition between the two species causes their abundances to become less positively or more negatively correlated, but this effect is influenced by several other population parameters. For example, we found that dispersal or other movement weakens the effect of competition on the interspecific correlation, and also increases the distance over which the species are (positively or negatively) correlated. We also found a close connection between the spatial scaling of population synchrony within a species and between species. Our results show that the relationships between the different factors influencing interspecific correlations in abundance are not simple linear ones, but our model enables us to disentangle them and predict how they will affect population fluctuations in different situations (Figure 1).

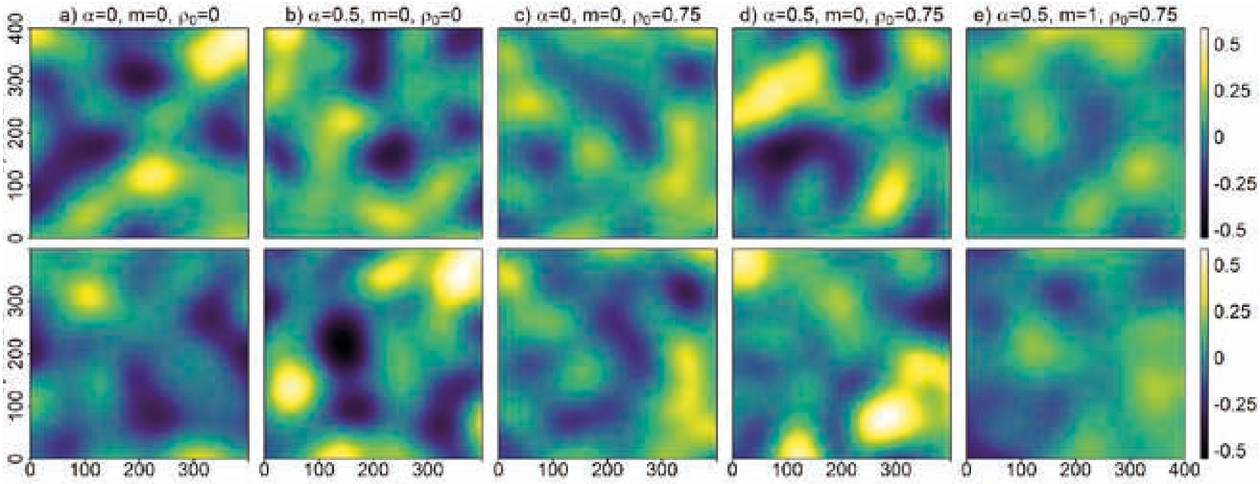

Figure 1. Simulations of the spatial population dynamics of two species with ($\alpha=0.5$) and without ($\alpha=0$) competition, dispersal ($m=1$) and positive correlation in how the two species experience the same environmental conditions ($\rho_0=0.75$).

SPATIAL DYNAMICS OF MARINE FISH IN THE BARENTS SEA

This project focuses on understanding the spatial dynamics of fish species within the Barents sea community. The spatial synchrony of population dynamics has important implications for ecological processes such as the spread of diseases and extinction probability. Understanding how this synchrony relates to life histories is therefore essential for both ecological theory and species management. In Marquez et al. (2019) we explored how generation time, growth rate and mortality rate predicted the spatial scaling of abundance and yearly changes in abundance of eight marine fish species in the Barents Sea (Figure 2). Our results showed that the population dynamics of fish species with 'slow' life histories were synchronized over greater distances than those of species with 'fast' life histories, linking the distribution of abundance of each species to specific life history characteristics. General patterns of this type can help in the development of broad conservation and harvesting strategies that consider multiple interacting species.

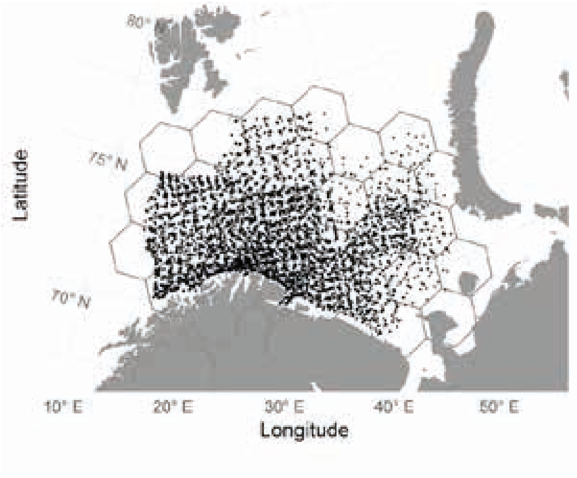

Figure 2. Spatial distribution of data from the Barents Sea used to study spatial population synchrony of eight species of fish.

