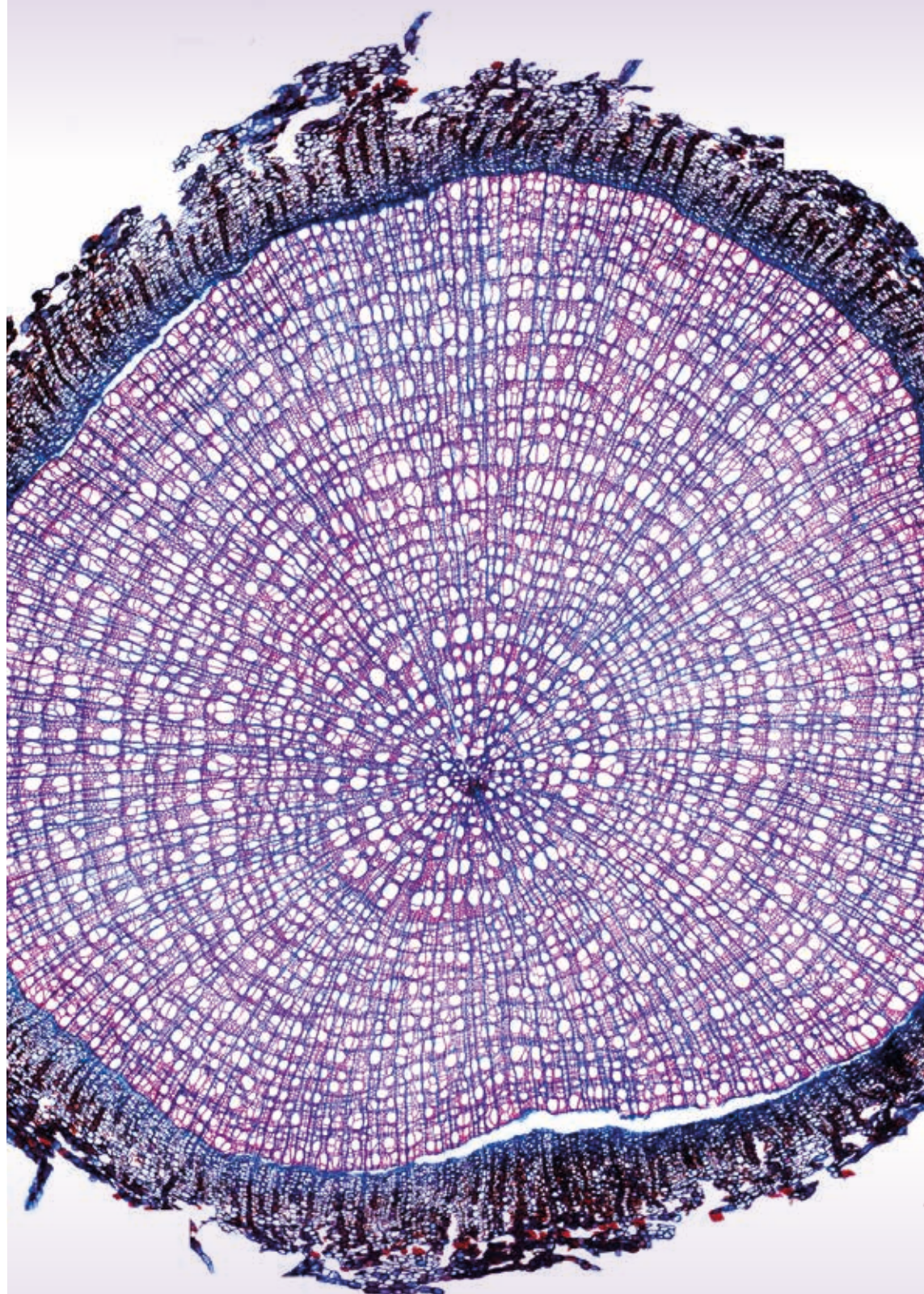


Annual Report 2018



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:

This cross-sectional view of the dwarf shrub *Salix polaris* won the British Ecological Society photographic competition in 2018, in the category The Art of Ecology, with the picture's title "*Can you feel the harsh climate of the high Arctic?*".

Shrub ring growth is highly irregular under the influence of the high-arctic climate. The story started onboard a sailing boat at the northern distribution margin of any shrub, in Svalbard, Norway. Long months in the laboratory followed for Mathilde Le Moullec and Lisa Sandal, cutting, staining and digitalizing our 2 mm wide cross-sections (100 x magnification). Art became science, and developed as time-series, retrospectively tracking vascular plants' biomass (Le Moullec et al. 2019, JEcol).

COMMENTS FROM THE DIRECTOR:



Bernt-Erik Sæther
Director CBD

A central focus for the work of the leadership of CBD in 2018 was to follow up the recommendations from the midterm evaluation that were published in October 2017. Although CBD received the highest ranking (Exceptional), the Evaluation Panel still provided some useful suggestions for changes and improvements. The research at CBD has been structured in three Research Areas (RA): population ecology, evolutionary biology and community dynamics. The Evaluation Panel suggested that the greatest potential for CBD to produce high-impact results was to address research questions located at the intersection among the RAs. CBD is in a unique position to do this because the major theoretical foundation for CBD is applicable in all the three RAs. The leadership of CBD therefore agrees with the recommendation from the evaluation panel and has in 2018 continued to strongly emphasize and facilitate collaboration among researchers across the RAs.

It is therefore with great pleasure I note that several of the publications in 2018 reveal strong ongoing interactions between researchers at different RAs. For instance, an important research question at CBD has been to analyse phenotypic evolution (RA2) using models based on ecologically realistic assumptions including fluctuating environments and density dependence similar to those used to analyse population dynamics in RA1. An important contribution to achieve this goal was a paper published by Gamelon et al. in the journal *Evolution*, which provided a method for analyses of phenotypic selection allowing for different optima in multiple characters.

Another important research topic that recently has emerged at CBD is questions related to the presence of so-called pace-of-life syndromes characterizing patterns of phenotypic covariation among individuals within species along a "slow-fast continuum". In 2018 a summary of much of the state of the art of research on this topic at CBD was published in a special issue of *Behavioral Ecology and Sociobiology* entitled "Topical Collection Pace-of-life Syndromes: a framework for the adaptive integration of behaviour, physiology, and life history" edited by M. Dammhahn, N.J. Dingemanse, P-T. Niemelä and D. Réale. In this issue Araya-Ajoy et al. presented an approach to link measures used in demography to characterize individual covariation among morphological, physiological and behavioural traits to classify individuals along such a "slow-fast continuum". Similarly, using a meta-analytic approach Tarka et al. found that males had a faster pace of life for development of life history traits, behaviour and physiology than females. In contrast, the opposite sexspecific trend was present in adult life history traits (e.g. life span). This means that the sexes may have different life history optima, resulting in the potential for sexual conflicts (Immonen et al.), which in turn can lead to sexspecific patterns in the covariances among phenotypic traits (Hämaläinen et al.).

The evolutionary significance of intersexual conflicts was the theme of a paper published by several researchers at CBD in the *Proceedings of the National Academy of Sciences USA*. Here, they show that in the Neotropical vine *Dalechampia scandens* the size of the seeds is partly determined by imprinted genes with antagonistic effects over maternal resource allocation. They further demonstrate that the strength of these genes depends on the intensity of the inter-sexual conflict over maternal resources experienced which in turn depends on the frequency of cross-pollination in the populations. These effects have important implications for local adaptation in offspring size in the presence of gene flow between populations with different mating systems.

A pattern that emerges from the publications in 2018 is that approaches and problems originating from the research field of behavioural ecology have received increased attention by researchers at CBD. For example, this includes questions related to allocation of parental

care (Ratikainen et al., *Proceedings of the Royal Society Biological Sciences*), the effects of multiple paternity on material allocation in wild boars (Gamelon et al., *Behavioural Ecology*) and the influence of predation on extra-pair copulations (Abbey-Lee et al., *Functional Ecology*). Such approaches, based on a detailed understanding of how behavioural variation affects the fitness of individuals, can without any doubt provide useful understanding of mechanisms that can be extremely helpful in obtaining realistic parameter spaces for many of the evolutionary and ecological models developed at the centre.

Both the panel performing the midterm evaluation and CBD's Scientific Advisory Committee (SAC) have pointed out that the scientific progress in RA3 (Community Dynamics) in the first period of the centre has been less than within the other two research areas, even though they considered the potential for scientific breakthroughs to be highest within RA3. The list of publications for 2018 indicates this trend is now changing. For instance, approximately 42 % of the papers published this year dealt with questions relevant for RA3. In order to further improve the integration among the RAs we also hired a post doc specifically to work on models involving evolution of community structure (dr. Christophe Coste).

The focus by the leadership on RA3 was the reason for the annual meeting of the Scientific Advisory Committee (SAC) being held in Longyearbyen at Svalbard May 1-3 2018. Spitsbergen is the location for the largest field project in this RA "Community dynamics in a rapidly warming high Arctic: trophic synchrony in time and space", which is mainly funded by a grant from the Research Council of Norway to researcher Brage Bremset Hansen through the programme FRIPRO. The central focus of this project is to understand how variation in climate affects trophic interactions in Arctic ecosystems. This site visit contributed important inputs, especially on design of field experiments as well as on future key questions to be addressed by CBD in this field of research. Furthermore, a seminar jointly organized by The University Centre in Svalbard (UNIS) and CBD clearly identified several research questions of mutual interest, which could form the foundation for more extensive collaboration between the two institutions in the future.

Researchers at CBD operate several study systems both in the field and in laboratories. Several papers published in 2018 are based on analyses of data from these studies. This involves papers on thermal reaction norms based on analyses of laboratory data of *Daphnia magna* (Fossen et al., *Journal of Evolutionary Biology* and Burton et al., *Journal of Experimental Biology*), age-dependent demography of the moose population on the island of Vega in northern Norway (Markussen et al., *Oecologia*), and population biology of house sparrows along the coast of Helgeland in northern Norway (Kvalnes et al., *Journal of Avian Biology*, Lundregan et al., *Molecular Ecology*).

A recommendation from the midterm evaluation was that researchers at CBD should be more involved in problems related to management of biological diversity. One example of such involvement was provided by the CBD-members O'Hara and Solberg. They were involved in a consortium that was able to show in a paper published in *Science* that movements of mammals in areas with a comparatively high human footprint were far less than the extent of their movements in areas with less impacts of humans

An important prerequisite for much of the research activity at CBD is the availability of external funding. In 2018 members of CBD were awarded several grants. Professor C. Pélabon obtained funding from the Research Council of Norway through the FRIPRO-programme for the researcher project "Understanding evolvability". In addition, associate professor Mike Martin and dr. Eivind Undheim received grants as Young Research Talent by the Research Council of Norway for the projects "Darwin Plants: Probing the genomic basis of rapid evolutionary diversification in the Galápagos daisy trees (genus *Scalsia*)" and Lacewing Venom: "Linking molecular and phenotypic evolution", respectively. Professor Robert B. O'Hara was also granted a project through NTNU's Digital Transformation initiative (<https://www.ntnu.edu/digital-transformation>) involving 5 PhD-students. In addition, the Norwegian Environment Agency also funded in 2018 the demographic study of the moose population on the island of Vega in northern Norway.



Moose at Hestmannøy. June 2016



Sparrows perching on a fence in Træna. February 2019.

In 2018, the large integrated project *Sustainable management of renewable resources in a changing environment* SUSTAIN (www.sustain.uio.no) funded by the Research Council of Norway approached its final stage. Here CBD is one of three principal nodes (the two others are the Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, and the Department of Arctic and Marine Biology, UiT Arctic University of Norway). An important contribution of CBD to this project has been the development of models for sustainable harvesting in a fluctuating environment that include species interactions in space. In 2018, 3 papers were published on this topic, showing that harvesting can influence the dynamics also of non-harvesting species and hence strongly affect structures of ecosystems.

An approach that is becoming more common in ecological and evolutionary studies is comparative analyses using meta-analytical approaches facilitating including data from a large number of studies. Researchers at CBD have been heavily involved in such an initiative through the FRIKLIM project *Evolution in a changing environment* funded by the Research Council of Norway. Here the aim is to study how fast evolutionary responses to expected changes in climate can evolve along ecological gradients. A central element in this project is to build up a database of long-term studies of the population biology of hole-nesting birds across Europe. This work was greatly facilitated by the participation of the Director in a network of researchers funded by the German Centre for Integrative Biodiversity Research (iDiv) in Leipzig, Germany.

Several members of CBD received external recognition in 2018. Professor Ovaskainen received the prize for mathematics and life sciences by the Finnish Academy of Science and Letters. The Director received the NTNU award for outstanding research in 2018. PhD-student Thomas R. Haaland received 'Honorable mention' for 'Student paper of the year 2018' in *American Naturalist*. In addition, NTNU appreciated non-scientific activities of researcher at CBD. Professor J. Wright received the Best Teacher of the Year Award 2017-2018 from the Faculty of Natural Sciences and was appointed by NTNU as Merritert Underviser (lecturer in education award). Researcher A.M. Lee and G. Rosenqvist received the NTNU's Prize for gender equality and diversity as member of the committee for gender equality at the Department of Biology.

