cbd
CENTRE FOR BIODIVERSITY DYNAMICS

Annual Report 2015

Norwegian
Centre of
Excellence

NTNU – Trondheim
Norwegian University of
Science and Technology

CBD IN SHORT

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

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

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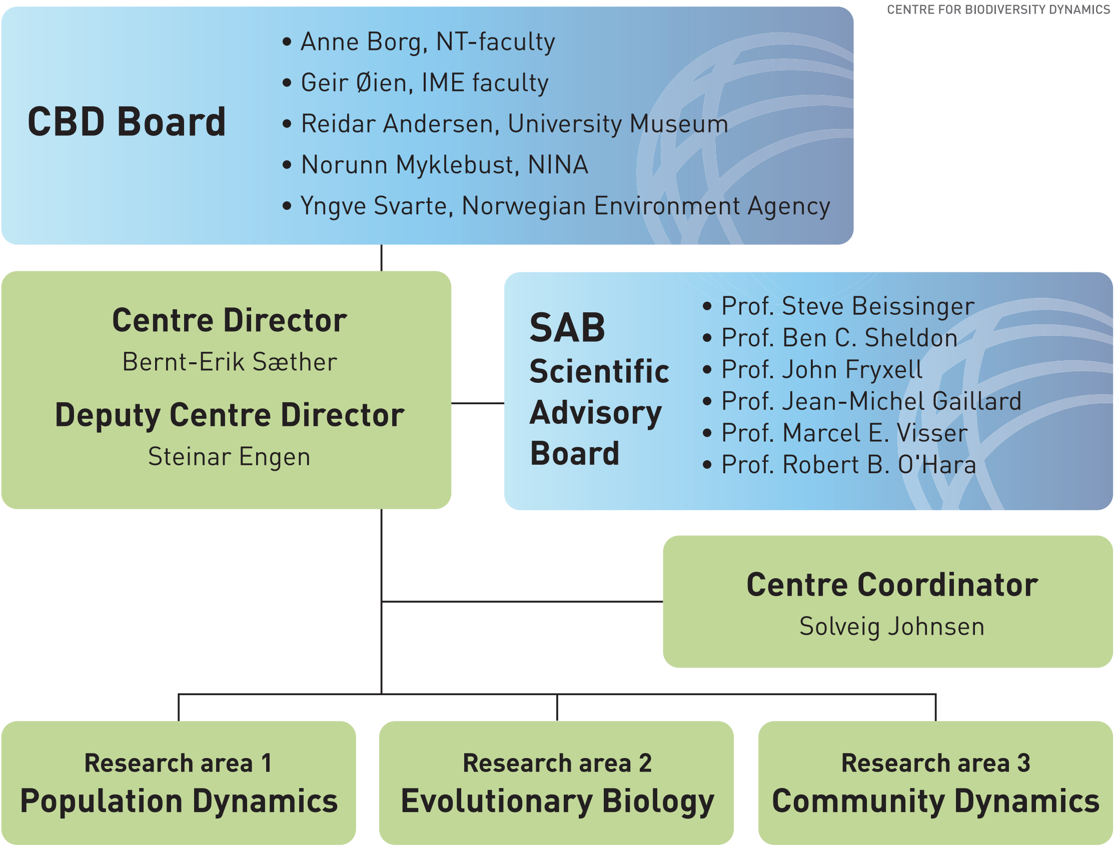
1. MANAGEMENT AND ADMINISTRATION

MANAGEMENT STRUCTURE

CBD is organized as a separate research centre analogue to a department with Faculty of Natural Science, NTNU, as host faculty. CBD involves collaborations between two partners: NTNU and the Norwegian Institute for Nature Research (NINA). Management of the centre is run by the Centre Director (Sæther) together with the Deputy Centre Director (Engen) and the Centre Coordinator (Johnsen). The organizational structure of the centre is flat. The operational unit of CBD is the research groups belonging to CBD's core members, who are researchers with faculty positions at NTNU or positions as senior researchers at NINA. A Steering board including members from each of the involved faculties at NTNU (including the Museum), NINA and the Norwegian Environment Agency oversees that activity at CBD is operated according to the project description funded by the Research Council of Norway. A central task for the Steering board is also to promote the collaboration among the different departments and to integrate in CBD relevant research at NINA that can be important for achieving the scientific goal of CBD. The Scientific Advisory Board, consisting of 6 internationally leading scientists, contributes to develop a strategy for the scientific development of the centre, facilitating the leadership to achieve the scientific aims. SAB - is also heavily involved in implementing appropriate means of actions to fulfil the strategy plan and act as external advisors for the management of CBD.



CBD Board
- Anne Borg, NT-faculty
- Geir Øien, IME faculty
- Reidar Andersen, University Museum
- Norunn Myklebust, NINA
- Yngve Svarte, Norwegian Environment Agency

Centre Director
Bernt-Erik Sæther

Deputy Centre Director
Steinar Engen

SAB Scientific Advisory Board
- Prof. Steve Beissinger
- Prof. Ben C. Sheldon
- Prof. John Fryxell
- Prof. Jean-Michel Gaillard
- Prof. Marcel E. Visser
- Prof. Robert B. O'Hara

Centre Coordinator
Solveig Johnsen

Research area 1
Population Dynamics

Research area 2
Evolutionary Biology

Research area 3
Community Dynamics

CBD Board

CBD Board from the left, Geir Øien, Dean of faculty of IME, NTNU, leader of the Board Anne Borg, Dean of Faculty of Natural Sciences and Technology, NTNU, Reidar Andersen, Director of NTNU University Museum, Norunn Myklebust Managing Director of the Norwegian Institute for Nature Research (NINA). Inserted: Yngve Svarte, Deputy Director, Norwegian Environment Agency.

CBD Scientific Advisory Board

CBD Scientific Advisory Board. From the left: Prof Robert O'Hara, Biodiversity and Climate Research Centre, Frankfurt, Germany, Prof. John Fryxell, Univeristy of Guelph, Canada, Prof. Jean-Michel Gaillard, CNRS Lyon, France, Prof. Marcel Visser, Netherlands Institute of Ecology (NIOO-KNAW), The Netherlands, Prof. and Director of CBD Bernt-Erik Sæther, Dept of Biology, NTNU, Prof. Ben Sheldon, University of Oxford, UK, and Prof. Steve Beissinger, University of California, Berkely, USA (Chairman of SAB).

ADDRESS FROM THE CHAIR

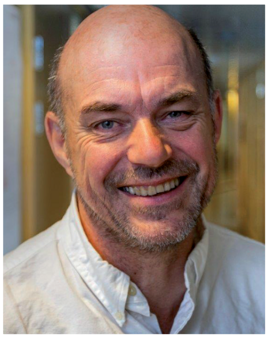
Centre of Biodiversity Dynamics (CBD), hosted by Faculty of Natural Sciences and Technology at NTNU, brings together outstanding researchers in ecology and evolutionary biology and in biomathematics and statistics to answer fundamental questions on, as its name reflects, dynamics of the biodiversity in our natural environment. CBD is a major contributor to NTNUs strategic area "Sustainability" and at the heart of the university vision "Knowledge for a better world".