RECOMMENDED READING:

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NEW AT NTNU

Stefanie Muff, September 2019

Being new at CBD, and how I got here

I had the honour to join CBD in September 2019, when I started my new position as an associate professor in statistics at the Institute for Mathematical Sciences. Becoming a member of the CBD felt like arriving at the right destination in my professional life. I finally have the possibility to use my quantitative skills to help addressing problems that I am really interested in, and I can do this embedded in an excellent group of world-class researchers.

My path so far was definitely not a very linear one, and looking back I see a couple of short-cuts that I could potentially have taken. However, all the detours helped me fill my backpack with insight that I now find valuable. For example, after having studied pure mathematics, I know that it is a privilege to collaborate and interact with applied scientists, and after a phase without doing research, I see crystal clear that it is the thing I am most passionate about. Being an ecological statistician (or am I a statistical ecologist?) perfectly

Jane Reid, October 2019

Time for a change and new challenges

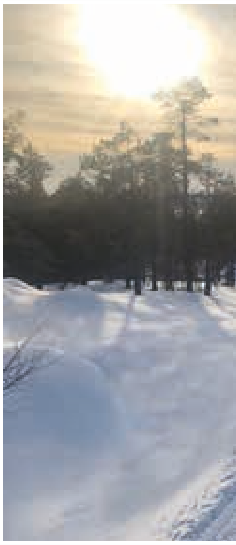
October 2019, and it was time for my big move to CBD. I had been at the University of Aberdeen for over a decade and it was time for a change, with some new challenges and opportunities to look forward to.

Until then, if someone had asked 'What is your most-visited European city', my answer would have been Trondheim. I doubt this would be a typical answer! But, for me, it reflects the existence of many common research interests with CBD, and so I had previously visited for conferences and research meetings, and twice as a PhD opponent. So, when the chance to move to CBD came, it was an easy decision to say yes.

Easy decisions still come with costs though, and it was tough to leave my lovely group in Aberdeen, and to move further from my field sites. It is an extra challenge to move as an ecologist; long-term field study sites cannot be moved, and cannot be easily reproduced elsewhere. So now, some longer-distance fieldwork and interactions are required!

But, the benefit of moving to CBD was evident as soon as I arrived. For the first few months, it has been wonderful to work in such a friendly and stimulating environment. I was immediately immersed into some challenging discussions about science, and about the next steps for CBD. Well, I did say I wanted some new challenges!

It has been fun to discover more about what everyone at CBD is doing – some things that I knew about already, and many more that I didn't. I will look forward to these discussions developing over coming months and years, and to some new exciting projects that we can build together!



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and uniquely unifies my interests in mathematics and the sciences and makes my work meaningful to me.

Taken together, CBD is an excellent place to work and blossom for someone like me. From a sabbatical in 2017 I also knew that not just the scientific, but also the social environment is exceptional. It was accordingly easy to settle here, not least because Trondheim is such a pleasant place to live. Starting in fall 2019 therefore felt more like «coming back» than «being new», and I was warmly welcomed and integrated from day one. I am very grateful for being here and look forward to many inspiring years.

Lisa Dickel, October 2019

From fishing spiders to fluffy sparrows

I came to CBD having just left Norway after my MSc in Applied ecology at the Inland Norway University of Applied sciences and returning to Germany. So, I got into the car to drive up from southern Germany all the way to Trondheim, changing from late summer to something more winter-ish on the way. While moving towards the north, it certainly got warmer (blooded) for me taxonomically, as I changed over from fishing spiders and trees to fluffy sparrows.

How was it to come to Trondheim?

After living in the countryside of Norway for the last few years, Trondheim has been a metropolis for me, and I have greatly enjoyed walking through the dark streets full of lights and snow (and ice and rain), stopping here and there in the small coffee shops along the way, following the river, as well as spending long evenings in my office and chatting with people at the coffee machine, to get to know them as well as to learn the basic vocabulary of the place, as the world of genetics had been hidden from me so far!

How was it to come to CBD?