ORGANIZATIONAL CHART 2018



MANAGEMENT AND ADMINISTRATION: THE LEADER GROUP



Bernt-Erik Sæther
Director
Professor



Bob O'Hara
Deputy Director
Professor



Ivar Herfindal
Leader, Research Area 1,
Researcher



Christophe Pélabon
Leader, Research Area 2,
Professor



Vidar Grøtan
Leader, Research Area 3,
Associated Professor



Lisbeth Pedersen
Centre Coordinator/
Consultant



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Management Departement
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Norunn Myklebust
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and Electrical Engineering
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Marcel E. Visser
Professor
Head of Department
Animal Ecology
Netherlands Institute of
Ecology (NIOO-KNAW)
The Netherlands



Ophélie Ronce
Research director
CNRS
University of Montpellier
France

SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

Current group members:

PI: Professor Bernt-Erik Sæther

Researcher Marlène Gamelon

Postdoc Thomas Kvalnes

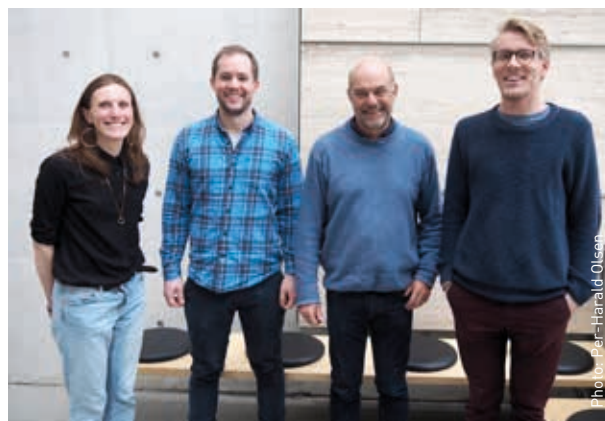
Postdoc Hanna Froy

PhD candidate Lara Veylit

PhD candidate Stefan Vriend

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

An important characteristic of this research group is heavy involvement with other research groups from all the three Research Areas. These interactions include collaboration in the development of theoretical models as well as statistical analyses of empirical data.



Lara Veylit, Thomas Kvalnes, Bernt-Erik Sæther, Stefan Vriend

Not present: Marlène Gamelon and Hanna Froy

MAJOR SCIENTIFIC CONTRIBUTIONS

A major contribution from this research group was the publication of theoretical models for harvesting of populations that include space and interactions with other species. This work was done in close collaboration with professor Engen and researcher A.M. Lee. For a summary of these results, see the Research Group Stochastic Theories. These models provide an important contribution of CBD to the achievement of the goals for the SUSTAIN-project.

Researchers at CBD have access to several unique long-term time sets of individual-based demographic data. One such data set was provided by Kurt Jerstad and Ole Wiggo Røstad, who have been studying the dipper in Lyngdalsvassdraget in southern Norway for nearly 40 years. In this system winter temperature affecting the icing conditions during winter has been identified as an important environmental driver for the population dynamics. Using a novel statistical approach that enables consideration of several traits simultaneously Gamelon et al. published in *Evolution*, show that also population density strongly affects phenotypic selection in this population.

Another type of analysis of longterm data was based on records of shot wild boar in an area in northeastern France. In this species littermates compete during pregnancy to extract maternal resources from the placenta. As a consequence, unequal extraction of

resources can lead to developmental differences among offspring and thus within-litter variation in offspring mass. Gamelon et al. combined long-term monitoring data with paternity analyses to examine whether the increase in the number of fathers within a litter explained the increase in within-litter variation in offspring mass observed in large litters. A clear pattern that emerged was that heavy females mated earlier during the rut, produced larger litters with a higher number of fathers and more variable fetus mass than lighter females. Within-litter variation of offspring mass increased with gestation stage and litter size, suggesting differential allocation of maternal resource among offspring "in utero." However, there was no effect of the number of fathers on the within-litter variation in offspring mass. Thus, differential maternal allocation to offspring during pregnancy is unlikely to be related to paternal identity in this species.

RECOMMENDED READING:

Gamelon, M., et al. . 2018. Does multiple paternity explain phenotypic variation among offspring in wild boar? *Behavioral Ecology* 29, 904–909.

Gamelon, M., et al. 2018. Environmental drivers of varying selective optima in a small passerine: A multivariate, multiepisodic approach. *Evolution* 72, 2325–2342.

RESEARCH GROUP: ECO-EVOLUTIONARY DYNAMICS

Members in 2018:

PI: Professor Sigurd Einum
 Postdoc Tim Burton
 PhD candidate Erlend Fossen
 PhD candidate Semona Issa
 Engineer Hanna-Kaisa Lakka

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

MAJOR SCIENTIFIC CONTRIBUTIONS

One of the major scientific contributions from our group in 2018 was the description of genetic variation in how organisms respond to a change in environmental temperature through phenotypic plasticity. Theoretical models on the evolution of phenotypic plasticity predict a zone of canalization where reaction norms cross, and genetic variation is minimized in the environment a population most frequently encounters. Empirical tests of this prediction have been missing, in particular for life-history traits. We addressed this prediction (Fossen et al. 2018) by quantifying thermal reaction norms of three life-history traits (somatic growth rate, age and size at maturation) in different clones from a single Norwegian population of *Daphnia magna*, and testing for the occurrence of an intermediate temperature at which genetic variance in the traits is minimized. The study confirmed the presence of strong genotype-environment interactions, and a zone of canalization at a temperature that corresponds well with mean summer temperatures experienced by the population. This suggests that the population has evolved under stabilizing selection in temperatures that fluctuate around this mean temperature. The results suggest local adaptation to temperature in the studied population and allow predicting evolutionary trajectories of thermal reaction norms under climate change. Specifically, the expected increase in the mean summer temperature in Norway should bring the mean summer temperature above the current zone of canalization. Such an increase in temperature, assuming that higher growth rate at the new temperature is beneficial, should select for clones with steeper slopes ('warm specialists'). Therefore, the mean slope of the reaction norm should increase until the new optimum phenotype is almost reached. Then, stabilizing selection around the new optimum should favour intermediate plasticity, leading to a progressive decrease in the mean slope and an increase in the elevation of the average reaction norm. This process, referred to as genetic assimilation, should result in an optimum phenotype being reached in the new environment. Furthermore, if



Semona Issa, Tim Burton, Sigurd Einum.
 Not present: Erlend Fossen, Hanna-Kaisa Lakka

there is genetic variation in how the organism perceives the environment, the zone of canalization itself should respond to selection and over time become equal to the new mean environmental temperature. Alternatively, the zone of canalization may change to the new mean environment through genetic drift, increased fitness costs of maintaining plasticity in the new environment or by changes in the genetic architecture of reaction norms.

Another major contribution from our group was the development of a method for automating the measurement of upper thermal limits in small aquatic organisms. This is a trait that we expect will be of high importance for ecological and evolutionary responses to the increasingly variable temperatures expected under climate change, and that we will continue to study in years to come. Upper thermal limits are frequently defined by the cessation of movement at high temperature, with measurement being performed by manual observation. Consequently, estimates of upper thermal limits may be subject to error and bias, both within and among observers. Our method utilizes video-based tracking software to record the movement of individuals when exposed to high, lethal temperatures. We develop an algorithm in the R computing language that can objectively identify the loss of locomotory function from tracking data. Using independent experimental data, we validate our approach by demonstrating the expected response in upper thermal limits to acclimation temperature.

RECOMMENDED READING:

- Burton, T., Zeis, B. and Einum, S. 2018. Automated measurement of upper thermal limits in small aquatic animals. *Journal of Experimental Biology* 221, UNSP jeb182386.
- Fossen, E.I.F., Pélabon, C. and Einum, S. 2018. An empirical test for a zone of canalization in thermal reaction norms. *Journal of Evolutionary Biology* 31, 936–943.

RESEARCH GROUP: DEMOGRAPHIC RESPONSES TO A CHANGING ENVIRONMENT

Current group members:

PI: Researcher Ivar Herfindal

Senior researcher Erling Johan Solberg

Senior researcher Erlend Birkeland Nilsen

Senior researcher Brett Sandercock

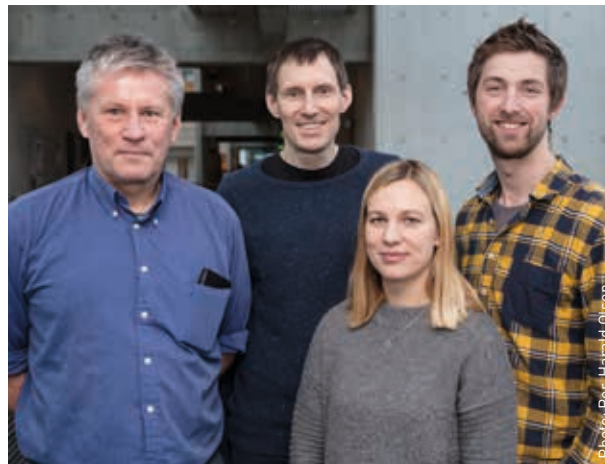
Senior researcher Hanno Sandvik

PhD candidate Stine Svalheim Markussen

PhD candidate Endre Grüner Ofstad

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

The main research focus is related to the fact that individual traits and population properties are inevitably linked to environmental conditions that vary in time and space. Understanding these links and the consequences they have for population dynamics is important, particularly in a world where human impact on ecosystems increases due to habitat change, climate change or harvesting of natural resources. We combine theoretical modelling and empirical data analysis to address questions related to demographic variation, often focussing on management and conservation of natural populations.



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

MAJOR SCIENTIFIC CONTRIBUTIONS

Harvesting is the most important factor for individual survival and population dynamics in many wildlife populations. Whereas previous research on the topic often has assessed consequences on population size and growth rates, or survival, genetic tools now allow investigation of individual consequences also on reproductive performance. This allows a more complete approach for understanding fitness-consequences of harvesting, also among the male segment. The close monitoring of the moose population at Vega offers unique possibilities to investigate causes and consequences of individual variation in vital rates in a population that experiences strong regulation by harvesting, and this was the main topic of the PhD thesis of Stine Svalheim Markussen, which was successfully defended in 2018.

One of the main findings in the doctoral work of Markussen was that there are consistent individual

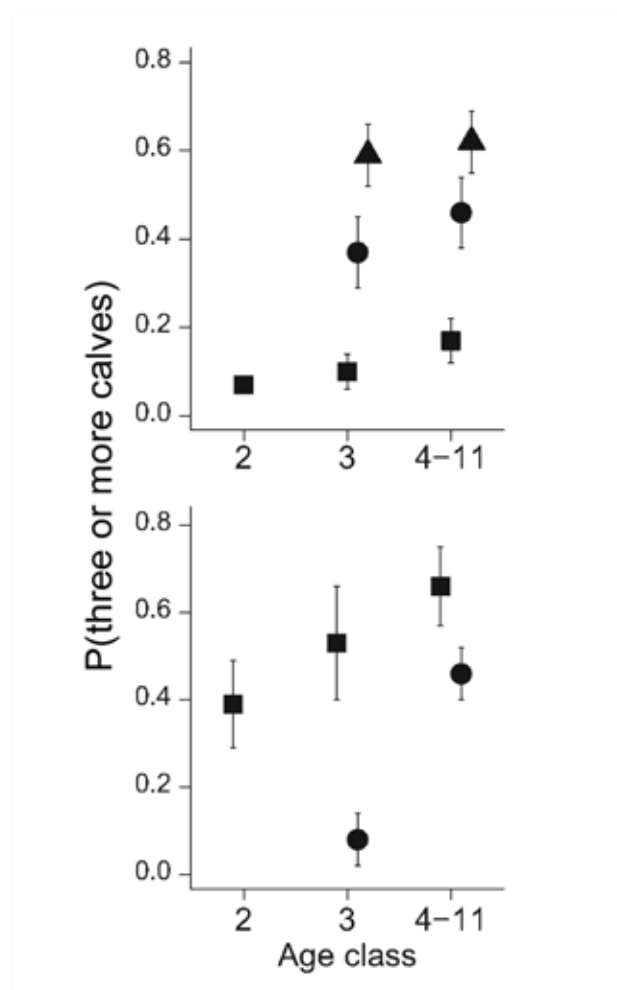
differences in vital rates among females, and that these differences have consequences for the likelihood of being harvested. The result is that females that start reproducing early, and that frequently produce twins, have a higher survival compared to females that delay the onset of reproduction and have a lower reproductive rate. Surprisingly, such patterns were also found in male moose, which indicates that there are males that are considered of particularly high quality by females already when young, and that continue to have a high mating success throughout their lifespan. Males also had a lower probability of being shot. Combined, these factors generate very high individual variation in lifetime reproductive success. Performing males were in general heavier and had larger antlers compared to low-performing males. PhD candidate Endre Grüner Ofstad explores the role that behaviour plays for generating such individual differences, and in particular the use of

habitat. His work (currently under review) shows complex relationships between the scale of movement (i.e. the home range size), and the selection of different habitat types, and how these have fitness consequences both with respect to reproductive performance and to the survival during the hunting season.

The strong participation of researchers from NINA in our group provides an even closer link to practical management and conservation of wildlife. For instance, work on the management and harvesting of willow ptarmigan showed that the effectiveness of management strategies, in this case the bag limit, depended on the population densities in a way that increased the harvest rate at low densities. This introduces more uncertainty into management strategies, however, when aware of such processes they can be incorporated into the strategies in order to quantify risk of overharvesting. In a study on tree swallows in Canada, Sandercock and co-authors showed how changes in the immigration rates provided the most important contribution to the dramatic decline in the population sizes over a 24 year period, emphasizing the severe consequences that isolation can have on population viability when conditions affecting vital rates change.