In 2015 CBD has operated as a well-established centre of excellence. Main contributors to the centre are researchers at Department of Biology, Department of Mathematical Sciences, NTNU University Museum and Norwegian institute for nature research (NINA). Additional projects have been added to the portfolio this year, further expanding the research activities at the centre. 2015 has been scientifically highly rewarding, with a number of research highlights meeting the ambitious goals set by the centre. We expect that these scientific results in the coming years will serve as foundation for the management of habitats in general and for vulnerable species in particular in a world with an increasing human population and a rapidly changing climate.

The progress of this research environment is of great inspiration to our students and scientific personnel. The board is looking forward to further excellent scientific achievements by the centre extending the understanding of dynamic factors affecting biodiversity, which may guide sustainable nature management.

Anne Borg
Dean,
Faculty of Natural Sciences and Technology
Chair Board

DIRECTOR'S COMMENTS



Bernt-Erik Sæther
Director CBD

After an establishment phase, 2015 can be considered as the first ordinary running year of CBD. As in the initial 1.5 year of the centre, the weekly lunch seminars are crucial for initiating and maintaining cross-disciplinary research collaboration. The operational running of the research on a daily basis mainly occurs in research groups, organized around the more senior scientists at CBD. The extensive international collaboration at CBD was also continued by the organization of four international workshops, frequent visits of international researchers and extensive co-authoring of papers with research collaborators outside Norway.

The project "Sustainable management of renewable resources in a changing environment: an integrated approach across ecosystems" (SUSTAIN) was initiated in 2015. This is a large integrated project funded by the Research Council of Norway, which is lead by professor Nils Christian Stenseth, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo. The aim of this project is to use an ecosystem perspective to develop sustainable harvesting strategies that can mediate the effects of the expected changes in climate on the dynamics of exploited species. CBD is together with CEES and University of Tromsø (under the leadership of Professor Rolf Anker Ims) one of three national nodes in this project, which also include collaborations with several Norwegian applied research institutes. CBD will have particular responsibility for the boreal forest ecosystem and in developing harvest models.

Although significant progress happened within all of the three major Research Areas (RA) at the centre, the largest advances occurred in 2015 in RA 2. A major research goal for this RA is to provide a conceptual framework to analyze evolutionary processes in fluctuating environments. In 2015 three significant advances were made at the centre on the way towards this overall goal of RA2: *The first advance* was the development of a new model for phenotypic evolution in an environment that varies stochastically over time provided by Jarle Tufto in a paper published in the journal *Evolution*. A characteristic of an individual such as body mass or clutch size subject to selection may have a genetic component but its expression may also be strongly influenced by the environment the individual encounters, especially during its early stages of life. So far, the effects of such phenotypic plasticity on the rate of evolution have been poorly understood. The modelling approach of Tufto enables us to include traditional Darwinian genetic evolution, phenotypic plasticity expressed by how fast the character responds to a change in an environmental variable and, finally, evolution of the variance among phenotypes (bet hedging) into a common theoretical framework. An important conclusion from this modelling exercise is that plasticity often is the dominant response to changes in the environment. Another advantage of this model is that several of the parameters can be estimated from data that can be collected in natural populations. Together with Luis-Miguel Chevin and Marcel E. Visser, Tufto showed (in a paper published in *Evolution*) using a long-term data set of the timing of egg-laying in Dutch great tits that there could be temporal autocorrelations in the selection as well as considerable phenotypic plasticity in fitness-related traits.

The second major advance in our understanding of evolution in a fluctuating environment (RA2) was provided by Jonathan Wright and collaborators in a paper published in the *Proceedings of the National Academy of Sciences of the United States of America*. They used extensive simulation studies to show how predictability and the time scale of environmental variation affected the type of evolutionary response. An important conclusion emerging from these studies was there exists so-called evolutionary tipping points that will prevent populations to cope in an evolutionary sense to changes in the environment.

The third advance in RA2 was related to identification of general principles affecting natural selection as a process. Darwin proposed selection among individuals with different fitness as the major mechanism causing adaptations to changes in the environment. It is therefore surprising that more than 150 years after Darwin proposed his groundbreaking theory we still lack a general understanding of how natural selection actually works especially in natural populations. This is perhaps the major reason for why we only to a limited degree understand factors affecting the recorded variation in nature in evolutionary rates. An important advance in our general understanding of evolution as a process was provided by Bolstad et al. in a paper published in the *Proceedings of the National Academy of Sciences of the United States of America*. In a large artificial selection experiment involving more than 50000 fruitflies they were able to show a large ability of the wing shape to respond to selection in the allometric intercept (representing the shape of the wing at a given size), whereas the response

Field work at Helgeland

to the allometric slope (size dependent shape) was more complex. Surprisingly, when selection was stopped, the flies responded by returning rapidly back after just 15 generations to the ancestral state. This shows that different selective pressures acting on correlated traits may constrain evolution along specific directions.

One of the key questions in RA2 is to understand how selection varies in time and space. This has in particular been the focus for the research by professor Christophe Pelabon. Fluctuating selection has been suggested as one of the major mechanisms explaining evolutionary stasis. Several studies have reported substantial temporal fluctuation in the estimates of selection strength and direction, but some evidence indicate that much of this variation may be strongly influenced by estimation error in the estimates of the selection coefficients so that directional selection in fact may be quite stable over time. Phenotypic selection studies repeating observations in space and time are therefore urgently needed to estimate how and at which rate directional selection fluctuate in the wild. Pollination ecology has provided a particularly powerful approach to estimate patterns of selection, because selection of flowers by the pollinators generates strong selection on floral traits responsible for the attraction of the pollinator (signaling or rewarding traits). Using *Dalechampia scandens* (Euphorbiaceae) as model species, Pelabon and collaborators have been studying patterns of selection in several populations of this species in Costa Rica during the autumns of 2014 and 2015. They have combined classical phenotypic selection experiments with molecular analyses (microsatellites) aiming at understanding the link between the population and meta-population genetic structure and the diversity of pollinator fauna. Together with the quantitative genetic experiments conducted in the greenhouse in Trondheim, these field observations should allow testing several of models explaining the population divergence under drift and selection.

An important, but difficult task in studies of evolutionary studies is to identify mechanisms for how genetic variation affects fitness related traits. So far, two approaches has been followed to obtain such relationships: (1) Assuming that individual variation in basal metabolic rate (BMR) provides an overall characteristic of many behavioural and physiological characters in birds, the fitness–correlates and the heritability of individual variation in BMR have been analysed in detail. (2) The length of telomeres has also been associated with individual variation in fitness. Accordingly, a study published by Ringsby and collaborators in *Proceedings of the Royal Society Series B* indicates that increased telomere length is associated with reduced body size in house sparrows.

In RA1 one of the major goal is to develop models and statistical procedures to account for fluctuations in age-structure of populations subject to density dependence in an environment that varies stochastically. Such age-distribution variations are important in analyses of temporal variation in population size because changes in the dynamics caused by variation in the environment is often confounded by the effect of variation in vital rates due to fluctuations in the age distribution. In a paper published in *Oikos,* Lee et al. were able to describe the fluctuations in the number of individuals of different ages in a population of Svalbard reindeer.