Not really knowing what I was going to, I found a great variety of people working on sparrows, having heated debates about egg-laying-dates and being otherwise occupied with many other birds (and to be fair: also some other things). After traveling through a variety of taxa, I am fascinated by the variety of interests being found in this one; and it is great that I also finally get to explore the bird world for the next few years!

I am happy that CBD and I chose each other to turn myself into an ornithologist (there might still be some hope for me) as well as a genetically informed ecologist. I will focus on understanding the impacts of immigrants into small, inbred populations, with the example of the Mandarte Song sparrows, being supervised by Jane Reid and Henrik Jensen (CBD), Lukas Keller (University of Zurich), Pirmin Nietlisbach and Peter Arcese (University of British Columbia).

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WORKSHOPS AND CONFERENCES 2019

MEETING AT THE CENTER OF ADVANCED STUDY OSLO

“EVOLVABILITY: A UNIFYING CONCEPT IN EVOLUTIONARY BIOLOGY“

Organized by C. Pélabon (NTNU, CBD) and T.F. Hansen (UiO).

The project at CAS aims at unifying the theory of evolutionary potential, i.e. evolvability, and promoting this concept as one of the major concepts in the evolutionary theory. To reach this aim, the group is reviewing the historical basis and philosophical underpinnings of the various perspectives on evolvability and synthesizing what we have learned during the past 25 years about evolvability and its consequences in broad research areas. The research group is organized around four research areas: evolutionary quantitative genetics, evolution and development (evo-devo) and systems biology, macroevolution and a theory-of-science group who investigates the historical development of the concept and facilitates the communication between the other research fields. Major actors in the development of the evolvability concept (G.P. Wagner, J. Cheverud, M. Pigliucci, A. Wagner, R Dawkins) have visited CAS during this meeting.

WORKSHOP

PREDICTION OF CLIMATE CHANGE EFFECTS ON THE DYNAMICS OF SPECIES WITH COMPLEX LIFE HISTORIES

Classical population models are typically based on the assumption that demographic traits can be described as a function of some specific variables such as age or body mass. This ignores that there may be consistent differences among individuals across years in their fitness contributions, for instance dependent on some unmeasured traits.
Such individual heterogeneity in demography causes a huge challenge when predicting population responses to changes in the environment (e.g. caused by climate change) because it potentially introduces time lags in the population dynamics. This makes it difficult to distinguish the dynamical consequences of environmental variation from those caused by individual heterogeneity in demography. Dr. Stephanie Jenouvrier, Woods Hole Institute, USA and professor Bernt-Erik Sæther at CBD therefore decided to organize a workshop on the topic *“Prediction of climate change effects on the dynamics of species with complex life histories”.*

The objectives of the workshop were:

1. Assemble a combination of theoreticians and researchers having access to long-term data to construct families of population models to assess the dynamical consequences of individual heterogeneity in demography. A requirement already identified in the outset is that the models should be possible to be parameterized by real data.
2. Develop a statistical approach that can be used to estimate the same set of parameters from a wide suite of species
3. Explore the dynamical consequences of individual heterogeneity in demography across species along the slow-fast continuum of life history variation.
4. Use these models to identify life history characteristics of those species in which individual heterogeneity in demography most strongly affects the projections of future responses to climate change

18 scientists accepted the invitation to participate at the workshop, which was held in Trondheim December 3-5 2019. The participants included a nice mixture of theoreticians and empiricists with access to some of the most extensive datasets of individual-based demography that exist for any species.

Some of the participant at the individual heterogeneity workshop in Trondheim in December 2019.

Substantial progress was made during the workshop, and in many respects the advances on this difficult topic were even larger than the organizers on had anticipated beforehand. This included:

1. A general statistical model was developed that potentially could be parameterized for a wide array of species using a Bayesian Integrated Population Model-approach.
2. Two different kinds of individual heterogeneity in demography were identified. *Fixed heterogeneity* arises from consistent differences among individuals across years due to variation arising at a single point of time (usually during the first year of life). *Dynamic heterogeneity* is caused by temporal variation in individual quality, e.g. generating long-lasting variation among cohorts in their contribution to the long-run population growth rate.
3. An important realization occurred at the workshop. Including individual heterogeneity in demography seems to represent greater challenges than previously realized and may pose particular problems in assessing the effects of stochastic fluctuations in environmental conditions. A central conclusion was therefore that these effects must be examined theoretically in order to explore the consequences for making projections about the effects of climate changes on the dynamics of species with complex life histories.
4. Several studies based on traditional stochastic population models have revealed a large effect of expected changes in climate on the viability especially of species with complex life histories. Thus, the effects of individual heterogeneity in demography must be included in models to examine the robustness and generality of these large dynamical effects of climate change.