RECOMMENDED READING:

- Eriksen, L.F., Moa, P.F. and Nilsen, E.B. 2018. Quantifying risk of overharvest when implementation is uncertain. *Journal of Applied Ecology* 55, 482–493.
- Markussen, S.S., Herfindal, I., Loison, A., Solberg, E.J., Haanes, H., Røed, K.H., Heim, M. and Sæther, B.-E. 2018. Determinants of age at first reproduction and lifetime breeding success revealed by full paternity assignment in a male ungulate. *Oikos*, In press.
- Markussen, S.S., Loison, A., Herfindal, I., Solberg, E.J., Haanes, H., Røed, K.H., Heim, M. and Sæther, B.-E. 2018. Fitness correlates of age at primiparity in a hunted moose population. *Oecologia* 186, 447–458.
- Taylor, L.U., Woodworth, B.K., Sandercock, B.K. and Wheelwright, N.T. 2018. Demographic drivers of collapse in an island population of Tree Swallows. *The Condor* 120, 828–841.



The probability that a male moose sires three or more calves a given year in relation to age. In the upper panel, squares, circles and triangles represent males that sired one, two, and three or more, calves in the previous state, respectively. In the lower panel circles and squares represent males starting to reproduce at age three and two, respectively.

RESEARCH GROUP: STOCHASTIC THEORIES

Current group members:

PI: Professor Steinar Engen
 Professor Jarle Tufto
 PhD Ane Marlene Myhre
 PhD Yihan Cao

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

This research group produces models and statistical methods used by several of the other research groups at CBD. A central focus is to develop a common theoretical framework based on application of stochastic theories in a wide array of empirical systems.



Ane Marlene Myhre, Steinar Engen, Yihan Cao
 Not present: Jarle Tufto

MAJOR SCIENTIFIC CONTRIBUTIONS

Sustainable harvest in a spatially structured environment

As part of CBD's input to the large integrated project SUSTAIN the group has developed models generalizing previous spatial results in two directions, a competition model (Jarilo et al. 2018) and an analysis of spatial effects of different harvesting strategies (Engen et al. 2018). The goal in both these generalizations has been to study spatial scaling of population density expressed as synchrony in population fluctuations. The competition model is a rather complex theoretical model but still gives some very informative results. It is shown that the effects of interspecific competition on the geographical scale of population synchrony are dependent on the pattern of spatial covariation of environmental variables. If the environmental noise is uncorrelated between the competing species, competition generally increases the spatial scale of population synchrony of both species. Otherwise, if the environmental noises are strongly correlated between species, competition generally increases the spatial scale of population synchrony of at least one, but also often of both species. If the species are subject to proportional harvesting, this may synchronize population dynamics over large geographical areas, affecting the vulnerability of harvested species to

environmental changes. In Engen et al. (2018) it is shown that harvesting reduces the population synchrony scale if it depends more strongly on population fluctuations than the density dependence of the growth rate in the absence of harvesting. Constant and proportional harvesting always increase the spatial scale in a theta-logistic model for density regulation. Exact scaling results are also derived under harvesting for the Beverton-Holt and the Ricker stock-recruitment models that are commonly applied, e.g. in fisheries. Our results indicate that harvest in areas with large abundances should be encouraged to avoid increase of the spatial scale of synchrony in the population fluctuations that can lead to unexpected quasi-extinction of populations over large areas. Our results quantify this harvesting impact giving the resulting scales of spatial synchrony of population fluctuations.

Community dynamics

In an applied study Solbu et al. (2018) in collaboration with NINA using previous theoretical results on community dynamics developed over time at CBD, bird communities across Norway have been analyzed with focus on heterogeneity in species abundance models with dynamical parameters varying among species. It was demonstrated how similarity in community composition over time, used as a measure of temporal diversity or turnover rate, could be estimated when accounting for heterogeneity in dynamical parameters among species. Heterogeneity affects estimated environmental stochasticity σ_e^2 , and how the temporal dynamics are modelled. Spatial variation in species abundance within sampling areas can obscure temporal dynamics of communities. Using Norwegian bird communities as a case study, it is shown how to interpret the sample correlation of the bivariate Poisson lognormal distribution, fitted to pairs of transects, and why separation of the transects into spatially similar subgroups can be beneficial. The partitioning of the variance of the species abundance distributions showed that heterogeneity among species in temporal dynamics accounted for roughly 75% of the variation, close to estimates for other taxa.

RECOMMENDED READING:

- Engen, S., Cao, F. J. and Sæther, B.-E. 2018. The effect of harvesting on the spatial synchrony of population fluctuations. *Theoretical population Biology* 123: 28-34.
- Engen, S., Lee, A.M. and Sæther, B.-E. 2018. Spatial distribution and optimal harvesting of an age-structured population in a fluctuating environment. *Mathematical Biosciences* 296, 36-44.
- Jarillo, J. , Sæther, B.E., Engen, S. and Cao, F.J. 2018. Spatial scales of population synchrony of two competing species: effects of harvesting and strength of competition. *OIKOS* 127: 1459-1470.
- Solbu, E. B., Diserud, O. H., Kålås, J. A. and Engen, S. 2018. How can heterogeneity among species affect community dynamics? – Norwegian bird communities as a case study. *Ecological Modelling* 388:13-23.

RESEARCH GROUP: EVOLUTIONARY DYNAMICS OF QUANTITATIVE TRAITS

Current group members:

PI: Professor Christophe Pélabon
 Researcher Geir H. Bolstad
 Postdoc Øystein H. Opedal
 PhD candidate Elena Albertsen
 PhD candidate Christoffer H. Hilde

Aim: *To understand the evolutionary dynamics of complex traits.*



Christophe Pelabon, Geir Bolstad, Elena Albertsen, Christoffer Høyvik Hilde og Astrid Raunsgard . Not present: Øystein Hjorthol Opedal

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 such traits.

Using both experimental and comparative approaches, the group aims at operationalizing measures of the evolutionary potential or evolvability. The group has published two papers on the subject in 2018 and organized a workshop on allometry in Trondheim in February and a symposium at the ESEB conference in Montpellier in August on Evolvability.



MAJOR SCIENTIFIC CONTRIBUTIONS

Evolution of flower morphology in a fluctuating environment

Seed size is a particularly important life history trait in plants whose evolutionary dynamic remains poorly understood. Seed size is under different sources of selection both extrinsic and intrinsic to the organism. For example, seed size determines the amount of resource available for the embryo at germination and thus affects the ability of seedlings to establish and to compete before the formation of true leaves. Seed size may also affect the rate of germination after dispersal and the duration of seed dormancy. On the other hand, seed size may be influenced by the size-number trade-off and by competition among pollen donor over maternal resources.

The Neotropical vine *Dalechampia scandens* represents a particularly interesting organism to study the evolutionary dynamics of seed size. Blossoms of *D. scandens* produce a maximum of nine large seeds (ca. 40 mg) that vary in size within plants, but also among plants within populations, and among populations and species. With various quantitative genetic experiments, we have shown the additive genetic variance in seed size was limited, but that seed size was genetically correlated with the size of the blossoms. Using inter-population crosses, we recently showed that seed size was affected by imprinted genes involved in a tug-of-war over maternal resources. In this tug-of-war, maternal genes limit the resources allocated to individual seeds while paternal genes increase the resource allocation to the seeds, possibly at the expense of other seeds from other pollen donors. Importantly, the strength of the alleles promoting or reducing maternal allocation depends on the level of outcrossing in the population, that is, the frequency and the strength of the inter-pollen donor competition. While within-population crosses do not show such an effect because maternal and paternal genes have reached an equilibrium in the tug-of-war, crosses among populations with different levels of outcrossing reveal such an effect (Figure 1).

RECOMMENDED READING:

Raunsgård, A., Opedal, Ø.H., Ekrem, R.K., Wright, J., Bolstad, G.H., Armbruster, W.S. and Pélabon, C. 2018. Intersexual conflict over seed size is stronger in more outcrossed populations of a mixed-mating plant. *Proceedings of the National Academy of Sciences of the United States of America* 115, 11561–11566.

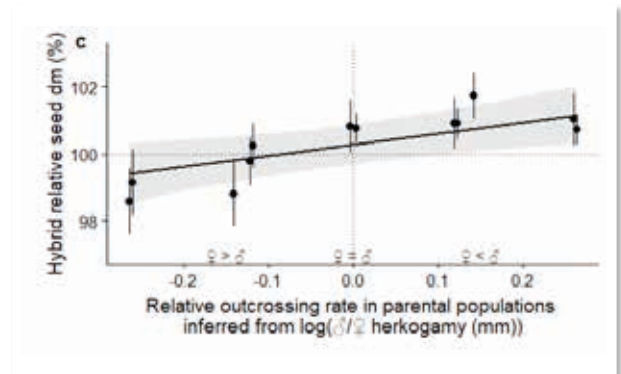


Figure 1: Results of the experimental tests of the tug-of-war and recognition-avoidance mechanisms. The hybrid relative seed size of crosses among populations of *D. scandens* is regressed against the relative outcrossing rate of parental populations to test the tug-of-war hypothesis. Data are from the diallel among four populations. The hybrid relative seed size is the hybrid seed diameter (dm) expressed as a percent of the average seed diameter within the maternal population. Shaded areas represent 95% confidence intervals for the regression models. Each point represents the mean (\pm SE) relative seed diameter for each cross-combination. The relative outcrossing rate of the parental populations is estimated as \log_e (Paternal population herkogamy / Maternal population herkogamy). The outcrossing rate of the paternal population is estimated as the mean herkogamy (millimeters). See Raunsgård et al. 2018 for more information.

RESEARCH GROUP: LINKING ECOLOGICAL AND GENETIC DYNAMICS

Current group members:

PI: Professor Henrik Jensen
 Professor Stig W. Omholt
 Professor Ingelin Steinsland
 Associate Professor Thor Harald Ringsby
 Associate Professor Arild Husby
 Associate Professor Michael D. Martin
 Researcher Ingerid J. Hagen (NINA)
 Researcher Hannu Mäkinen
 Postdoc Alina Niskanen (University of Oulu)
 PhD candidate Peter S. Ranke
 PhD candidate Sindre L. Sommerli
 PhD candidate Dilan Saatoglu
 PhD candidate Maria L. Selle
 PhD candidate Michael P. Pedersen
 PhD candidate Sarah Lundregan
 PhD candidate Vanessa Bieker
 Senior engineer Henrik Pärn
 Senior engineer Bernt Rønning



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

Not present: Stig W. Omholt, Ingelin Steinsland, Arild Husby, Michael D. Martin, Ingerid J. Hagen, Hannu Mäkinen, Alina Niskanen, Peter S. Ranke, Sindre L. Sommerli, Maria L. Selle, Vanessa Bieker, Henrik Pärn, Bernt Rønning

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 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: 1) needed to parameterize and test models developed by other RGs at CBD; 2) attractive for scientists who wish to use our unique data in international and national collaborative projects that test hypotheses and answer questions in various fields in biology.

MAJOR SCIENTIFIC CONTRIBUTIONS

Life-history dynamics in natural populations

Understanding how life history characters affect population dynamics (aim of RA1), and how selection may result in evolutionary change in fluctuating environments (aim of RA2) are fundamental goals in evolutionary biology. Using individual data from one of CBD's long-term study populations of house sparrows at the coast of Helgeland, we investigated the interaction

between offspring size (measured as egg volume) and environmental conditions on offspring mortality and phenotype (Kvalnes et al. 2018). Offspring size is a key trait in life-history theory, and an important maternal effect on offspring fitness and phenotype in birds and other oviparous animals. The performance of offspring often increases with size, but a fluctuating environment may introduce temporal variation in the optimal phenotype. We found that increased offspring size reduced

offspring mortality in early life, with more pronounced effects under heavy precipitation. However, the optimal offspring size for low offspring mortality until recruitment shifted from large to small as temperature increased. Our results reveal a potential for eco-evolutionary dynamics in offspring size, as populations adapt to fluctuating environmental conditions. The ultimate outcome of this dynamic process will also depend on variation in parental fitness and trade-offs with other life-history traits, particularly clutch size. By increasing our understanding of these mechanisms, we provide novel insights into the eco-evolutionary dynamics of life history strategies in parental reproductive investment.

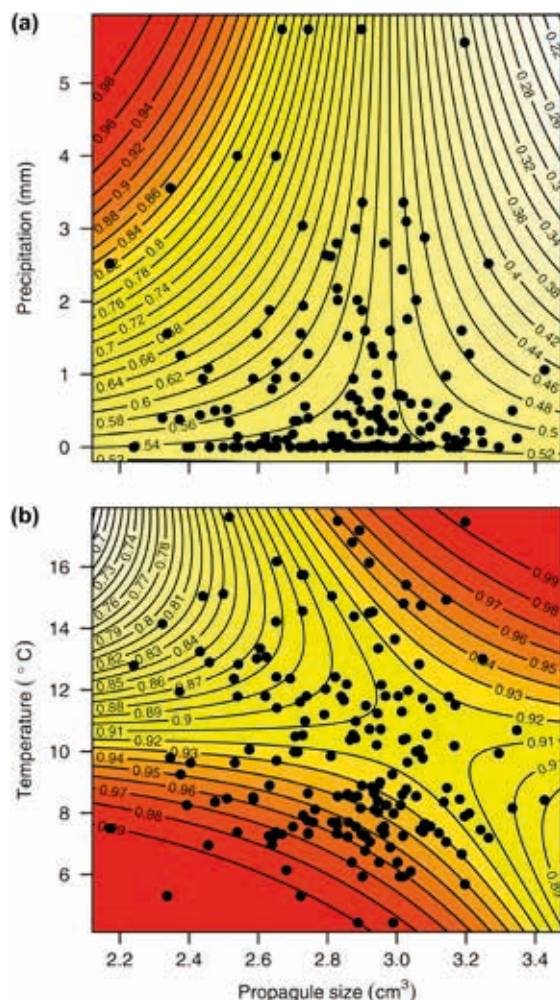


Figure 1. The predicted consequences of offspring size (measured as egg volume) on offspring mortality from hatching until (a) fledging and (b) recruitment in a population of house sparrows in Norway (Kvalnes et al. 2018). The effect of offspring size on mortality depends on the weather conditions during the early life of nestlings (age 0 to 5 days of age). Heat map with con-tour lines for mortality (red = high, white = low) as a result of the interaction between offspring size and temperature or precipitation; other explanatory variables in the models were kept at their mean value.