An important aim of CBD is to improve our understanding of the impacts of various kinds of human activities on changes in biological diversity. A focus for several projects has been to develop tools for predicting the ecological consequences of the expected changes in climate. Important insights in how complicated such effects can be for the long-term viability of populations were gained by a study of Danish goshawks published by I. Herfindal and collaborators in the *Journal of Animal Ecology*. In this population temperatures experienced in April early in life translates into effects on the reproductive of the female at older ages, causing long delays in the demographic responses to an environmental change occurring in a single year.

A central focus in RA1 is to establish and maintain model systems, designed to provide the foundation for parameterizing the models developed at the centre. Generalizing the results from these models has also been facilitated by the collaboration within a large network of researchers conducting long-term population studies of birds and mammals. In particular, the collaboration with professor Marcel E. Visser (member of the Scientific Advisory Board), Netherlands Institute of Ecology, Netherlands, who is running some of the longest running studies based on individual-based demographic data that exist for any free living vertebrate, was in 2015 extensive.

The major field system operated by CBD has been the studies of the metapopulation dynamics of house sparrows at the coast of Helgeland in northern Norway. This study, running since 1993 at 18 islands, was continued at a full scale also in 2015. In addition, experimental manipulation of the adult sex ratio in 8 house sparrow populations of different size was finalized this year. Furthermore, an artificial selection experiment on increased basal metabolic rate had also its last field season in 2015. Finally, a "common garden"-experiment in which selection on BMR was studied by introducing individuals with large and low BMR at an island on the coast of Trøndelag was continued in 2015.

Another important long-term study of individual-based demography is conducted on the island of Vega at Helgeland, northern Norway, where survival and reproduction of individual moose have been followed since 1992. This study, generously funded by The Norwegian Environmental Agency, has recently been expanded to equip almost all individuals with GPS-collars. This facilitates studies of how individual variation in home range quality affects the individual fitness of cows and bulls. Unfortunately, due to lack of snow, we were not able to band any individuals in 2015.

The level of field activities in Svalbard was particularly high in 2015. First, the annual marking and recapturing of reindeer were performed in April together with the collaborating institutions (NPI, NINA, NMBU, James Hutton Institute). Second, a boat expedition took place in the remote Eastern parts of Svalbard in July. This expedition resulted in successful collection of a multitude of data and plant/reindeer samples, essential for our projects investigating large-scale anthropogenic impacts on this ecosystem that includes analyses of spatial synchrony in tree-ring growth in a dwarf shrub and spatiotemporal changes in reindeer abundance and population genetics related to climate and past overharvest. Third, together with collaborators at the University Centre in Svalbard

Field work at Helgeland

Live captures and handling of water voles at the coast of Helgeland, northern Norway

(UNIS), a long-term vegetation experiment was initiated in the fall, with the aim to combine retrospective time-series analysis with experimental data to understand how plant species of particular importance to herbivores are influenced by projected changes in climate. The treatments include winter rain-on-snow (experimental ground-icing) and summer warming (using open top chambers). These studies also form an important link to analyses of trophic interactions in Research Area 3.

In 2015 CBD established a new study system on the spatial variation in the demography and population dynamics of water voles at the coast of Helgeland. By using pit-tags a large proportion of all individuals at several islands were individually known, which makes it possible to analyse how different factors such as dispersal and environmental variation correlated in space affect spatial synchrony in population fluctuations. An advantage with this system is that experimental manipulations of many of the structuring processes are logistically feasible.

In Research Area 3 of the CBD "Community dynamics" the central goal is to deduce patterns in the temporal and spatial variation of species composition of communities from the characteristics of the dynamics of the single species. An important advance towards fulfillment of this goal was provided by Ovaskainen et al., who developed a statistical method that also utilizes joint-species distribution models with a latent variable parameterization (published in *Methods in Ecology and Evolution*). Instead of a spatially explicit approach, a spatially hierarchical study design is applied. With this method, it is possible to identify large networks of species-to-species associations at different spatial scales. This approach was used to analyse spatial variation in co-occurrence of fungal species across Europe. These studies nicely illustrate how this kind of methods can be used to disentangle how different drivers affect the species co-occurrences and hence structure of communities.

In my opinion, these snapshots of research contributions from CBD during 2015 fully illustrates that the cross-disciplinary approach in the interface between several disciplines of biology and mathematical sciences embedding most of the projects at the centre has a great potential in producing important scientific advances. These results have also received public interest. For example, researchers at CBD has in 2015 appeared at least monthly in national broadcasts, and research results have been presented in several newspaper articles.

The paper *Evolutionary consequences of non-selective harvesting in density-dependent populations* published in *American Naturalist* by Steinar Engen, Russell Lande and Bernt-Erik Sæther was awarded by the Wildlife Society the prize for the outstanding publication in wildlife ecology and management in 2014.

1 PhD-student (Erik Blystad Solbu) at CBD graduated in 2015.

2. SCIENTIFIC ACTIVITY

RESEARCH AREA 1: POPULATION ECOLOGY

The aim of RA1 is to develop and apply models to describe dynamics of populations in time and space in fluctuating environments.

Questions

- How does the age-specific variation in the stochastic contributions to the population growth rate differ along the slow-fast continuum of life history variation?
- To what extent can age-specific variation in the contribution of different age-classes to the total density dependence affecting the population dynamics, be explained by the position of the species along the slow-fast continuum of life history variation?
- How can spatial patterns in the population dynamics be predicted from the species' position along the slow-fast continuum of life history variation?
- How will expected changes in climate affect spatio-temporal variation in population fluctuations?

Achievements

- Methods are developed that can describe the dynamics of density dependent age-structured populations including fluctuations in age distribution based on a combination of population counts and capture-mark-recapture analyses of marked individuals.
- It is shown for a bird species (the goshawk) that climate conditions experienced early in life can cause carry-over effects later in life that strongly affect individual variation in important components of fitness.

TOWARDS A MECHANISTIC UNDERSTANDING OF UNGULATE POPULATION GROWTH: AN INTEGRATED POPULATION MODEL

Brage Bremset Hansen, Aline Lee, Vidar Grøtan

Robust estimation of the drivers of vertebrate population dynamics is challenging. In particular, analyses of a large number of long-term studies have led to the rather disappointing conclusion that it is extremely difficult to develop precise projections of future population sizes as response to e.g. climate change when only based on time-series of population fluctuations. This is because other factors affecting the population dynamics, such as density-dependence and demographic stochasticity, are statistically difficult to separate out in this kind of data, particularly in long-lived species, where age-structure fluctuations may induce lagged fluctuations in population size. Such fluctuations can easily be interpreted as climate effects or density-dependence while in fact being consequences of factors affecting the population years ago. Thus, projections of the effects of climate changes on the dynamics of animal populations require demographic models that include a mechanistic understanding of climatic influences on key life history parameters. In a paper published in *Oikos* (Lee et al. 2015) we developed an integrated population model for a population of wild Svalbard reindeer, and demonstrated how this type of model can be used to extract more information from data by combining different data sets in a joint model, and separate different sources of variability in population estimates. Our model combines individual mark-recapture data with population counts and harvesting data within a Bayesian modelling framework (Fig. 1), and accounts for observation error, environmental and demographic stochasticity and age structure. From this model we obtain estimates of age-specific and total population sizes, as well as age-specific survival and fecundity over time (Fig. 2). The model provides estimates of age structure at a finer