The workshop in Trondheim was planned as the first of two. The organizers were also awarded grants for a follow-up Lorentz-workshop in Leiden, The Netherlands, on February 3-7 2020. The aim of this second workshop was to introduce the results and approaches from Trondheim to a wider audience and get access to a wider range of data.

Science and conservation of biodiversity and socio-cultural values. An NTNU-IPBES seminar

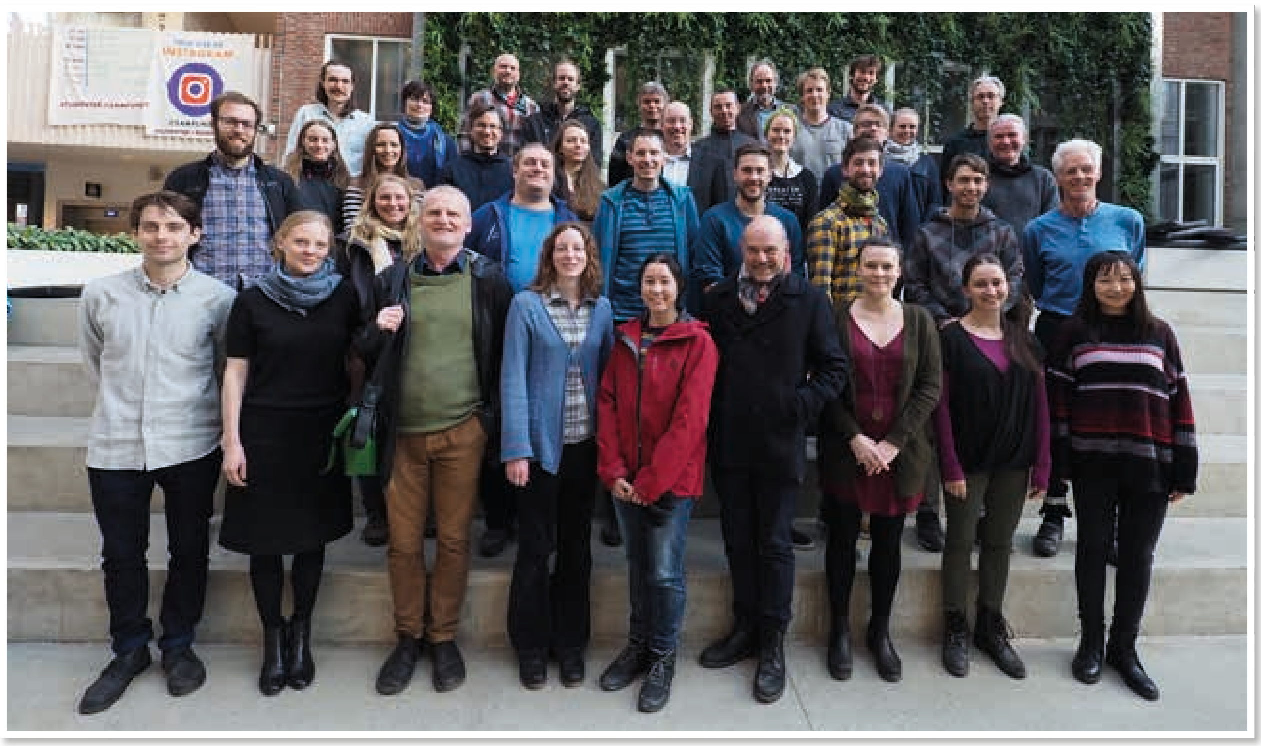
On February 27. 2019 CBD organised, with generous support from the strategic programme "NTNU Sustainability", a seminar to draw the attention to science-policy interactions in light of IPBES' 2019 Global Assessment Report on Biodiversity and Ecosystem Services. The main aim was to link scientific and societal needs communicated from e.g. IPBES and the Norwegian Environmental Agency, and an overarching question during the seminar was " How can scientists contribute to give policy makers the tools, models and knowledge they need to make wise decisions on how to best conserve nature and nature-cultural values?"

The seminar included two keynote speakers as well as presentations by scientists and other people involved in the IPBES Capacity Building unit that gave valuable insight into the scientific and societal processes behind their assessment reports. Researchers from NTNU presented different approaches of the current state of methodology and need for further development, also regarding data availability and sharing. These ranged from basic ecology, to applied and interdisciplinary fields with strong ties to societal developments.