Genetic basis of ecologically important characters

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

Using our house sparrow reference genome sequence, we developed a custom high-density (200K) single nucleotide polymorphism (SNP) genotyping array for house sparrow (Lundregan et al. 2018). Such a genomic resource is rare for any wild vertebrate species, and provides a unique tool for understanding e.g. the genetic mechanisms underlying adaptive phenotypic variation. Bill morphology is a heritable and ecologically important trait in birds, and closely linked to individual fitness. Previous studies have revealed several genes that may influence bill morphology, but the similarity of gene and allele effects between species and populations is unknown. We used our custom 200K SNP array to examine the genetic basis of bill morphology in nearly two thousand house sparrows in our study metapopulation off the coast of Northern Norway (Lundregan et al. 2018). We found high genomic heritabilities for bill depth and length, which were comparable with previous pedigree estimates. Candidate gene and genome-wide association (GWA) analyses yielded six significant loci, four of which have previously been associated with craniofacial development. Three of these loci are involved in bone morphogenic protein (BMP) signalling, suggesting a role for BMP genes in regulating bill morphology. However, these loci individually explain a small amount of variance. In combination with results from genome partitioning analyses, our results indicate that bill morphology is a polygenic trait. Any studies of eco-evolutionary processes in bill morphology are therefore dependent on methods that can accommodate polygenic inheritance of the phenotype and molecular-scale evolution of genetic architecture.

Due to its history of multiple introductions to novel environments worldwide, the house sparrow is an excellent model species to study rapid local adaption. Australian populations of house sparrow were introduced from Europe 150 years ago, and in collaboration with researchers in Australia, we used our genomic resources to identify putative loci subject to selection across an extensive range of temperate, arid and tropical climates following the introduction (Andrew et al. 2018). By using both population differentiation (PD) and ecological

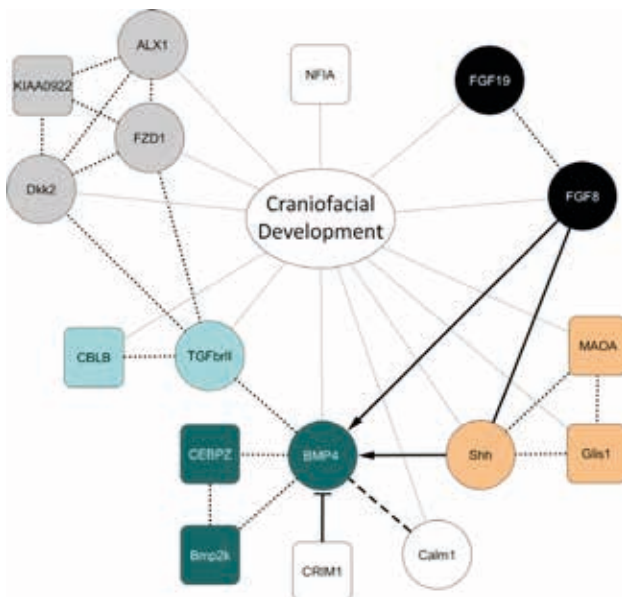


Figure 2. Pathway diagram displaying links between candidate genes (circular nodes) for bill morphology (craniofacial development). Square nodes represent flanking genes for significant SNPs associated with bill morphology in our genome wide association (GWA) analyses and that have previously been linked to craniofacial development (Lundregan et al. 2018). Full grey edges indicate link to craniofacial development, full black edges indicate direct protein-protein interaction, bars and arrows indicate negative and positive regulation, dashed edges indicate coexpression, and dotted edges indicate involvement in the same signalling pathway. Nodes are coloured according to main signalling pathway: FZD1, Dkk2, ALX1 and KIAA0922 are all involved in the Wnt pathway, TGFbr1 and CBLB are part of the TGF pathway, BMP4, Bmp2k and CEBP2 belong to the BMP pathway, FGF8 and FGF19 are part of the FGF pathway, and Shh, Glis1 and MAOA all belong to the Shh pathway. White nodes indicate candidate genes that do not share a main signalling pathway with another candidate, or for which main signalling pathway is unknown.

association (EA) methods we identified nearly 1000 outlier SNPs, of which 38.3% were physically linked (within 20 kbps) to 575 known protein-coding regions in the house sparrow reference genome. Interestingly, some outlier genes had been previously identified in genome scan studies of broadly distributed species or had strong links to traits that are expected to be important to local adaptation, for example, heat-shock proteins, immune response and HOX genes. Our results identify an opportunity to use the house sparrow as a model to further study genetic processes involved in local adaptation, and clearly show that our genomic resources provide great prospects for studying genome-level questions in house sparrow populations world-wide.

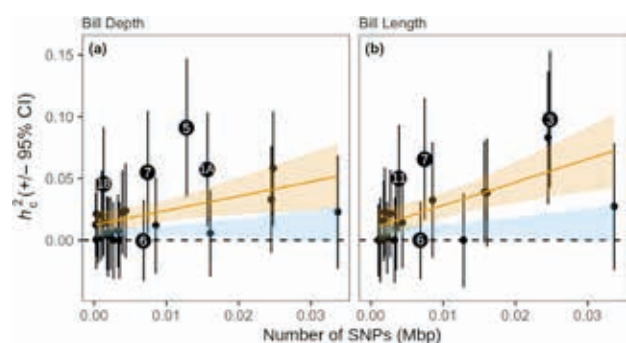


Figure 3. Results from analyses where variation in bill morphology of house sparrows in a metapopulation in northern Norway was partitioned across chromosomes in the house sparrow genome (Lundregan et al. 2018). Figures show the relationship between explained variation in bill morphology and chromosome size for (a) bill depth and (b) bill length. Numbers indicate chromosome number. The yellow-shaded area shows 95% C.I. for OLS regression between the number of SNPs and the proportion of variance explained by each chromosome (h^2_c), with black bars indicating 95% C.I. for each h^2_c estimate. Blue-shaded area indicates 95% quantiles generated by resampling of the null distribution under the hypothesis of no relationship between chromosome size and variance explained.

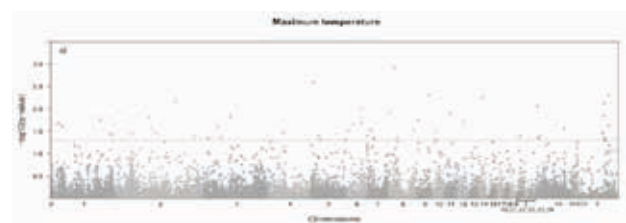


Figure 4. Results from an analysis where we tested for putative loci involved in rapid adaptation to high temperatures in Australian house sparrows (Andrew et al. 2018). Each dot in the Manhattan plot shows the significance level of a SNP-marker when tested for a relationship with summer maximum temperature (y-axis) and its location in the genome (x-axis). More than 162,000 SNPs distributed across most chromosomes in the house sparrow genome were used in the analysis. Significant loci lie above the dashed line.

RECOMMENDED READING:

- Andrew, S.C., Jensen, H., Hagen, I.J., Lundregan, S. and Griffith, S.C. 2018. Signatures of genetic adaptation to extremely varied Australian environments in introduced European house sparrows. *Molecular Ecology* 27, 4542-4555.
- Kvalnes, T., Røberg, A.Å., Jensen, H., Holand, H., Pärn, H., Sæther, B.-E. and Ringsby, T.H. 2018. Offspring fitness and the optimal propagule size in a fluctuating environment. *Journal of Avian Biology* 49, e01786.
- Lundregan, S.L., Hagen, I.J., Gohli, J., Niskanen, A.K., Kempainen, P., Ringsby, T.H., Kvalnes, T., Pärn, H., Rønning, B., Holand, H., Ranke, P.S., Båtnes, A.S., Selvik, L.-K., Lien, S., Sæther, B.-E., Husby, A. and Jensen, H. 2018. Inferences of genetic architecture of bill morphology in house sparrow using a high density SNP array point to a polygenic basis. *Molecular Ecology*, 27, 3498-3514.

RESEARCH GROUP: MODELLING BEHAVIOUR IN STOCHASTIC ENVIRONMENTS

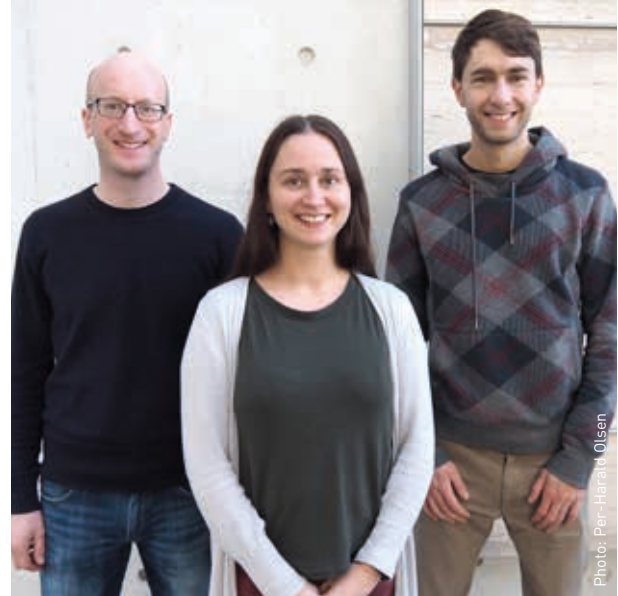
Current group members:

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.

In 2018, Assistant prof. Martin Lind from Uppsala University joined the group as a visiting researcher. He is 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.



Martin Lind, Irja Ida Ratikainen, Thomas Haaland

Ratikainen, his lab is testing novel theory in the powerful *Caenorhabditis remanei* and *C. elegans* empirical model systems.

MAJOR SCIENTIFIC CONTRIBUTIONS

Adaptations to unpredictable environmental fluctuations represent some of the most intriguing problems in evolutionary biology and some of the most relevant for understanding biodiversity dynamics in the light of climate change. At the individual level, this involves the use of ‘insurance’ strategies against negative effects of environmental variation when fitness functions are skewed (see Fig. 1). However, across generations it is usually predicted that genotype fitness is maximized in the form of ‘bet-hedging’ adaptations. We found that insurance causes the optimal phenotype to shift from the peak to down the less steeply decreasing side of the fitness function, and that conservative bet-hedging produces an additional shift on top of this, which decreases as adaptive phenotypic variation from diversifying bethedging increases. When diversifying bet hedging is not an option, environmental canalization to reduce phenotypic variation is almost always favored. Importantly, using skewed fitness functions, we provide

the first model that explicitly addresses how conservative and diversifying bethedging strategies might coexist.

Epigenetic inheritance is another common adaptation to environmental fluctuations, but its influence on evolutionary dynamics is not well known. To synthesize the current state of the field and point out promising directions for future research, we edited a special issue entitled “Evolutionary consequences of epigenetic inheritance” in *Heredity* (Lind and Spagopoulou 2018). The focus of this special issue was the evolutionary forces selecting for epigenetic inheritance, its costs and importance for adaptation.