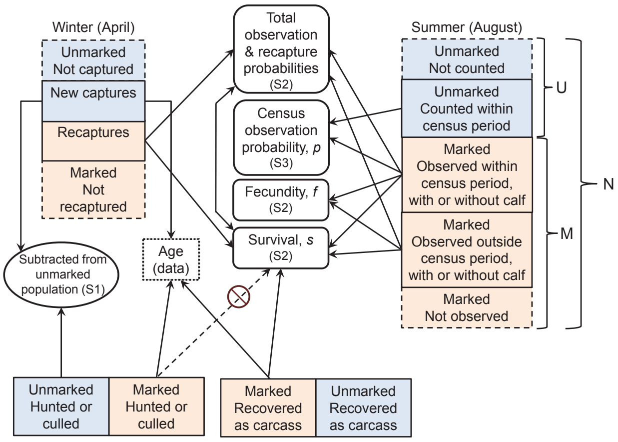


Figure 1. Overview of the different types of data and where they enter the integrated population model for wild Svalbard reindeer. The figure does not show all possible routes of information flow. From Lee et al. (2015, Oikos).

scale than in the census data, which only separates between calves and adults, and enables us to estimate calf survival for the period before they are marked and enter the individual mark-recapture data.

The integrated population model framework provides an improved approach to studying age-structured populations that are imperfectly censused and where the demography of only a sample of individuals is known. Using data from independent censuses of the same population we were able to evaluate population estimates obtained from the model, showing that it is successful at correcting for different types of observation error. Our model results suggest that allocating resources to the collection of supplementary mark-recapture data could improve the reliability of population projections more than making regular population censuses as exhaustive as possible. Our work also demonstrates how integrated Bayesian population modeling can be used to identify and disentangle sources of variation in individual performance and population size.

This represents an important step towards increasing the predictive ability of population growth models for long-lived species experiencing changes in environmental conditions and harvesting regimes. Accordingly, we are currently applying an extension of this population model to first disentangle how age-specific effects of density-dependence and different climatic drivers, and hence age structure fluctuations, contribute to the observed patterns of Svalbard reindeer population growth, for then to predict future population dynamics given different climate scenarios (the "REINCLIM" project, financed by the Research Council of Norway (RCN)). Furthermore, we examine by simulation how different harvest levels and harvest quota systems may interact with climate change to impact age structure fluctuations and thereby change both the short-term and longer-term patterns of population growth ("SUSTAIN" project, an integrated project financed by RCN).

FURTHER READING:

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

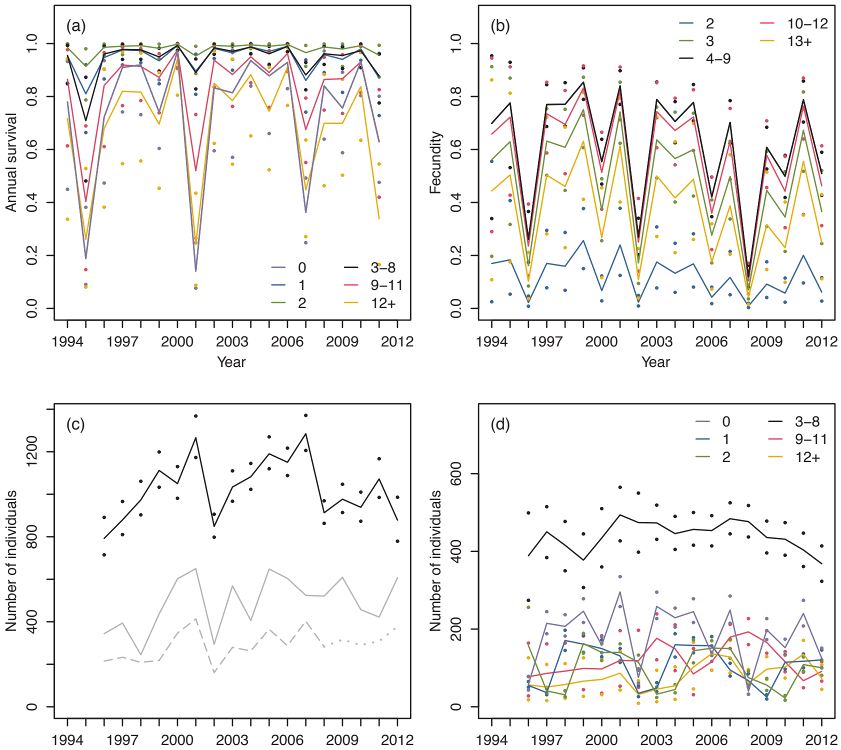


Figure 2. Age-specific estimates for the female segment of a wild Svalbard reindeer population. From Lee et al. (2015).

ESTIMATING TEMPORAL TRENDS IN POPULATION DYNAMICAL PARAMETERS

Erik Blystad Solbu

Stochastic population dynamical models are used to describe fluctuations in population size over time and ultimately predict how species are expected to persist in the future. The model parameters are often assumed to be constant, or stationary, when fitting the model to data. However, the stationary assumption can be unrealistic in environments where anthropogenic activities have altered the habitat considerably over time, such as deforestation, or in abrupt changes in single events, e.g. an oil spill. Different anthropogenic activities can affect different aspects of the population dynamics. We have modeled the effect of different temporal changes in parameters, on the population dynamics in a paper published in 2013 in *Mathematical Biosciences*. Using contemporary estimation techniques, we have now presented how different characteristics of species and the data collected affect the ability to detect temporal trends in parameters.

A large number of scenarios were studied using simulations, in particular species response to environmental perturbations, in this case the strength of density regulation, and the length and quality of the data. Species were assumed to have a mean return time to equilibrium of either three (fast) or ten (slow) years. The changes considered where stepwise change in growth rate and either gradual or stepwise change in carrying capacity. A stepwise change in growth rate can for instance illustrate the release of some toxin reducing the offspring survival of a species, while a change carrying capacity can be due to habitat reduction, either abrupt or gradual. The estimation techniques applied assumed the Bayesian paradigm of statistical inference, which also allowed us to compare the effect of having expert knowledge about some aspect of the species prior to the estimation.

Regarding population growth rate, the study showed that detecting changes in this parameter required observations of the population density at low abundance both before and after the change. The result illustrates that time series data are not ideal when growth rate is assumed to be changing due to anthropogenic activities. Instead data on the individual level should be acquired. Estimating and detecting gradual (trend) or stepwise changes in carrying capacity depends on the dynamics of the species being studied. For species with fast dynamics, i.e. short return time to equilibrium, the number of data points required to estimate the change accurately where 20 to 30 observations, a species with slow dynamics were not necessarily significant even with 50 observations. Thus, when studying species with high age of maturity, changes in the dynamics will require monitoring over decades, unless the total abundance is low or the change brings the population close to extinction. Furthermore, we showed that increases in carrying capacity where more difficult to detect than decreases, which again implies that a recovery of a species would be harder to confirm, i.e. requiring more data. Although the results in our work might be sobering, they are important for ecologists and decision makers alike.