With ecological models such a large part of forecasting fluctuations in biodiversity, keynote speaker Professor Carsten Rahbek (Centre for Macroecology, Evolution and Climate, University of Copenhagen) spoke about the need for more consistency in modelling, given that even the most tried and tested models can give very different forecasts of species distributions when compared. He highlighted the example of the red-backed shrike, which ecological models suggested would be flourishing by 1990, and ended up facing significant habitat loss and range restriction. Professor Rahbek also called for more emphasis on the negative impacts of land use on biodiversity and ecosystem services, reminding the audience that whilst climate change is a growing threat, the majority of species losses that are happening today are a product of human habitat destruction and fragmentation.

Professor William Sutherland (Department of Zoology, University of Cambridge) was the day's second keynote speaker, and spoke in favour of more precision and less broad statements in such assessment reports, calling into question some of the recent claims that had been made of species declines in areas where scientific evidence was vague and largely unsupported. He instead called for more focus on areas where scientific knowledge is more readily available. Professor Sutherland also questioned reliance on supposed 'expert knowledge', citing Phillip E. Tetlock's work Expert Political Judgement as a warning sign of placing faith in a small number of individuals rather than relying on scientific consensus.

The importance of maintaining scientific rigour in the process of making ecosystem assessments was emphasized by several speakers during the seminar. These aspects are particularly important and challenging when communicating scientific results or assessments to a broader audience. In such situations, scientists may be faced with a dilemma of either downplaying the uncertainty or exaggerate their results in order to grab the public's attention.



Participants at the NTNU-IPBES seminar on Science and conservation of biodiversity and socio-cultural values.

FAIR DATA MANAGEMENT AND OPEN SCIENCE IN ECOLOGY, WILDLIFE MANAGEMENT AND CONSERVATION

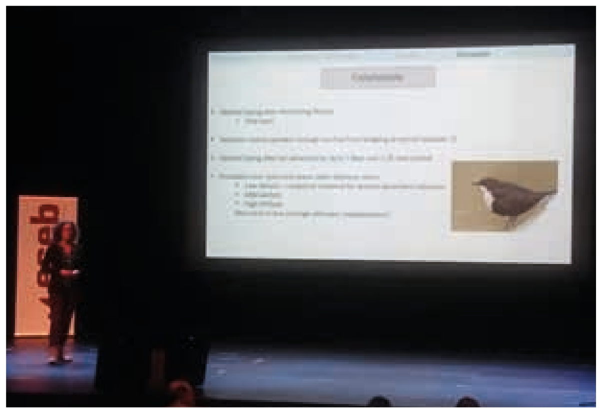
A workshop focussing on open biodiversity data was organised in June 11.-12. 2019 at Norwegian Institute of Nature Research (NINA) Trondheim. The workshop was formally organised by the Living Norway Ecological Data Network, with support from NTNU Sustainability and CBD as a co-organiser. The FAIR data principles are that biodiversity data should be Findable, Accessible, Interoperable and Reusable.

The seminar included ca. 70 participants over the two days, and speakers represented and key actors in Norwegian society on biodiversity data such as the Norwegian Environments Agency, Norwegian Biodiversity Information Centre, NTNU and CBD, NINA, Norwegian University of Life Sciences (NMBU), and University of Bergen. Additionally, international participants from the Global Biodiversity Information Facility (GBIF) and the Nordic e-Infrastructure Collaboration (NeIC) presented their work and view on the FAIR issue. The seminar had two main focuses: 1) how should biodiversity data be managed in order to increase FAIRness, and 2) how to increase the implementation of FAIR among community members.

As well as sharing knowledge on how data management can be done hands-on, participants on the workshop raised awareness on potential collaborators and provided input on further development of existing solutions. Moreover, the awareness of promoting FAIR principles as means of increasing transparency was stressed, because this is fundamental for understanding and trust between policy makers and scientists.

The other main topic of the workshop was education as a tool for increasing the awareness and implementation of FAIR data. This section was to a large extent oriented towards the university representatives. During these sessions it was stressed that the principles of FAIR data management should be taught from early in the university curriculum. This would also ensure that data and knowledge from student project for instance from Bachelor's or Master's thesis will be available for future research and knowledge-based management and conservation.