Studies on phenotypic plasticity normally focus on single traits and few populations. Together with researchers from University of Sheffield, we studied multi-trait plasticity on a landscape scale in the freshwater

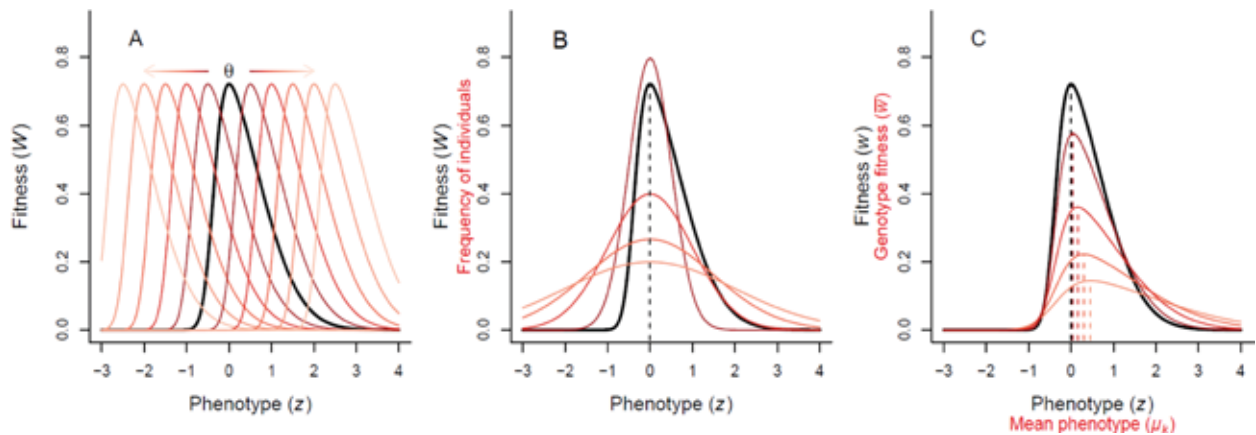


Figure 1: Asymmetric fitness functions and uncertainty in fitness returns produces insurance. Both A), environmental variation moving the position of the fitness function around, and/or B) phenotypic variation among individuals of a genotype (red curves), can cause uncertainty in the fitness returns, leading to C) arithmetic mean fitness to favor insurance. Insurance therefore takes the form of an adjustment of the mean phenotypic value away from the peak of the deterministic fitness function (to the right in this case) down the shallow side to avoid accidentally falling off the cliff-edge. The thick black line in all panels is the deterministic fitness function, a skew-normal function. In A, environmental variation causes the position of the fitness function to fluctuate (arrows, colored lines, darker to lighter lines representing range of fluctuations). In B, phenotypic variation among individuals leads to different individuals gaining different fitness rewards. Colored lines represent distributions of individuals with increasing standard deviations (darker to lighter). Therefore, in C the colored lines are arithmetic mean fitness across individuals for genotypes with a fixed phenotypic variance, from darkest to lightest. Maxima of these functions are indicated by the dotted lines. See Haaland et al. 2018 for more details.

crustacean *Daphnia pulex*, and found local adaptation in the genetic variation of multi-trait plasticity related to predation regime, recently published in *Nature Ecology & Evolution* (Reger et al. 2018).

In another series of models, we have shown that parental investment should be plastic according to partner quality, but that the response should be highly dependent on the exact partner effect on either investment costs or offspring fitness. We have also shown how partner quality should affect the quality vs. quantity trade-off in offspring investment (Ratikainen et al. 2018). These results are important because parental investment can contribute both to evolution by sexual selection but also to natural selection because parental investment decisions can either enhance or reduce differences in individual quality.

RECOMMENDED READING:

- Haaland, T.R., Wright, J., Tufto, J. and Ratikainen, I.I. 2018. Short-term insurance versus long-term bet-hedging strategies as adaptations to variable environments. *Evolution*, in press.
- Lind, M.I. and Spagopoulou, F. 2018. Evolutionary consequences of epigenetic inheritance. *Heredity* 121, 205-209
- Reger, J., Lind, M.I., Robinson, M.R. and Beckerman, A.P. 2018. Predation drives local adaptation of phenotypic plasticity. *Nature Ecology and Evolution* 2, 100-107.
- Ratikainen, I.I., Haaland, T.R. and Wright, J. 2018. Differential allocation of parental investment and the trade-off between size and number of offspring. *Proceedings of the Royal Society B: Biological Sciences* 285, 20181074.

RESEARCH GROUP: ADAPTATIONS TO (UN)PREDICTABLE ENVIRONMENTAL CHANGE

Current group members:

PI: Professor Jonathan Wright

Postdoc Yimen Araya-Ajoy

PhD candidate Mette Helene Finnøen

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

This 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



Jonatan Wright, Mette Helene Finnøen, Yimen Araya-Ajoy

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

Pace-of-life variation in life histories within and among species

We take a novel perspective to life history evolution that combines recent theoretical advances in fluctuating density-dependent selection with the notion of pace-of-life syndromes (POLs) in behavioural ecology. These ideas posit phenotypic co-variation in life history, physiological, morphological and behavioural traits as a continuum from the highly fecund, short-lived, bold, aggressive and highly dispersive 'fast' types at one end of the POLS to the less fecund, long-lived, cautious, shy, plastic and socially-responsive 'slow' types at the other. We propose that such variation in life histories and the associated individual differences in behaviour can be explained through their eco-evolutionary dynamics with population density – a single and ubiquitous selective factor that is present in all biological systems. Contrasting regimes of environmental stochasticity are expected to affect population density in time and space and create differing patterns of fluctuating density-dependent selection, which generates variation in fast versus slow life histories within and among populations. We therefore predict that a major axis of phenotypic co-variation in life history, physiological, morphological and behavioural traits (i.e. the POLS) should align with these stochastic fluctuations in the multivariate fitness landscape created by variation in density-dependent selection (Fig.1). Phenotypic plasticity and/or genetic (co-)variation oriented along this major POLS axis are thus expected to facilitate rapid and adaptively integrated changes in various aspects of life histories within and among

populations and/or species. The fluctuating density-dependent selection POLS framework we presented therefore provides a series of clear testable predictions, the investigation of which should further our fundamental understanding of life history evolution and thus our ability to predict natural population dynamics.

Several life history metrics can be used to place species in the fast-slow continuum and we asked whether individual variation in POL can also be studied using similar life history measures. We therefore translated some commonly used measures in demographic studies into individual level estimates. We studied fecundity rate, generation time, lifespan, age at first reproduction, fecundity at first reproduction, and principal component scores integrating these different metrics. Using simulations, we show how demographic stochasticity and individual variation in resources affect the ability to predict an individual's POL using these individual level estimates. Their accuracy depends on how environmental stochasticity varies with the species' position on the fast-slow continuum and with the amount of (co) variation caused by individual differences in resources. These results highlight the importance of studying the sources of life history covariation to determine whether POL explains the covariation between morphological, physiological and behavioral traits within species. Our simulations also show that quantifying not only among-individual, but also among-population patterns of life history covariation helps with the interpretation of demographic estimates in the study of POLs.

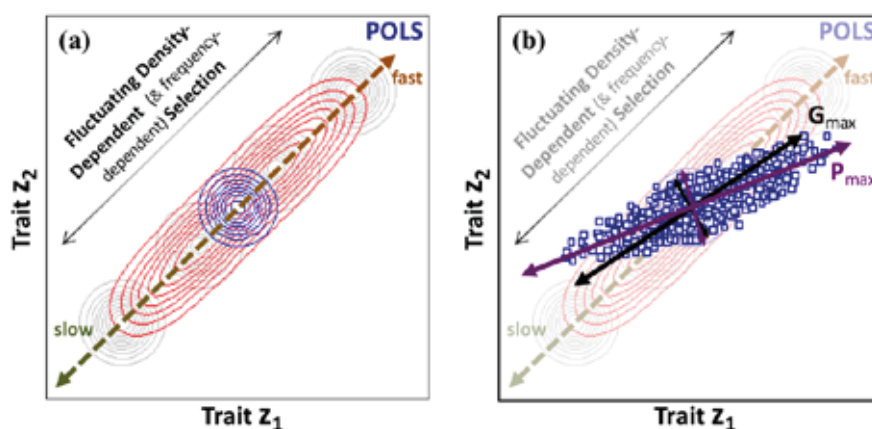


Figure 1. Illustration of covariation and correlated selection between two life history traits (z_1 & z_2). (a) Fluctuations in the position of Gaussian fitness surfaces (grey) creates a ridge of arithmetic mean fitness surface (red), but does not affect the geometric mean fitness surface (blue) producing a potential pace-of-life syndrome (POLS) dashed two-headed arrow varying from fast-types resulting from low density-dependent selection (orange) to slow-types resulting from high density-dependent selection (green), plus possible frequency-dependent selection. (b) Imposed on top of (a), individual phenotypes (open blue squares), with the purple two-headed arrow indicating the major axis of phenotypic trait covariation (P_{max}), and the black two-headed arrow the major axis of genetic covariance (G_{max}).

Body size, allometric relationships and evolvability

Body size plays a key role in the life histories, ecology and evolution of all organisms. Therefore, quantifying the sources of morphological (co)variation, dependent and independent of body size, is of key importance when trying to understand and predict responses to selection. We combined structural equation modeling (SEM) with quantitative genetics analyses to study morphological (co)variation in a meta-population of house sparrows (*Passer domesticus*). As expected, we found evidence of a latent variable 'body size', causing genetic and environmental covariation between morphological traits (Fig.2). Estimates of conditional evolvability show that allometric relationships constrain the independent evolution of house sparrow morphology. We also found spatial differences in general body size and its allometric relationships. On islands where birds are more dispersive and mobile, individuals were smaller and had proportionally longer wings for their body size. While in islands where sparrows are more sedentary and nest in dense colonies, individuals were larger and had proportionally longer tarsi for their body size. We corroborated these results using simulations and show that our analyses produce unbiased allometric slope estimates. This study highlights that in the short term allometric relationships may constrain phenotypic evolution, but that in the long-term selection pressures can also shape allometric relationships.

RECOMMENDED READING:

- Wright, J., Bolstad, G.H., Araya-Ajoy, Y.G. and Dingemanse, N.J. 2018. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews*, in press.
- Araya-Ajoy, Y.G., Bolstad, G.H., Brommer, J., Careau, V., Dingemanse, N.J. and Wright, J. 2018. Demographic measures of an individual's "pace of life": fecundity rate, lifespan, generation time, or a composite variable? *Behavioral Ecology and Sociobiology* 72, 20132645.
- Araya-Ajoy, Y.G., Ranke, P.S., Kvalnes, T., Rønning, B., Holand, H., Myhre, A.M., Pärn, H., Jensen, H., Ringsby, T.H., Saether, B.-E. and Wright, J. 2018. Characterizing morphological (co)variation using structural equation models: Body size, allometric relationships and evolvability in a house sparrow metapopulation. *Evolution*, In press.

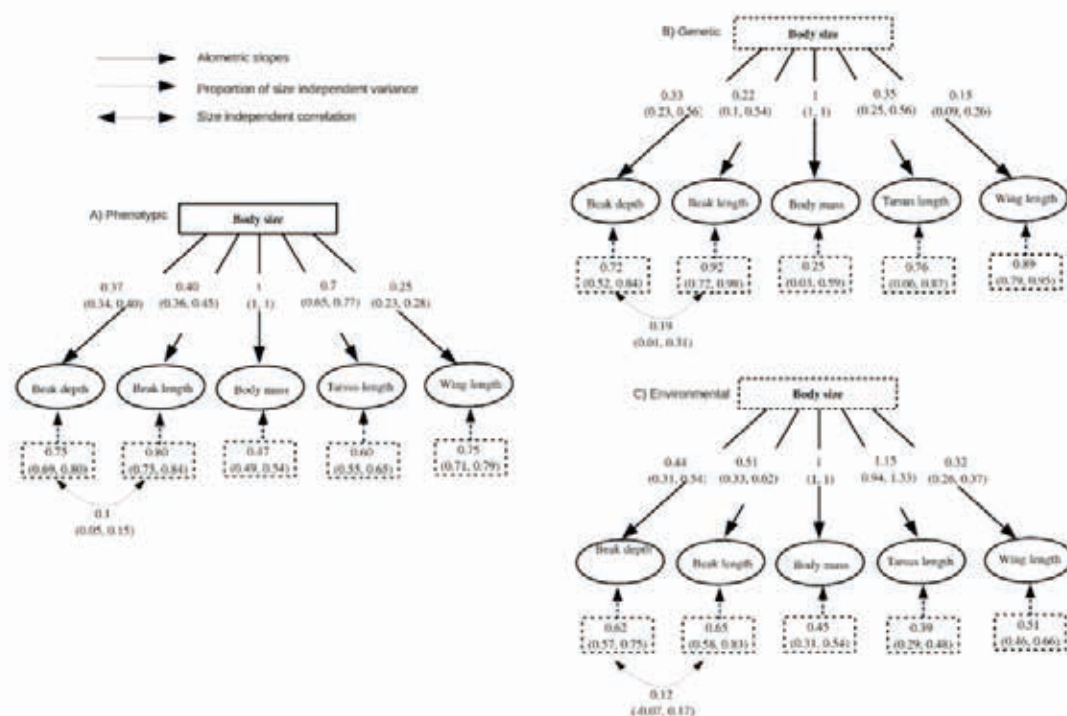


Figure 2. Structural equation model (SEM) diagrams for the effect of the latent variable body size on the morphological measurements and size-independent variances and covariances. SEM models involve (co)variation at A) the phenotypic level, B) the environmental level, and C) the genetic level. Solid line single-headed arrows represent the effect of body size on the different morphological measurements (i.e. allometric slopes) scaled to body mass. Dashed line single-headed arrows represent the proportion of size-independent variation in traits, and dashed line double-headed arrows represent size-independent correlations between pairs of traits. Estimates are the mean and 95% credible intervals in parenthesis.

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

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



Tanja Petersen, Lisa Sandal, Anders Gravbrøt Finstad, Bob O'Hara, Emily Grace Simmonds, Vidar Grøtan, Emma-Liina Marjakangas, Sam Perrin, Christophe Coste
 Not present: Otso Ovaskainen, Ola Diserud

MAJOR SCIENTIFIC CONTRIBUTIONS

Even undisturbed communities will show variation over time due to inherent stochasticity operating on the dynamics of the species included in the community. To study effects of e.g. human disturbances, such as habitat fragmentation, as well as effects of long term changes in climate it is thus important to establish baseline estimates of temporal turnover in communities. Solbu et al. studied temporal turnover in bird communities in seven different areas in Norway where sampling have been systematically performed in order to document possible long-term changes in Norwegian fauna. These undisturbed areas cover a wide range of climatic variation. The study showed that temporal turnover within an area in these bird communities was slow, meaning that abundant species remained abundant while less abundant species tended to maintain a low abundance over the 20-year study period. An increasing temporal turnover rate in the future could be an indication of e.g. effects of species invasions or climate change.