FURTHER READING:

Solbu, E.B., Engen, S. & Diserud, O.H. 2013. Changing environments causing time delays in population dynamics. *Mathematical Biosciences* **244**: 213–223.

Solbu, E.B., Engen, S. & Diserud, O.H. 2015. Guidelines when estimating temporal changes in density dependent populations. *Ecological Modelling* **313**: 355-376.

RESEARCH AREA 2: EVOLUTIONARY BIOLOGY

The aim of RA2 is to develop and apply models for phenotypic evolution in fluctuating environments.

Questions

- How can the evolutionary response to selection on a quantitative character be decomposed into age-specific components, accounting for demographic stochasticity?
- How does density-dependent selection affect phenotypic evolution in fluctuating environments?
- Does the rate of phenotypic evolution in response to a change of the environment depend on the position of the species along the slow-fast continuum of life history variation?

Achievements

- Theories are developed for the influence of plastic responses and bet-hedging on phenotypic evolution.
- A theory is developed for phenotypic evolution by *r*- and *K*-selection in fluctuating environments, showing that harvesting can induce phenotypic evolution even without any phenotypic -specific outtake of individuals
- An experiment shows that the evolutionary response to artificial selection are can be constrained by the genetical architecture of the trait.

MODELLING JOINT EVOLUTIONARY RESPONSES TO AND ESTIMATING AUTOCORRELATED FLUCTUATING SELECTION

Jarle Tufto

Understanding how populations respond to environmental change is a fundamental question in evolution. It is also critical in predicting how biological populations will respond to ongoing anthropogenic global warming. Darwin hypothesized that the adaptive process occurs mainly through natural selection acting on heritable variation in a population. Without knowing the laws of heredity, he believed that selection would quickly erode variation and that this process therefore would be slow and dependent on continual input of new variation through mutation. However, for traits determined by a large number of loci of small effect in sexual populations, theory and empirical evidence from artificial selection experiments and from studies of contemporary evolution in natural populations suggest that a response to selection can be sustained for many generation without erosion of genetic variation, moving the mean phenotype outside the initial range of phenotypic values within only a few generations.

Phenotypic expression may depend on the environment experienced by an organism during development. If there is genetic variance in the reaction norm parameters describing how the mean phenotype depends on an environmental variable and this variable is correlated with later selective phenotypic optima, the norm of reaction will respond to selection and adaptive phenotypic plasticity can evolve. Such plasticity represent a second mechanism by which organisms can cope with environmental change.

In highly variable environments, genotypes producing a random distribution of phenotypes may theoretically have higher long-term geometric mean fitness than genotypes producing a fixed phenotype because at least some copies of the genotype by chance are likely to match the current phenotypic fitness optimum. An empirical example of such bet-hedging strategies is random seed germination in desert plants.

The above evolutionary response modes to fluctuating selection have been dealt with mostly separately in previous theory. In Tufto (2015), I formulate a model of joint evolution in three latent quantitative genetic determining the overall phenotype *z*. Trait *a* (the reaction norm elevation) accommodates conventional Darwinian genetic evolution, trait *b* (the reaction norm slope) evolution of

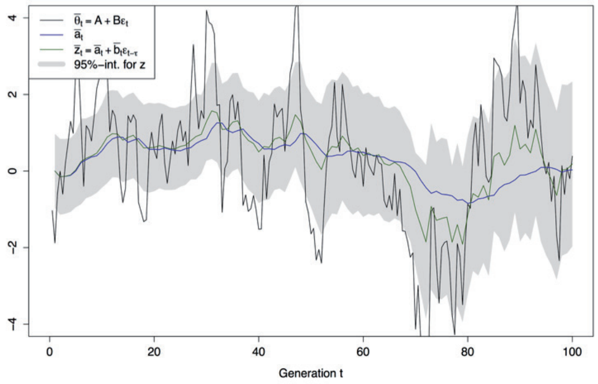


Figure 3. Responses to fluctuations in the optimal phenotype (black curve) through genetic evolution in mean reaction norm elevation (blue curve), through genetic evolution and plasticity combined (green curve) and additionally, through changes in the phenotypic variance (grey shaded area)

adaptive plasticity, and trait *c* evolution in the phenotypic variance (bet-hedging). The environment and the optimal phenotype fluctuates temporally according to a Gaussian stationary autocorrelated process (Fig. 3). I derive analytic approximations expressing the mutual dependencies between the three response modes, exact in the limit of small genetic variances in *b* and *c*. Conventional Darwinian genetic evolution generates a covariance across generations between the mean reaction norm elevation $\bar{a}_t$ and the environment ε_t. Only with perfect plasticity is genetic evolution and this covariance reduced to zero. The mean reaction norm slope evolves to a level fluctuating around the slope of the regression of the optimal phenotype θ on the environment at time of development $\varepsilon_{t-\tau}$ minus the slope of the regression of $\bar{a}_t$ on the environment at development generated by genetic evolution. Finally, provided that stabilizing selection is sufficiently strong, the phenotypic variance evolves to a level determined by residual variation in $\bar{a}_t$ and plasticity. These results generalizes previous theoretical results on genetic evolution (Lande & Shannon, 1996), plasticity (Gavrilets & Scheiner, 1993), and evolution of the phenotypic variance (Bull, 1987).

Solving for the joint evolutionary outcome, there is considerable overlap between the three response modes throughout large parts of the parameter space with plasticity being the dominant response mode for realistic parameter values. If microenvironments experienced by different individuals deviates from the current global macroenvironment, this shifts the joint evolutionary outcome away from plasticity in favour of genetic evolution if environmental fluctuations are slow. Bet-hedging becomes restricted to a small part of the parameter space where genetic evolution and plasticity is limited (fast environmental fluctuations).

In Chevin, Visser & Tufto (2015), using generalized linear mixed models and INLA, we estimate several of the parameters in the above theoretical models during one episode of selection from 40 years of data on in a Great tit population in the Netherlands. We assume that number of given by

$$ln(w) = \mu_t + (\beta_z + \beta_{zx}x_t + \zeta_t)z + \beta_{zz}z^2$$

This translates to a Gaussian fitness function acting on onset of breeding *z* with an optimum possibly depending linearly on an environmental covariate x_t such as spring temperature. To accommodate fluctuating autocorrelated selection, the random effect on the slope ζ_t in the regression was modelled as a first order autoregressive process. Reparameterizing in terms of quantities of biological interest, the width of the fitness function was estimated to 20.6 days, the autocorrelation between years to 0.30, the mean optimal onset of breeding across years to April 19.4, the change in the optimal onset of breeding per change in early spring temperature to -5.01 days per degree Celcius, and the standard deviation of overall fluctuations in the optimal onset of breeding across years (resulting from both temperature variation and residual variation) to 8.62 days. Estimates of the optimal onset of breeding across years are displayed in Fig. 4.