The 2019 Congress of the European Society for Evolutionary Biology (ESEB2019)

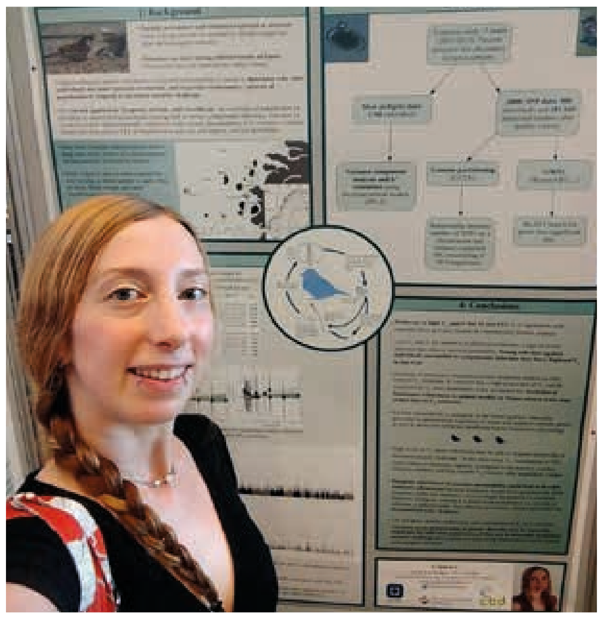


Researchers from CBD were well represented at ESEB2019 in Turku, Finland, where more than 1300 people met to present and discuss a wide range of topics in evolutionary biology. Three symposia at the congress were organized by CBD-members. In addition, CBD-members gave plenary and invited talks, and presented their research on posters.

The symposium *"Genetics of small populations"* was aimed at providing a review of the state-of-the-art regarding genetic processes in small populations to understand the extent of current genetic problems in natural populations, considering the relative importance of genetic and demographic processes for population viability. To reach this goal, the symposium brought together researchers in different fields to discuss the latest experimental, observational, and theoretical work on causes and consequences of changes in genetic variation in small populations. The symposium was organized by CBD-members Henrik Jensen and Alina Niskanen in addition to Lumi Viljakainen.

The goal of the symposium *"Quantitative trait effect size distributions and their impact on evolutionary processes"* was to review experimental, empirical and methodological studies that focus on how genetic architecture might impede or facilitate evolutionary processes. Quantitative traits have historically been modelled assuming a large number of genes of small effect. However, there are examples of moderate to large effect loci segregating in populations which suggest that there is likely to be a diversity of species- and trait-specific effect size distributions. The work presented at the symposium synthesized how the genetic architecture of traits, and the genetic constraints between traits, impact evolutionary processes including, for example, the rate of adaptation, maintenance of genetic variation and the predictability of evolution. The symposium was organized by CBD-member Arild Husby in addition to Anna Santure.

Ageing is a key challenge of this century, and in the symposium *"Evolutionary ecology of ageing: from mechanisms to life-history consequences"* the purpose was to increase our comprehension of the mechanisms of ageing and their evolutionary basis. This was done by giving an overview of the existing research in the field, focusing on both the molecular and physiological determinants of ageing. A result of the symposium was that we have a better understanding of the causes of the wide variation which is observed in ageing rates between and within species. The symposium was organized by Hannah Froy in addition to Sophie Reichert and Antoine Stier.



NATIONAL AND INTERNATIONAL COLLABORATION

Extensive international collaboration is a key element in the research strategy of CBD. One of the best indications of this is the steady flow of visitor from abroad. In 2019, three of these gave a CBD-lecture, intended for a wider audience from the research institutions in environmental science located in Trondheim. Several of the visitors also gave presentations at the weekly lunch seminars of CBD. An important asset is also the annual meeting of the Scientific Advisory Committee (SAC), which provides an important perspective from outside on the scientific activities at CBD. In 2019 SAC especially focused on providing input on PhD- and post doc-projects based on more than two days of presentations. The comments were greatly appreciated and had a wide impact on the research activities at the centre.

One of the best illustrations of the huge network of international collaborators with CBD is the large number of co-authors from abroad on papers published by researchers at the centre. In 2019 CBD-researchers co-authored papers with scientists affiliated with institutions in 24 countries.