As part of a broad theme issue 'Trophic rewilding: consequences for ecosystems under global change' on Philosophical Transactions of Royal Society B, Marjakangas et al. presented a new framework for prioritizing species and areas to inform species reintroduction. Trophic rewilding has been suggested as a restoration tool to restore ecological interactions and reverse defaunation and its cascading effects on ecosystem functioning. One of the ecological processes that is jeopardized by defaunation is animal-mediated seed dispersal. The authors proposed a

framework that combines joint species distribution models with occurrence data and species interaction records to quantify the potential to restore seed-dispersal interactions through rewilding and apply it to the Atlantic Forest, a global biodiversity hotspot. Using this approach, they identified areas that should benefit the most from trophic rewilding and candidate species that could contribute to cash the credit of seed-dispersal interactions in a given site. Sites within large fragments bearing a great diversity of trees may have about 20 times as many interactions to be cashed through rewilding as small fragments in regions where deforestation has been pervasive. Mammal and bird species were ranked according to their potential to restore seed-dispersal interactions if reintroduced while considering the biome as a whole and at finer scales. This prioritization framework can aid future conservation efforts in rewilding projects in defaunated tropical rainforests and can be used by stakeholders to support decision-making in conservation.

The "Transforming Citizen Science for Biodiversity" project (start autumn 2018) is part of a larger initiative on Digital Transformation at NTNU and is being lead by Bob O'Hara. The project is an interdisciplinary research programme that will develop tools and methods to improve the way that members of the general public collect data on what they observe in the natural world, and the way this data is used to inform us about the natural world and how it is changing. The amount of data being generated and uploaded to databases such as the

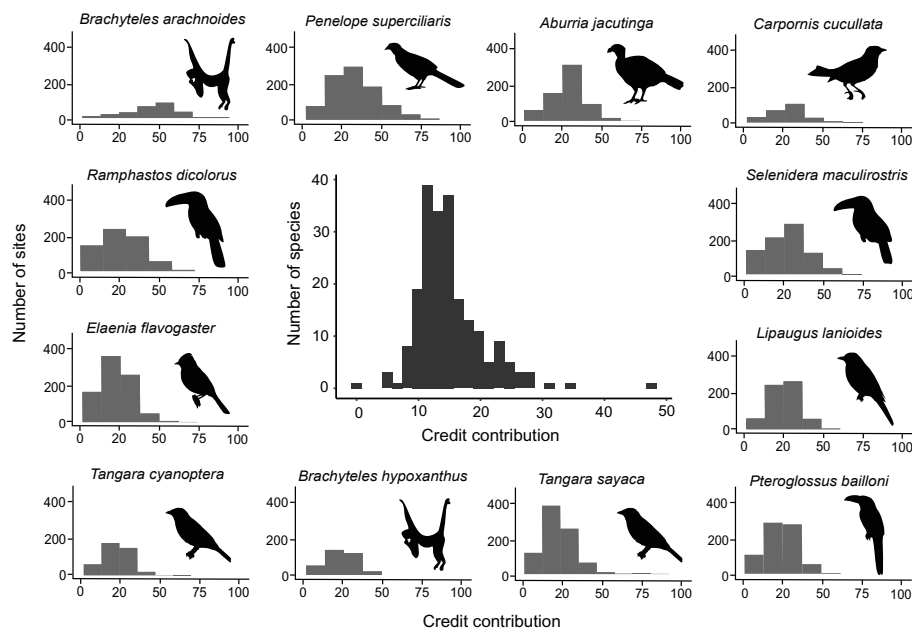


Figure 1. Distribution of the frugivore contributions to the credit of seed-dispersal interactions across prediction sites in the Atlantic Forest. The large histogram in the centre shows the distribution of the average credit contribution of each species considering all sites. Smaller histograms show the distributions of credit contribution for the 12 highest scoring species across prediction sites.

Norwegian Artsobservasjoner is massive, and this and the unsystematic way the data are collected provides challenges when making inferences from the data. This project will (1) encourage citizens to collect data, (2) help scientists correctly interpret and use this data, and (3) provide information back to the citizens about how the

data they have collected is being used. The project is a collaboration between four departments at NTNU and two organisations (NINA and Artsdatabanken) that are heavily involved in the collection and use of citizen science data. Five students will be employed to work on the following topics: (1) Tools for a Biodiversity Atlas: based at the Dept. of Mathematical Sciences / CBD, with collaboration from NBIC (2) Quality Control in Citizen Science data: based at the Dept. of Mathematical Sciences / CBD, with collaboration from NBIC (3) Transforming the Geography of Citizen Science: based at the Dept. of Geography with collaboration from NINA (4) Extending Digital Data collection in Citizen Science: based at the Dept. of Energy and Process Engineering, in collaboration with NINA (5) Transforming Ecology with Citizen Science: based at the Museum of Natural History / CBD, in collaboration with NINA.

RECOMMENDED READING:

- Marjakangas, E.-L., Genes, L., Pires, M.M., Fernandez, Fernando A S, de Lima, Renato A F, de Oliveira, Alexandre A, Ovaskainen, O., Pires, A.S., Prado, P.I. and Galetti, M. 2018. Estimating interaction credit for trophic rewilding in tropical forests. *Philosophical Transactions of the Royal Society of London B* 373, 20170435.
- Ovaskainen, O. and Saastamoinen, M. 2018. *Frontiers in Metapopulation Biology: The Legacy of Ilkka Hanski*. Annual Review of Ecology, Evolution, and Systematics 49, 231–252.
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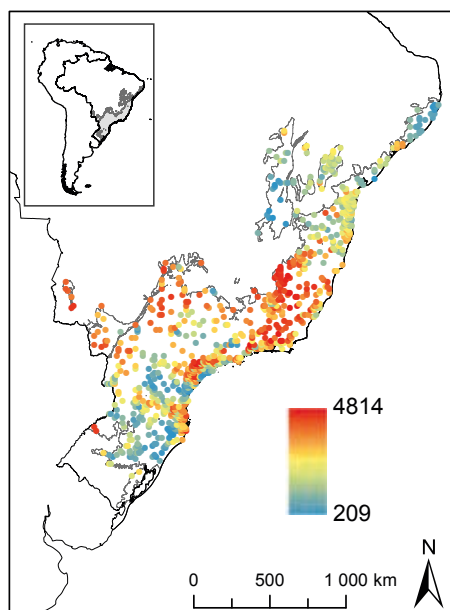


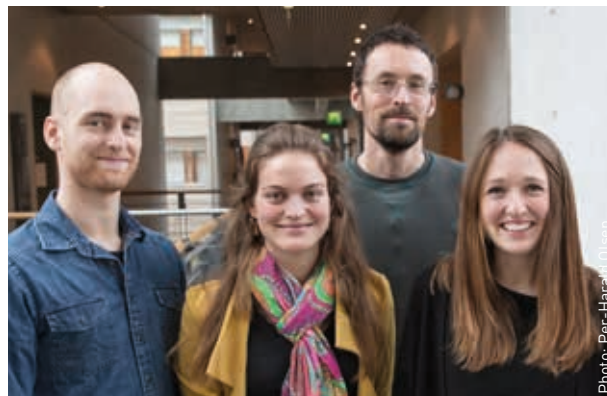
Figure 2. Spatial credit of ecological interactions to be cashed through rewilding across prediction sites in the Atlantic Forest. We calculated the interaction credit as the difference between a historical benchmark of species occurrences and their current predicted occurrences. The number of interactions expected to be restored by rewilding is depicted by a color gradient. The warmest colors represent credit hotspots, whereas the coldest colors represent sites where there are fewer seed-dispersal interactions to be restored through reintroductions.

RESEARCH GROUP: DYNAMICS OF ARCTIC ECOSYSTEMS

Current group members:

PI: Researcher Brage Bremset Hansen
 PhD candidate Mathilde Le Moullec
 PhD candidate Bart Peeters
 PhD candidate Kate Layton-Matthews

Aim: *To apply demographic modelling and multi-species stochastic approaches to understand how climate change influences spatiotemporal community dynamics, through direct as well as indirect effects (i.e. trophic interactions).*



Bart Peeters, Mathilde Le Moullec, Brage Bremset Hansen, Kate L. Matthews,

Our current main project INSYNCR (Research Council Norway, 2018-21) aims to use novel field-experimental approaches and time-series analyses to explore how climate drivers of key ecosystem components shape spatiotemporal dynamics of the entire tundra community in Svalbard. Collaborators include Univ. Aberdeen (UK), Univ. Groningen (NL), Univ. Iceland, CNRS Montpellier (FR), Norwegian Meteorological Institute, and Univ. Centre Svalbard.



Field experiment garden in Svalbard.



Photo: Brage B. Hansen

MAJOR SCIENTIFIC CONTRIBUTIONS

2018 was characterized by intensive field work activity and the establishment of a new field experiment, where we investigate how the tundra vegetation responds to extreme warm spells and rain-on-snow events in winter. In a cross-disciplinary paper by Peeters et al. (2018), published in *Environmental Research Letters*, we show how a rapidly warming winter climate in Svalbard has led to a sudden regime shift in precipitation patterns (i.e. more winter rain) and snow-pack properties (i.e. more frequent icing). We are now investigating implications for the spatiotemporal dynamics of key herbivore food plants, both through experiments and time-series analysis. In Le Moullec et al. (2018) in *Journal of Ecology* we demonstrate the great potential of 'tree-rings' in tiny dwarf shrubs as tool for such investigations.

In a paper by Hansen, Gamelon et al. in *Nature Communications* (in press), we find that observed responses to single extreme climate events in long-lived species, such as reindeer, may be poor predictors of long-term population dynamics and persistence. Using empirically parameterized, stochastic population models for wild Svalbard reindeer, the study shows that more frequent extreme rain-on-snow events actually reduce extinction risk and stabilize the population dynamics due to interactions with age structure and density dependence. Thus, internal density-dependent feedbacks act as a buffer against more frequent events, dampening the population fluctuations. In INSYNCR we are now exploring how these rather unexpected changes in population variability of such a key species may cascade through the tundra food-web and, thereby, alter the properties of community-level dynamics in time and space.

RECOMMENDED READING:

- Peeters, B., Pedersen, Å.Ø., Loe, L.E., Isaksen, K., Veiberg, V., Stien, A., Kohler, J., Gallet, J.-C., Aanes, R. and Hansen, B.B. 2018. Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. *Environmental Research Letters*, in press.
- Le Moullec, M., Buchwal, A., van der Wal, R., Sandal, L. and Hansen, B.B. 2018. Annual ring growth of a widespread high-arctic shrub reflects past fluctuations in community-level plant biomass. *Journal of Ecology*, in press.

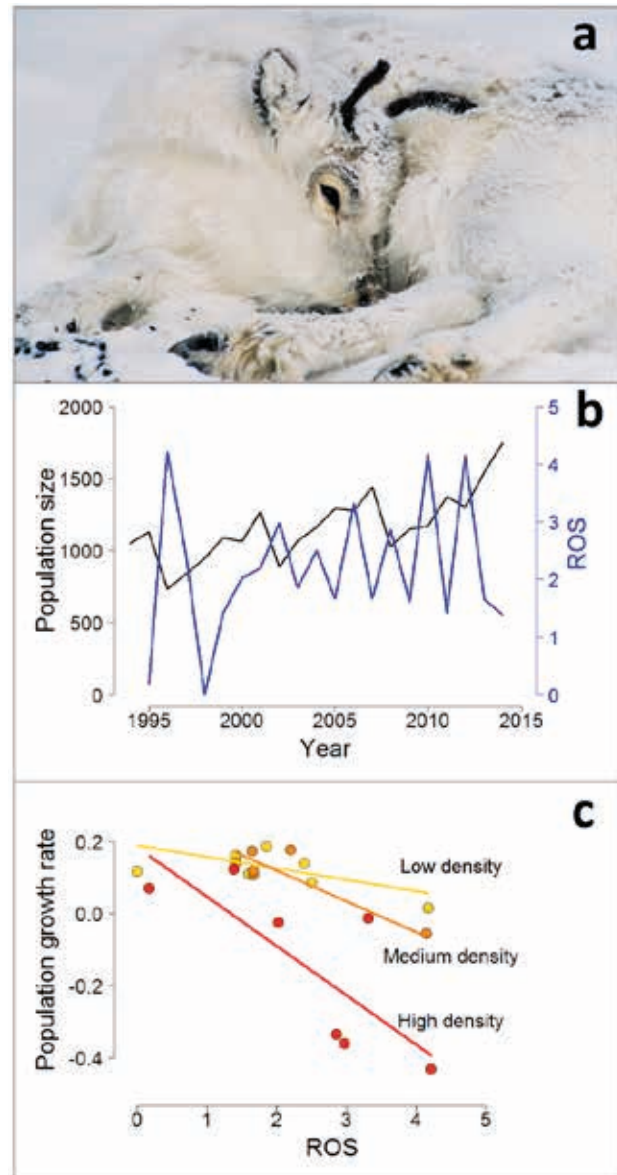


Figure 1. Density-dependent and age-specific effects of rain-on-snow (ROS) and ice-locked tundra shape the population dynamics of wild reindeer in Svalbard. As illustrated by this newly dead calf, icing may cause starvation and dramatic die-offs in vulnerable age classes, but only occasionally, because of internal density-dependent regulation. Figure from Hansen et al. (in press, *Nature Communications*).