Based on model selection criteria, this model provided a more parsimonious alternative than both simpler models without stabilizing selection, models without fluctuating selection, as well as models where first and second order regression coefficient in different years are free parameters. In contrast, because fluctuating Gaussi-

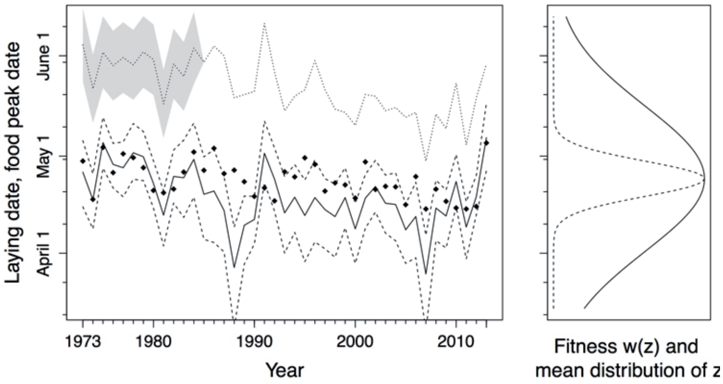


Figure 4. Left panel: Estimated optimal laying date (solid line) with 95% credible intervals (dahsed line), mean laying date (dots), and the estimated peak in catterpillar abundance (dotted line). Right panel: The estimated Gaussian fitness function (solid line) and a normal distribution with variance equal to the average phenotypic variance acrros years (dashed line), both centered around the mean optimal onset of breeding.

an stabilizing selection of constant strength translates to fluctuations in both linear and quadratic selection gradients as defined in the Lande & Arnold (1983), such traditional methods would require more parameters to fit the data. Additionally, our approach correctly accounts for sampling error in estimates of selection within each year.

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UNDERSTANDING THE EVOLVABILITY OF COMPLEX CHARACTERS

Christophe Pelabon

Understanding evolution in fluctuating environment requires understanding both the pattern of selection and the nature of heritable variation. In this context, evolvability is a central concept to understand adaptive evolution. Evolvability is the propensity of an organism or a character to evolve, and ultimately its ability to adapt. Consequently, our capacity to predict the fate of natural populations facing rapidly changing environments depends on our capacity to understand and measure evolvability. In quantitative genetics, the ability for adaptive evolution has been classically estimated by the heritability (h^2); the proportion of phenotypic variance due to additive genetic variance. If scaling additive variance with phenotypic variance seems a natural and effective way of accounting for the inherent relationship between the mean and the variance, it requires that other components of the phenotypic variance[1] do not vary systematically in relation to the additive variance. Because they do, measuring evolvability using heritability is similar of using a rubber scale that gets stretched when measuring something large (Hansen et al. 2011). Furthermore, heritability does not usefully generalize to multivariate characters and therefore does not allow linking evolvability to concepts such as evolutionary constraints, or modularity. Hansen, Houle and Pélabon have suggested that the square of the additive genetic coefficient of variation $IA = VA/\mu^2$, where VA and μ are the trait's additive genetic variance and mean, respectively, was a more interpretable measure of evolutionary potential because this measure is not on a rubber scale. Furthermore, this standardization provides particularly meaningful units to the different parameters of the evolutionary process (i.e. selection, genetic variation and evolutionary rate), and allows meaningful comparisons of these parameters across traits and populations (Hansen et al. 2003, 2011; Houle et al. 2011). Finally, evolvability can efficiently extend to multivariate characters, where pleiotropic interactions may constrain genetic variance and evolvability (Hansen & Houle 2008). One of the axes of research developed by the group of C. Pélabon and collaborators is to further

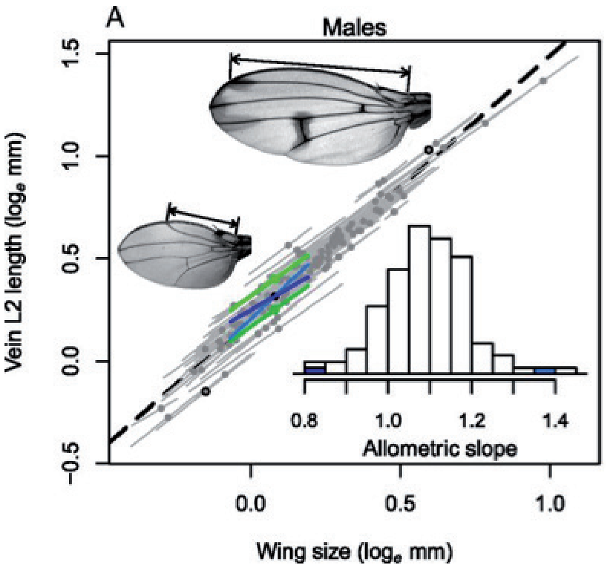

Figure 5: Allometric relationships between the length of the L2 vein (represented by the arrow on the wing) and the wing size within and among 111 drosophilid species. The selection responses are also presented for the selection on the intercept (green lines) and selection on the slope (blue lines). The histogram shows the among-species distribution of slopes with the final slopes of the up- and down-selected populations in blue (Bolstad et al. 2015).

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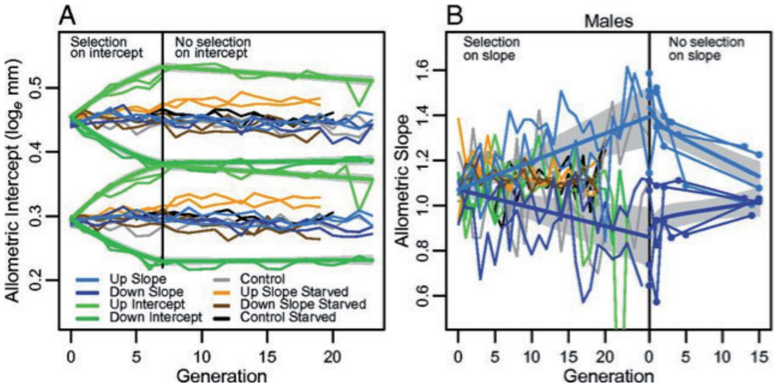
[1] The phenotypic variance $V_P = V_A+V_E+V_D+V_R$, where V_A, V_E, V_D, V_R, are the additive genetic, environmental, dominance and residual variances, respectively.

Figure 6. Change in allometric intercept (A), and allometric slope for males (B) for the two replicates of each selection regime. The populations were measured at each generation except during relaxed selection on slope, where measurements are indicated by circles.



understand the evolvability of complex traits by testing various hypotheses linking micro and macro evolution, as for example to understand whether the evolutionary stasis observed in some complex characters results from the absence of evolvability. In this context the group has studied the evolvability of allometry.