A large problem in many fields of biology is the lack of rapid and easy access to relevant data, which has restricted the possibilities for comparative analyses facilitating identification of general principles. To overcome these issues, the Netherlands Institute of Ecology (NIOO) together with CBD has created the SPI-Birds Network and Database, which is a new community-driven initiative that is successfully connecting researchers working on Studies of Populations of Individual birds. A central aim of SPI-Birds is to creates tailored pipelines to convert each unique data set into a standard format, and to provide a platform to find and access these datasets. Thus, SPI-Birds can be an example of a working model for data standardisation, exchange, and integration, facilitating international collaboration among researchers.

POPULAR SCIENCE

The outreach and popular dissemination of the results from CBD occurs mainly through two channels. First, CBD is one of the core research groups in the focus area "Biological diversity and ecosystem services" within NTNU Sustainability. This is one of four strategic research areas at NTNU, and is aimed at securing strategic interdisciplinary collaboration on different themes within the field of environmental sustainability. On behalf of NTNU Sustainability, CBD organized the workshop Science and conservation of biodiversity and socio-cultural values. An NTNU-IPBES seminar. This was aimed at researchers, students and environmental managers. A central message from this workshop was that the huge public attention received by the IPBES assessment report required rapid development of methods and procedures to assess and predict trends in biological diversity.

A second channel for interactions between CBD and end-users was the involvement by CBD-researchers at NINA with the public as well as environmental managers both at local, regional and national levels. In particular, the close involvement by senior researcher Erling J. Solberg with moose mangers has generated a flow of information and results from the moose project on the island of Vega, both at the local, regional and national level, which in turn should provide potential for having practical implications for moose management in Norway.

The project "Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems" (SUSTAIN) was a large integrated project funded by the Research Council of Norway (RCN). This project was by the Centre for Ecological and Evolutionary Synthesis (CEES) at the University of Oslo together with CBD and UiT The Arctic University of Norway as the two other principal nodes. On June 5, RCN organized a seminar with the researchers involved in the project and potential end-users of the project. Many researchers at CBD gave lectures and presentations at the seminar and were heavily involved in the general discussions. The major focus from CBD was the importance of securing accessibility and continuity of long-term time series describing temporal variation in ecological conditions and the necessity of considering interactions between different human activities (e.g. habitat loss and harvesting) to fully understand the consequences of the expected changes in climate on ecosystem structures and processes.


Reddet fra utryddelse

The research by CBD in the Arctic has also in 2019 continued to catch interest in media. Several studies by the Dynamics of Arctic Ecosystems group were covered by Gemini (Norwegian SciTech News), forskning.no, and numerous national and international news agencies. This included papers on barnacle goose population dynamics under climate change and Svalbard reindeer dietary and population-dynamic responses to extreme weather events. A study describing how reindeer numbers rebounded from harvest-induced extirpations got particularly widespread media attention, nationally as well as internationally, including a one-pager in the only Norwegian newspaper for kids, Aftenposten Junior (Fig).

List of CBD lectures 2019

- February 26th: Prof. Carsten Rahbek, University of Copenhagen, Centre for Macroecology, Evolution and Climate, "The role of mountains in understanding geographical patterns of biodiversity – and the need for process-based models"
- June 11th: Dr. Lynn Govaert, Department of Aquatic Ecology, Eawag, Switzerland: "Eco-evolutionary signatures in space/ communities"
- October 22nd: Dr. Mathew E. Wolak, Department of Biological Sciences, Auburn University, USA: "Quantitative Genetic Evolutionary Ecology: Fitness, immigration, inbreeding, and divorce in song sparrows".

Dissertations

Seven PhD candidates defended their thesis at CBD in 2019:

January 18th	**Peter Sjolte Ranke** *"Demographic and genetic and consequences of dispersal in house sparrows"*
Opponents	Professor Tomas Pärt, University of Agricultural Sciences, Sweden Professor Erik Matthysen, University of Antwerp, Belgium
January 25th	**Mathilde Le Moullec** *"Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony"*
Opponents	Professor Steeve Côté, Université Laval, Canada Professor Mads Forchhammer, UNIS, Norway
January 29th	**Endre Grüner Ofstad** *"Causes and consequences of variation in resource use and social structure in ungulates"*
Opponents	Professor Mark S. Boyce, University of Alberta, Canada Professor Carl Göran Ericsson, Swedish Agricultural University, Sweden
February 15th	**Elena Albertsen** *"Evolution of floral traits: from ecological contex to functional integration"*
Opponents	Professor Laura Galloway, Department of Biology, University of Virginia, USA Dr. Mario Vallejo Marin, Biological and Environmental Sciences, University of Sterling, UK
May 29th	**Thomas Ray Haaland** *"Adaptive responses to environmental stochasticity on different evolutionary time-scales"*
Opponents	Associate Professor Sasha R. X. Dall, University of Exeter, UK Dr. Florence Débarre, Collège de France, France
October 25th	**Bart Peeters** *"Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer"*
Opponents	Professor Marco Festa-Bianchet, Université de Sherbrooke, Canada Dr. Jean-Pierre Tremblay, Université Laval, Canada
November 22nd	**Emma-Liina Marjakangas** *"Understanding species interactions in the tropics: dynamics within and between trophic levels"*
Opponents	Professor Anne Magurran, University of St. Andrews, UK Assistant Professor Naia Morueta-Holme, University of Copenhagen, Denmark