- Hansen, B.B., Gamelon, M., Albon, S.D., Lee, A.M., Stien, A., Irvine, R.J., Sæther, B.-E., Loe, L.E., Ropstad, E., Veiberg, V. and Grøtan, V. (2018) More frequent extreme climate events stabilize reindeer population dynamics. *Nature Communications*, in press.

RESEARCH GROUP: DYNAMICS OF INTERACTING SPECIES

Current group members:

PI: Researcher Aline Magdalena Lee

PhD candidate Jonatan Fredricson Marquez

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

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.



Jonatan Fredricson Marquez, Aline Magdalena Lee

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. The extent to which the environment can synchronize population fluctuations depends on intrinsic characteristics of the populations, such as dispersal rate and distance, and strength of density regulation. However, an important factor that is often overlooked in this context is that species do not live in isolation. Most studies have focused on populations of single species,

and we lack knowledge of how species interactions and dispersal together influence responses to environmental fluctuations. We have therefore developed a new analytical model for understanding patterns of covariation in space between interacting species.

Using this model we are investigating how different factors influence the spatial covariation of competing species in fluctuating environments. Currently, we are focusing on effects of dispersal, strength of competition, and the differences or similarities between species in how they experience and respond to environmental fluctuations. We have shown that the spatial correlation between two competing species depends on all these factors. We have also found that the distance at which population synchrony of a single species goes to zero is closely connected to the distance at which the correlation between two competing species goes to zero.

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. We have been studying the relationship between spatial scaling in population dynamics and the slow-fast continuum of life history, where species are ranked from slow species with long generation times, high adult survival and low reproduction to fast species with short generation times, low survival and high reproduction. Our results so far show that population dynamics of species with slow life histories are synchronized over greater distances than those of species with fast life histories. Finding general patterns of this type in the covariation of ecological processes can help in the development of broad conservation and harvesting strategies.

RECOMMENDED READING:

Engen, S., Lee, A.M. and Sæther, B.-E. 2018. Spatial distribution and optimal harvesting of an age-structured population in a fluctuating environment. *Mathematical Biosciences* 296, 36–44.

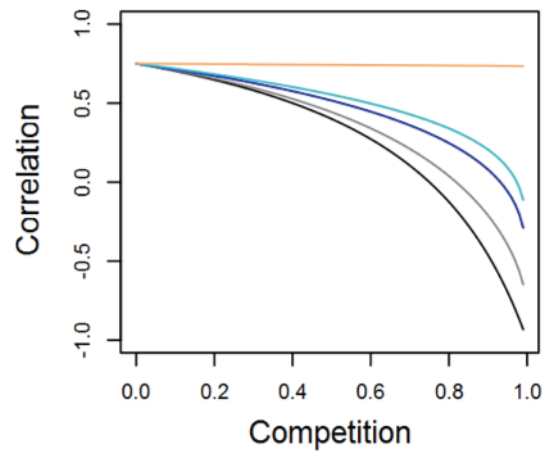


Figure 1. Correlation between the density of two competing species at a single point within the spatial field studied as a function of the strength of competition between them and with different rates of dispersal of spatial movement from black (no movement) to orange (continuous movement).

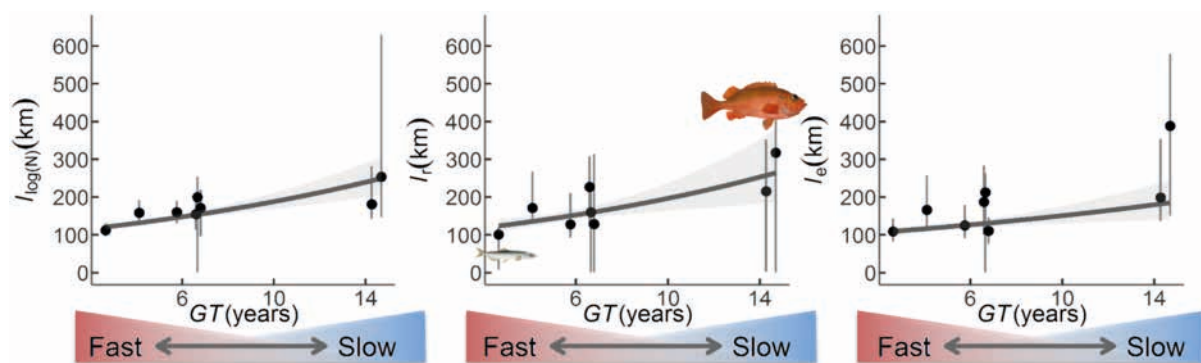


Figure 2. Relationship between generation time (GT) and spatial scaling in abundance (a), growth rate (b) and environmental noise (c) for eight species of fish in the Barents sea.

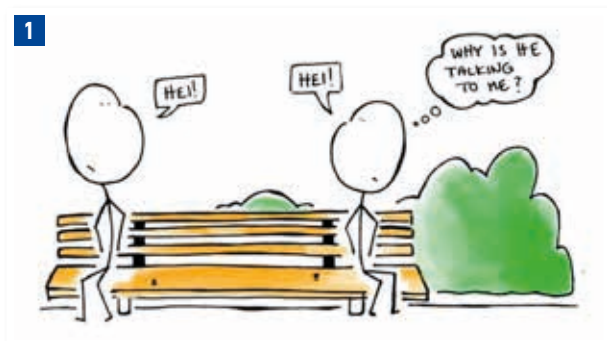
NEW IN TRONDHEIM

Hannah Froy and Christophe Coste, March 2019

A FRENCH AND A BRITISH POSTDOC JOIN THE CBD FAMILY

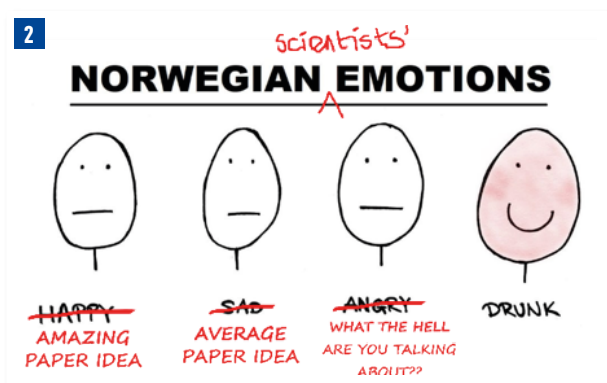
Oui arrived in Trondheim at the tail end of the summer. Just in time to see the sun, one last time, before it disappeared below the horizon for four months. During this summer's swan song, we discovered the "vakker natur" of Trøndelag, its soaring mountains, cascading waterfalls, mirror-like lakes, never-ending fjords, and bountiful foraging opportunities for delicious mushrooms and berries galore.

It took us much longer to comprehend fully the complex behavioural ecology of Norwegian society, both within and outside of CBD. Do not invade others' personal space (Fig. 1). Avoid small talk at all costs (hard to achieve for some of us south Europeans).



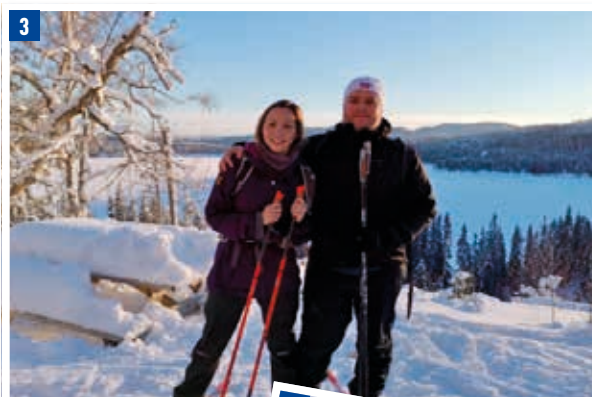
From "The Social Guidebook to Norway", Julien S. Bourrelle

Do not over-interpret your colleagues' reactions, facial expressions or body language (Fig. 2). Try and adapt to a shifted circadian rhythm: wake up at 6 – training – coffee – breakfast – CBD – coffee – CBD – coffee – lunch at 11.00 – coffee – CBD – coffee – leave work at 15.00 – training – dinner at 16.30 – coffee – training – coffee – training – shower – øl → fun times – bed.



Modified from "The Social Guidebook to Norway", Julien S. Bourrelle

Fortunately, as early as mid-November, Trondheim puts on its Juletid attire. Christmas trees, twinkly lights, pinnekjøtt, choir music... a koselig, hyggelig feeling all around. It is so sweet you forget that the days are, by now, only four hours long. But the sweetest of all blessings is on its way: four feet of snow blanketing the streets, the cathedral, the forest and the marka. With the snow comes the opportunity to bask in the favourite Norwegian pastime: cross-country skiing. A pair of skis, a pair of poles, a little "butter" under your soles and off you go. It is so much fun (Fig. 3), even though the first few downhill are a little bit hair-raising (Fig. 4).



CBD is a place of fusion. Biologists and mathematicians come together to work at the interface of population ecology, evolutionary biology and community dynamics in a unified scientific language. This is in stark contrast with the diversity of tongues spoken at the centre – even among Norwegians; there are many different dialects, in addition to two distinct written languages. Aline speaks Nynorsk, Vidar speaks Bokmål, Bernt-Erik speaks Trøndersk, Christophe (the elder) speaks Franglish, and Steinar speaks old-Norse. 'ow the 'ell are we supposed to hexpand the 'orizons of hecology in this tower of babel?

WORKSHOPS AND CONFERENCES 2018

NORDIC OIKOS CONFERENCE



The Nordic Oikos conference was held in February 2018 in Trondheim, Norway. The conference was organized by Gunilla Rosenqvist, Irja Ratikainen, Thomas Kvalnes and Stefan Vriend (CBD) in collaboration with Norwegian Institute for Nature Research with financial support from Nordic Society Oikos and the Norwegian Research Council.

The Nordic Oikos conference is a bi-annual congress that has been held since 2014. It is a meeting point for all Nordic ecologists and evolutionary biologists. Every other year the congress is hosted in a different Nordic country. The theme of the Nordic Oikos conference in 2018 was "The importance of ecological science in society", with a solid focus on the need for fundamental ecological science.

The conference was a big success with 300 participants from 20 countries, one third of the participants were students. Four scientifically outstanding keynote lecturers, Georgina Mace (University College London), William Sutherland (Cambridge University), Trine

Bilde (Aarhus University) and David Wardle (Nanyang Technological University) framed the conference with inspiring and thought provoking lectures. The main aim of the conference is to increase communication between Nordic ecologists. This was achieved through parallel sessions with talks as well as poster sessions and various social settings with a friendly atmosphere to allow for plenty of discussions and development of new networks. There were more than 70 contributed talks and 130 posters on a wide variety of topics. In addition, there were several pre-conference workshops on topics ranging from early career development to the Per Brinck symposium on "Coupling Ecology".

To consider gender equality at large events like Oikos 2018 is of great importance, both because of the career promoting effects for the participants but also because participants to the conference will serve as role models for the more junior scientists participating. The conference fulfilled the goal by the fact that among the people presenting at the conference were 50 % females, and both the organising committee and keynote speakers were 50:50 females/males.



Photo:



UNIS-CBD SEMINAR IN SVALBARD, MAY 2018



In connection with the annual CBD-SAC meeting in Longyearbyen in early May 2018, a two-day seminar/workshop was co-organized by UNIS (Øystein Varpe) and CBD (Brage B. Hansen). The main aim was to explore further scientific and educational collaboration between the two institutions.

Part one of this event was an open scientific seminar where delegates from both UNIS and CBD presented their view on the challenges and opportunities for biological research in the Arctic, with particular emphasis on climate change issues. This included talks by Varpe (UNIS), Sæther, Visser, Gaillard, and Fryxell, and a plenary discussion. About 60 people attended the seminar.





On day two of this cross-institutional get-together, an educational workshop was arranged. The SAC and leader group met delegates from UNIS (P.E. Eidesen, Ø. Varpe) to learn about the Centre of Excellence in Biology Education and, in particular, UNIS' experience with research-based teaching.

Finally, the SAC and leader group spent a day in the field, visiting a vegetation experiment site in Adventdalen (collaboration project between CBD and UNIS) as well as one of our reindeer study areas (Colesdalen).

PHD STUDENT WORKSHOP AT SAN JOSÉ UNIVERSITY IN COSTA RICA

In December 2018, post-doc Dr Yimen Araya-Ajoy and Prof Jonathan Wright organised and taught at a PhD student workshop about 'SEM & Path Analysis' at San José University in Costa Rica. Around 20 PhD students from San Jose and other universities attended, plus post-docs and staff members. Using interactive educational techniques they were taught the basics of these statistical methods along with research discussions concerning the application of these statistical methods in 'Allometric relationships and evolvability in house sparrows' and 'Theoretical approaches to social evolution'. Prof. David Westneat (University of Kentucky, USA) and Prof. Niels Dingemanse (LMU, German) also provided seminar discussions on additional applications to 'The analyses of individual life histories' and 'The quantitative genetics in behavioural syndromes'.

This workshop builds upon a similar sized PhD student workshop Dr Yimen Araya-Ajoy and Prof Jonathan Wright organised and taught at San José University in December 2017 concerning 'The hierarchical nature of evolution in natural populations: a mixed model approach'. It also extends contributions by Dr Yimen Araya-Ajoy and Prof Jonathan Wright to the long-standing Life History Theory PhD course run by University of Gröningen, NL



Yimen Araya-Ajoy

on Schiermonnikoog in March 2018, where they led a number of interactive teaching sessions on topics such as 'Life History Evolution in a Changing World' and 'The hierarchical nature of life histories: a mixed model approach'.