Throughout the natural world, shape, physiology and behavior are strongly related to the size of the organisms. These relationships are found both within individual during growth, within species and between species, and often remain unchanged in species separated for millions of years. For example, the hearts of small species beat much faster than those of large species, and the antlers of small deer species are smaller, relative to body size, compared to antlers of large species. In Drosophila species, the relationship between some aspects of the wing shape and the size of the wing are amazingly constant over a wide range of species spanning over more than 50 MYs of evolution (Fig. 5). With a large scale artificial selection experiment measuring more than 58,000 flies (*Drosophila melanogaster*), we tested whether the allometric relationship between shape and size was evolvable. With the exception of a previous experiment on guppy (*Poecilia reticulata*), this selection experiment was the first experiment that clearly distinguished the evolvability of the allometric slope (shape – size relationship) from the evolvability of the intercept (shape). While the allometric intercept proved to be highly evolvable, the response of the allometric slope was more complex. Yet, in 26 generations, the selection generated more extreme variation in the relationship between shape and size in fly wings than more than 50 million years of evolution (Fig.6). However, when selection was stopped, the relationship between shape and size returned to normal after just 15 generations. In contrast, lines selected for different shape (selection on the intercept) did not show such return to the ancestral stage. Therefore, the return of the allometric slope to the ancestral stage was interpreted as the effect of antagonistic pleiotropy affecting the development of the wing. This experiment clearly illustrates how correlated traits with different selective pressures may constrain adaptive evolution along specific direction in the morphospace.

A second line of research of Pelabon's group aims at understanding patterns of spatial and temporal variation in selection. Fluctuating selection has been suggested to be one of the mechanisms explaining evolutionary stasis (Futuyma 2010), and the study of Siepielski et al. (2009) reported substantial temporal fluctuation in the estimates of selection strength and direction. In a reanalysis of data gathered by Siepielski et al., Morrissey and Hadfield (2011) showed that this variation was mostly the result of estimation error and that, contrary to the initial conclusion, patterns of directional selection were particularly stable. Phenotypic selection studies repeating observations in space and time are therefore needed to estimate how and at which rate directional selection fluctuates in the wild. Pollination ecology provides a particularly powerful tool to estimate patterns of selection, because selection of flowers by the pollinators generates strong selection on floral traits responsible for the attraction of the pollinator (signaling or rewarding traits). Using *Dalechampia scandens* (Euphorbiaceae) (Fig. 7) as a model species, Elena Albertsen and Øystein H. Opedal, both PhD at CBD, have been studying patterns of selection in several populations at Costa Rica during the autumn 2014 and 2015 . They have combined classical phenotypic selection experiments with molecular

Figure 7: *Euglossa dilemma* visiting a blossom of *Dalechampia scandens* in the population of Puenta la Amistad in Costa Rica. Photo: Elena Albertsen

analyses (microsatellites) to understand the link between the population and meta-population genetic structure and the diversity of pollinator fauna. Together with the quantitative genetic experiments conducted in the greenhouse in Trondheim, these field observations should allow testing several of the models explaining population divergence under drift and selection.

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EVOLUTIONARY TIPPING POINTS IN THE CAPACITY TO ADAPT TO ENVIRONMENTAL CHANGE

Jonathan Wright

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. A paper on 'Evolutionary tipping points in the capacity to adapt to environmental change' involves a conceptually unifying individual-based simulation model concerning a variety of evolutionary responses to environmental change, which assumes a very simple genetic architecture (i.e. only 7 genes that turn on/off developmental plasticity and reversible plasticity, and determine reaction norm elevations and slopes, and phenotypic polymorphism). The main result is that different combinations of environmental predictability and the timescale of environmental variation produce distinct regions where a single class of response (reversible phenotypic plasticity, irreversible phenotypic plasticity, bet-hedging, or adaptive tracking) has a clear selective advantage over all others (Fig.8). The model also indicates that although populations can often cope with fairly large changes in these environmental parameters within each region, on occasions when they are forced across the boundaries between regions populations will collapse abruptly and go extinct. These conditions are characterized as 'evolutionary tipping points'. A potential implication of these results is that vulnerability to such cryptic threats may depend upon the specific genetic architecture and life history of the organisms involved. These insights should help identify and address some of the threats to natural populations from natural or human-induced changes in environmental conditions. They also demonstrate the value of evolutionary thinking in the study of effects such as global climate change.

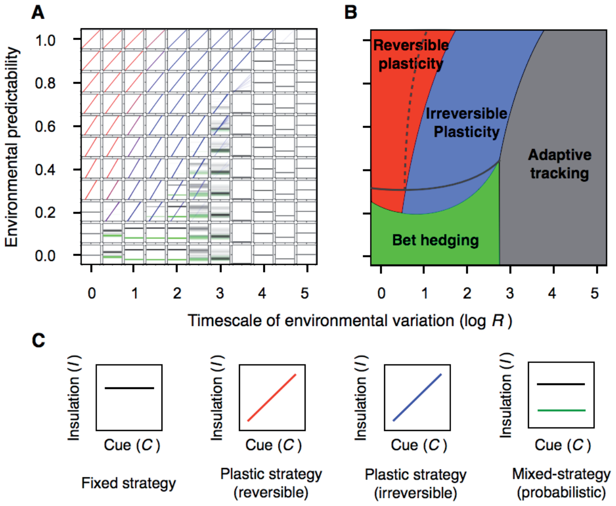

Figure 8. The four different classes of adaptive strategies that evolve in response to different timescales of environmental change (R=1 = one generation) and predictability (P=0 = completely unpredictable; P=1 = completely predictable). The norm of reaction plots for each part of parameter space depict the mean strategies of 5,000 individuals (at generation 50,000) from over 100 different simulations each. These reaction norms are colour-coded according to the type of strategy.

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UNDERSTANDING THE EVOLUTIONARY MECHANISMS THAT SHAPE LIFE HISTORY STRATEGIES – THE ROLE OF TELOMERE DYNAMICS

Thor Harald Ringsby and Maja Tarka

One of the questions that puzzle biologists is the great variation observed in life history strategies among species in the wild. A central principle in life history theory is that resources are limited, which results in trade-offs between costs and benefits of different life history components such as growth, self-maintenance and reproduction.

Many studies have focused on the trade-offs between reproductive investment and other life history traits. However, lately there has been an increased focus on investigating the relationships among growth, body size and longevity.

One challenge has been to understand the opposing pattern that typically exists in body size and longevity among and within species. A positive relationship exists between body size and longevity across taxonomic groups. However, within species, one often finds a negative relationship between body size and longevity. For instance in the domestic dog (*Canis lupus familiaris*) where artificial selection has resulted in huge variation in body size, we find that larger dog breeds have shorter lifespans, which has been shown to occur because they age faster.

We do not currently fully understand why large body size is associated with shorter lifespan within species and there could be several explanations involved. One explanatory route that has been proposed is the role of telomeres (see Box 1). It has been shown that telomere length at an early age can be predictive for longevity and that telomere loss is related to senescence and early death. Among dog breeds, telomere length has been reported to be shorter in large compared to small breeds. This may suggest that telomere dynamics could be central as a mechanistic mediator of the cost in terms of reduced lifespan associated with large body size. Accordingly, if organismal size is negatively correlated with telomere length, this could potentially constrain evolution of larger body size within species in nature.

Objectives

As a consequence of the above rationale, two essential questions can be raised:

The first question is whether intraspecific variation in body size covaries with telomere length measured at early age in a wild species under natural conditions. We investigated this question by applying an experimental approach where we analyzed the relationship between body size and telomere length in wild house sparrows (*Passer domesticus*) at the beginning and the end of a four year selection regime for larger parent size. The study was conducted at the remote island Leka in northern Norway during the years 2002 – 2005 (Fig. 9).