KEY FIGURES 2018

GENDER EQUALITY

The transition from postdoc period to faculty position has proven to be a critical point at which many women end up leaving academia. In an attempt to increase the number of women from CBD with permanent faculty positions in ecology or evolution, CBD has therefore chosen to offer positions as researchers, following the postdoc period. Furthermore, we actively seek to recruit more female senior scientists. We are extremely happy to welcome International Chair professor Jane Reid and Associate professor Stefanie Muff as new members of CBD.

The Department of Biology has an Equal Opportunities Committee with one member from CBD. In 2019 this committee organized a workshop on gender bias aimed at section leaders at the department. Representatives from CBD attended this workshop to learn more about how to work towards gender equity. The situation at CBD is improving, but we acknowledge that we still have work to do in this area.

KEY FIGURES

Key numbers in CBD	2019	
	F	M
Professors/Associate professors	6	17
Researchers	4	17
Postdocs	7	4
PhD candidates	19	18
Technial staff	1	2
Administration	2	
All staff at CBD	39	59
Total	98	
Scientific Advisory Bord	1	5

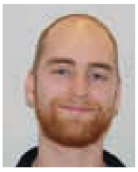
Costs and funding	in thousand
Costs:	
Salary and indir. costs	18 907
Other operating cost	3 829
Sum cost	22 736
Funding:	
NFR	11 608
NTNU	11 128
Sum funding	22 736

Funding associated projects	14 330

PHD CANDIDATES


Anne Catriona Mehlhoop
PhD candidate NINA


Astrid Raunsgard
PhD candidate NINA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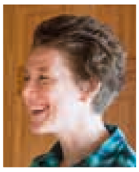
PhD candidate NIBIO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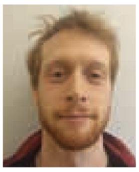
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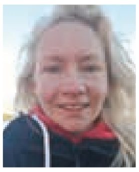
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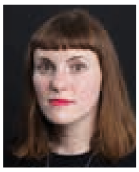
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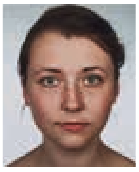
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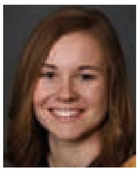
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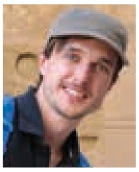
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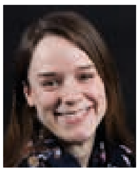
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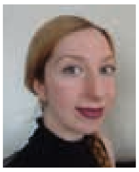
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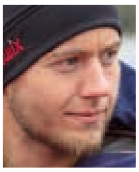
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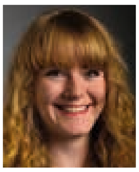
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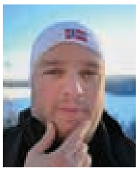
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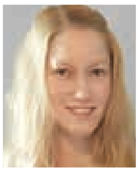
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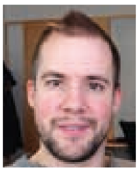
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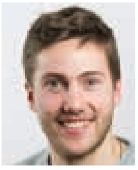

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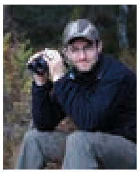

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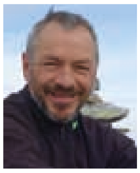

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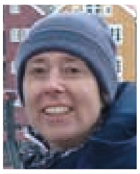

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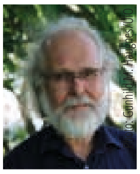

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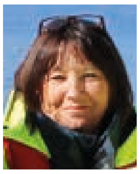

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PUBLICATION LIST

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