SYMPOSIA ORGANIZED BY MEMBERS OF CBD AT THE II JOINT CONGRESS ON EVOLUTIONARY BIOLOGY – MONTPELLIER 2018

About the conference:

The joint congress on evolutionary biology takes place every six years and brings together four of the world's largest academic societies in the field of evolutionary biology: the European Society for Evolutionary Biology, the American Society of Naturalists, the Society for the Study of Evolution, and the Society of Systematic Biologists. The first joint congress was in Ottawa, Canada in 2012. The second was held in Montpellier, France, on August 19-22 2018 and was organized by Ophelie Ronce and Yannis Michalakis. Ophelie is a member of the SAC of CBD.

The first symposium on **Evolutionary Rescue** was coorganized by: Richard Gomulkiewicz, Ruth Hufbauer, Ane Marlene Myhre (CBD) and Joost Raeymaekers (CBD)

Extinction—evolution's ultimate limit—is a pressing concern in this era of global change. Evolutionary rescue is adaptation to unfavourable changes in the environment that decrease population growth rate, preventing imminent extinction. Considerable research on evolutionary rescue has greatly advanced our understanding of the conditions under which adaptive evolution can prevent extinction. Our symposium brought together scientists from around the world behind some of the most exciting empirical and theoretical advances emerging in this field. These advances include empirical evidence from wild populations, understanding the roles of non-adaptive evolutionary processes and the roles



The group from their symposium

played by genome structure and genetic interactions, as well as elucidating how adaptive evolution can affect the course of decline when a population fails to avoid extinction.

The symposium opened with Graham Bell's excellent talk introducing the topic and summarizing the "state of the art" and our invited speaker Stephanie Carlson closed the symposium with an open-ended discussion of the role and evidence for evolutionary rescue in wild populations. In total the symposium consisted of seven speakers and three posters

Bell, G. – Evolutionary Rescue; **Rescan, M.** – Genetic variation alters the impact of environmental auto-correlation on extinction risk in an experimental system; **Ono, J.** – Adaptation to high concentrations of drug depends on ploidy in yeast; **Petkovic, N.** – The effect of sex on the extinction dynamics and evolutionary rescue of *Chlamydomonas reinhardtii* experimental populations depends on the rate of environmental change; **Holt, R.** – Temporal variation, dispersal, and the scope for evolutionary rescue; **Vinton, A.C.** – Evolutionary rescue amidst environmental stress depends on the life-history traits under selection; **Carlson, S.** – Evolutionary rescue in nature - case closed or jury still out?

The second symposium on **Evolvability, a unifying concept in evolutionary biology**, was co-organized by C. Pelabon (CBD, NTNU) and T.F. Hansen (UiO):

The aim of this symposium was to present the different concepts and definitions of evolvability and bring together researchers from different fields to present their research on evolvability and work on a unifying understanding of evolvability. In the short term, evolvability is a function of 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. Although these different notions of evolvability generate some misunderstandings and confusion, the interest of different fields in the same topic marks it as a "trading



The two organizers of the conference, Yannis Michalakis and Ophelie Ronce.

zone" where researchers can exchange ideas and develop a common language. The symposium consisted of eight oral communications and nine posters.

Pavlicev M. – How well can we predict the trait's selection response from the GP map? ; **Rolian C.** – (How) does evolvability evolve? Insights from the Longshanks mouse selection experiment; **Sztepanacz J.** – Cross-sex genetic covariances limit the evolvability of complex traits; **Payne J.** – A comparative analysis of empirical genotype-phenotype maps; **Nuño De La Rosa L.** – Populational models of developmental evolvability: towards an integrated theory of evolution; **Ares S.** – Nitrogen-fixing cyanobacteria optimize evolvability; **Staedler Y.** – Understanding the evolvability of flowers: a grand perspective of floral shape modularity; **Houle D.** – A dictionary of genetic effects as a predictor of mutational evolvability.

WORKSHOP - GENDER BIAS AT THE IBI DEPARTMENT

Two members of CBD, Gunilla Rosenqvist and Aline M. Lee, are members of a new Equal Opportunities Committee at IBI. In 2018 the committee has surveyed attitudes and experiences of gender bias at the department and organized a two-day workshop for employees to discuss improvements. The workshop brought in international experts to teach us about important issues such as implicit bias. CBD was well represented at this workshop. The committee has also worked on guidelines for avoiding implicit bias in the hiring process at the department. The committee members received NTNU's Equality and Diversity Award for their work in these matters.



NATIONAL AND INTERNATIONAL COLLABORATION

Researchers at CBD had extensive national and international collaborations again in 2018. Within Norway especially tight ties have been to the Centre for Ecological and Evolutionary Synthesis (CEES) at the University of Oslo. This collaboration has been focused around the large integrated project SUSTAIN lead by professor N. C. Stenseth at CEES, where CBD and UiT The Arctic University of Norway are the two other principal nodes. In addition, researchers at the two centres have collaborated on analyses of ecological and evolutionary consequences of climate and about development of models for describing evolutionary dynamics. Stenseth also holds a position (20 %) as International Chair at CBD.

CBD has also interacted with several other research institutions in Norway, including UNIS The University Centre in Svalbard, UiT The Arctic University of Norway, Nord University, Innland University of Applied Sciences and the Norwegian University of Life Sciences. In addition to the Norwegian Institute for Nature research (NINA), which is a partner of CBD, extensive research collaborations also occurred with other applied Norwegian research institutes, such as the Norwegian Institute of Bioeconomy Research (NIBIO), Norwegian Polar Institute, Norwegian Computing Centre, Institute of Marine Research, Norwegian Institute for Water Research (NIVA), NORUT Northern Research Institute and Norwegian Meteorological Institute.

In 2018, CBD collaborated with researchers located in almost all parts of the world. In particular, there were close interactions with researchers at University of Helsinki, Finland, and Uppsala University, Sweden. This was facilitated by Otso Ovaskainen (40 % until May 31 and then 20 %) and Arild Husby (20 %) having affiliations at CBD as Professor and Associate Professor, respectively.

In 2018, considerable effort by several members of CBD was put into building up and structuring a data-base of long-term individual-based studies of hole-nesting birds in Europe. This work has involved close interactions with more than 20 research groups across Europe and especially to the Netherlands Institute of Ecology (NIOO-KNAW) in Wageningen, the Netherlands. As part of this endeavor, the Director has participated in a network of researchers performing meta-analyses of climate influences on demography and population dynamics funded by the German Centre for Integrative Biodiversity Research (iDiv), which was led by dr. Viktoriia Radchuk, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany and professor Marcel E. Visser, NIOO-KNAW,

POPULAR SCIENCE

An important component of the outreach of CBD was its involvement in NTNU's strategic area "Sustainability", where the centre was one of the major research groups included in the focus area "Biological diversity and ecosystem services". As part of this, CBD participated in organizing the workshop "*Biodiversity – from knowledge to policy?*", which was well attended both by researchers, students and environmental managers. Here both the IPBES Chair Sir Robert Watson and the Director of CBD gave talks. The engagement in "Sustainability" has also provided CBD with a platform for regular interactions with the Norwegian Environment Agency.

A source for interactions with 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. For example, in 2018 senior researcher Erling J. Solberg gave 11 oral presentations related to management of moose. In total, researchers at CBD gave more than 85 talks for a wide variety of audiences, ranging from plenary lectures at large conferences to small numbers of people involved in practical problems related to managing biodiversity.

In 2018, CBD published a number of popular science writings (14), ranging from descriptions of interesting research to chronicles in national newspapers about questions related to science policies at the national level.

LIST OF CBD LECTURERS 2018

- Professor Dieter Ebert, Basel University, Switzerland
- Professor Jane Margaret Reid, University of Aberdeen, Scotland
- Professor Sean R Connolly, ARC Centre of Excellence for Coral Reef Studies, James Cook University Townsville, Australia

DISSERTATIONS

Two PhD candidates defended their thesis at CBD in 2018:

August 31st	Stine Svalheim Markussen: " <i>Causes and consequences of intersexual life history variation in a harvested herbivore population</i> "
Opponents:	Professor Fanie Pelletier, University of Sherbrooke, Quebec, Canada Ass. Professor Sandra Hamel, University of Tromsø, Norway
December 7th	Erlend Ignacio Fleck Fossen: " <i>Trait evaluability: effects of thermal plasticity and genetic correlations among traits</i> "
Opponents:	Professor Claus Wedekind, University of Lausanne, Switzerland Ass. Professor Yngvild Vindenes, University of Oslo, Norway

KEY FIGURES 2018

GENDER EQUALITY

In 2018 CBD had two female professors, Gunilla Rosenqvist (IBI) and Ingelin Steinsland (IME) and one female associate professor, Irja Ida Ratikainen (IBI). 22% of the researchers were female.

The core of CBD is still strongly male biased.

At the end of 2018, 53% of the PhD candidates and 38 % of the postdocs were female.

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

We are very pleased that in 2018 we have managed to recruit a female senior professor at CBD. She will begin in October 2019.

KEY FIGURES

Key numbers in CBD	2018
Senior Researchers	24
Postdocs	8
PhD candidates	26
Adm.tech staff	5
All staff at CBD	63
Scientific Advisory Board	6
Costs and funding	in thousand
Operational costs CBD	29 306
Funding	
NINA	750
NFR	9 385
NTNU	19 171
Operational costs Associated projects	7 650

CBD MEMBERS

PhD CANDIDATES



Anne Catriona Mehloop
PhD candidate NINA



Astrid Raunsgard
PhD candidate NINA



Bart Peeters
PhD candidate CBD



Bert van der Veen
PhD candidate NIBIO



Christoffer Høyvik Hilde
PhD candidate CBD



Dilan Saatlogu
PhD candidate IBI



Elena Albertsen
PhD candidate CBD



Emma-Liina Marjakangas
PhD candidate IBI



Endre Grüner Ofstad
PhD candidate CBD



Erlend Fossen
PhD candidate IBI



Jonatan Fredricson Marquez
PhD candidate CBD



Kate Layton-Matthews
PhD candidate IBI



Lara Veylit
PhD candidate CBD



Lars Rød-Eriksen
PhD candidate NINA



Lasse Frost Eriksen
PhD candidate NINA



Lisa Sandal
PhD candidate CBD



Maria Lie Selle
PhD candidate IME



Mathilde Le Moullec
PhD candidate IBI



Mette Finnøen
PhD candidate IBI



Michael Pepke Pedersen
PhD candidate CBD



Peter Sjolte Ranke
PhD candidate CBD



Sam Perrin
PhD candidate VM



Sarah Lundregan
PhD candidate IBI



Semona Issa
PhD candidate IBI



Sindre Sommerli
PhD candidate CBD



Stefan Vriend
PhD candidate CBD



Stine Svalheim Markussen
PhD candidate IBI



Tanja Kofod Pedersen
PhD candidate VM



Thomas Haaland
PhD candidate IBI



Vanessa Bieker
PhD candidate VM



Wouter Koch
PhD candidate Norwegian Biodiversity Information Centre



Yihan Cao
PhD candidate IME

POSTDOCS



Ane Marlene Myhre
Postdoc IBI/CBD



Christophe Coste
Postdoc CBD



Emily G. Simmonds
Postdoc IME



Hannah Froy
Postdoc CBD



Thomas Kvalnes
Postdoc CBD



Yimen Araya-Ajoy
Postdoc CBD



Øystein Hjorthol Opedal
Postdoc IBI

TECHNICAL STAFF



Bernt Rønning
Sr. Engineer CBD



Hanna-Kaisa Lakka
Engineer CBD



Henrik Pärn
Sr. Engineer CBD

RESEARCHERS



Alina Niskanen
Guest researcher



Aline Magdalena Lee
Researcher
CBD



Brage Bremseth Hansen
Researcher CBD



Brett Sandercock
Senior Research Scientist
NINA



Erlend Birkeland Nilsen
Senior Research Scientist
NINA



Erling Johan Solberg
Senior Research Scientist
NINA



Geir Hysing Bolstad
Researcher II
NINA



Hanno Sandvik
Researcher
NINA



Håkon Holand
Researcher CBD



Ingerid Julie Hagen
Researcher II NINA



Ivar Herfindal
Researcher CBD



Knut Anders Hovstad
Researcher NIBIO



Marlène Gamelon
Researcher
CBD



Martin Lind
Guest researcher



Ola Diserud
Senior Research Scientist
NINA



Tim Burton
Researcher IBI



Vebjørn Veiberg
Senior Research Scientist
NINA



Øystein Nordeide Kielland
Researcher VM



Hannu Mäkinen
Researcher CBD



CENTRE FOR BIODIVERSITY DYNAMICS

PROFESSORS / ASSOCIATE PROFESSORS



Anders Gravbrøt Finstad
Professor VM



Arild Husby
Ass. Professor (20%)
CBD



Bernt-Erik Sæther
Professor
CBD



Bob O'Hara
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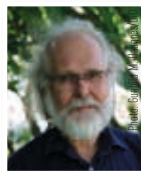
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PUBLICATION LIST

- Abarenkov, K., Somervuo, P., Nilsson, R.H., Kirk, P.M., Huotari, T., Abrego, N. and Ovaskainen, O. 2018. Protax-fungi: a web-based tool for probabilistic taxonomic placement of fungal internal transcribed spacer sequences. *New Phytologist* 220, 517–525.
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