Figure 9. An artificial selection study for larger parental size over four years resulted in significantly larger fledglings associated with significantly shorter telomere length. This may indicate that larger size comes with a penalty in terms of shorter predicted lifespan. The selection study was conducted in a wild house sparrow population at the island Leka in northern Norway during 2002 – 2005. (Photo: Thomas Kvalnes)

The second question is which environmental factors influence telomere length and to what extent telomere length is a heritable trait. Heritability is a prerequisite if telomere length is involved in the evolution of body size. For this question, we report from our long term study on great reed warblers (*Acrocephalus arundinaceus*) at Lake Kvismaren in South Central Sweden, where genetic and environmental variances of telomere length, based on an extensive pedigree, have been estimated (Fig. 10).

The artificial selection experiment in the house sparrow study system revealed that after four years of selection for larger parental body size (measured as tarsus length) the mean body size of their fledglings increased significantly at the end of the study (2005) compared to at the beginning of the study (2002) (Fig. 11a). Interestingly, as a correlated effect of the selection regime, the associated mean telomere length in fledglings decreased significantly (Fig. 11b). In fact, a negative relationship between body size and telomere length was present already in the beginning of the study (2002) which was extended to larger body sizes under the artificial selection regime. (Fig. 12). This is to our knowledge the first experimental study to show that a persistent negative correlation was present between body size and telomere length. Accordingly, given that shorter telomere length is negatively associated with lifespan this potential

Figure 10. A pedigree based analysis showed that telomere length is affected by non-genetic maternal effects but also have a significant genetic component, indicating that telomere length is trait that could evolve if under selection. This study is among the first showing that older mothers give their offspring longer telomeres, refuting the idea that telomere length is static in the ova. The study was conducted in a wild great reed warbler population at Lake Kvismaren, South Central Sweden, with data spanning 1985-2004. (Photo: Arne Hegemann)

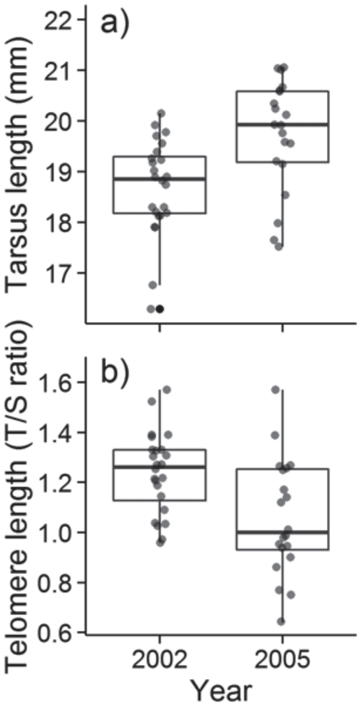

Figure 11. The average telomere size in fledgling house sparrows at the island Leka increased during a selection experiment measured at the beginning (2002) and the end (2005) of a 4 year selection period where parents were selected for larger size (a). As a correlated response the average telomere length, measures as the T/S ratio decreased significantly (b). Figure from Ringsby et al. 2015.

trade-off could play an important role in the evolution of optimal body size.

One underlying prerequisite for evolutionary change is that the traits involved are heritable. In house sparrows, as well in other bird species, body size has been shown to be heritable. In contrast, the heritability of telomere length has been investigated in only a handful of species, such as the sand lizard (*Lacerta agilis*), collared flycatcher (*Ficedula albicollis*), kakapo (*Strigops habroptilus*) and king penguins

Box 1.

Telomeres Telomeres are repetitive nucleotide sequences at the end of chromosomes and have the important function to protect chromosomes from fusion and decay. During cell division in eucaryotes the telomeres are not fully replicated, often known as "the end replication problem". Thus, telomere attrition has been linked to organismal growth per se. Telomeres can also be shortened due to environmental effects, such as oxidative stress, caused by free radicals which result in oxidative damage. Also physiological stress and disease has been shown to influence the loss of telomeres over time. Telomere loss has been associated with increased probability of mortality, and early age telomere length has been shown to be predictive of lifespan. It has been found that telomere length is highly variable between individuals, even very early in life. Hence, telomeres have an important role in the process of aging and can be an important functional mediator of trade-offs in life history traits such as lifetime reproductive success, lifespan and body size.

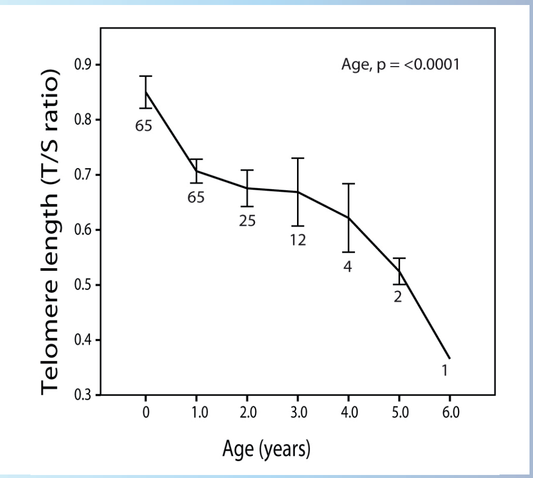

Figure: Telomere length decreases with age. Here an example from the great reed warblers. T/S ratio is a relative telomere length estimated by dividing the sample's telomere copy number (T) by its copy number of an ultra-conserved single copy nuclear sequence (S). Sample size for each age class is given below the error bars. Figure from Asghar et al. 2015 Proc Roy Soc B.

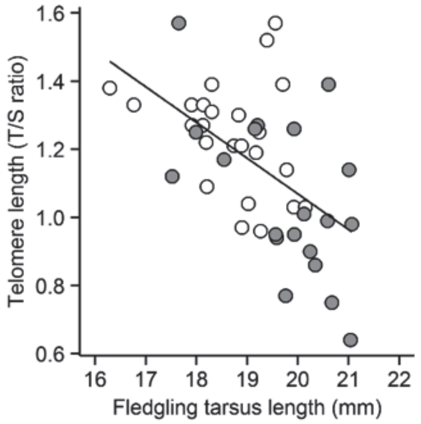

Figure 12. A negative relationship between body size and telomere length was present already in the beginning of the study (2002, open circles) and the negative relationship was present also in 2005, gray shaded circles). This suggests that a persistent negative correlation was present between body size and telomere length. Figure from Ringsby et al. 2015.

(*Aptenodytes patagonicus*). The heritability of telomere length in the reported house sparrow study will be investigated in the near future.

The only study in birds that has estimated heritability of telomere length with high precision is our long term study of the great reed warbler (*Acrocephalus arundinaceus*) in the Lake Kvismaren in South Central Sweden. In this study we aimed to identify and estimate both genetic and environmental components that affected the telomere length measured in nestlings. Since 1983, all individuals in the population have been individually monitored throughout their life. Among other things, we have measured morphology, ecology, behaviour, reproduction, immunology and lifespan. This thorough monitoring gives us not only a fully resolved pedigree (there are not more than 3% extra pair young in the population, and since 1986 we have molecularly confirmed all parentage), but also the possibility to measure all individuals at all different life stages. The

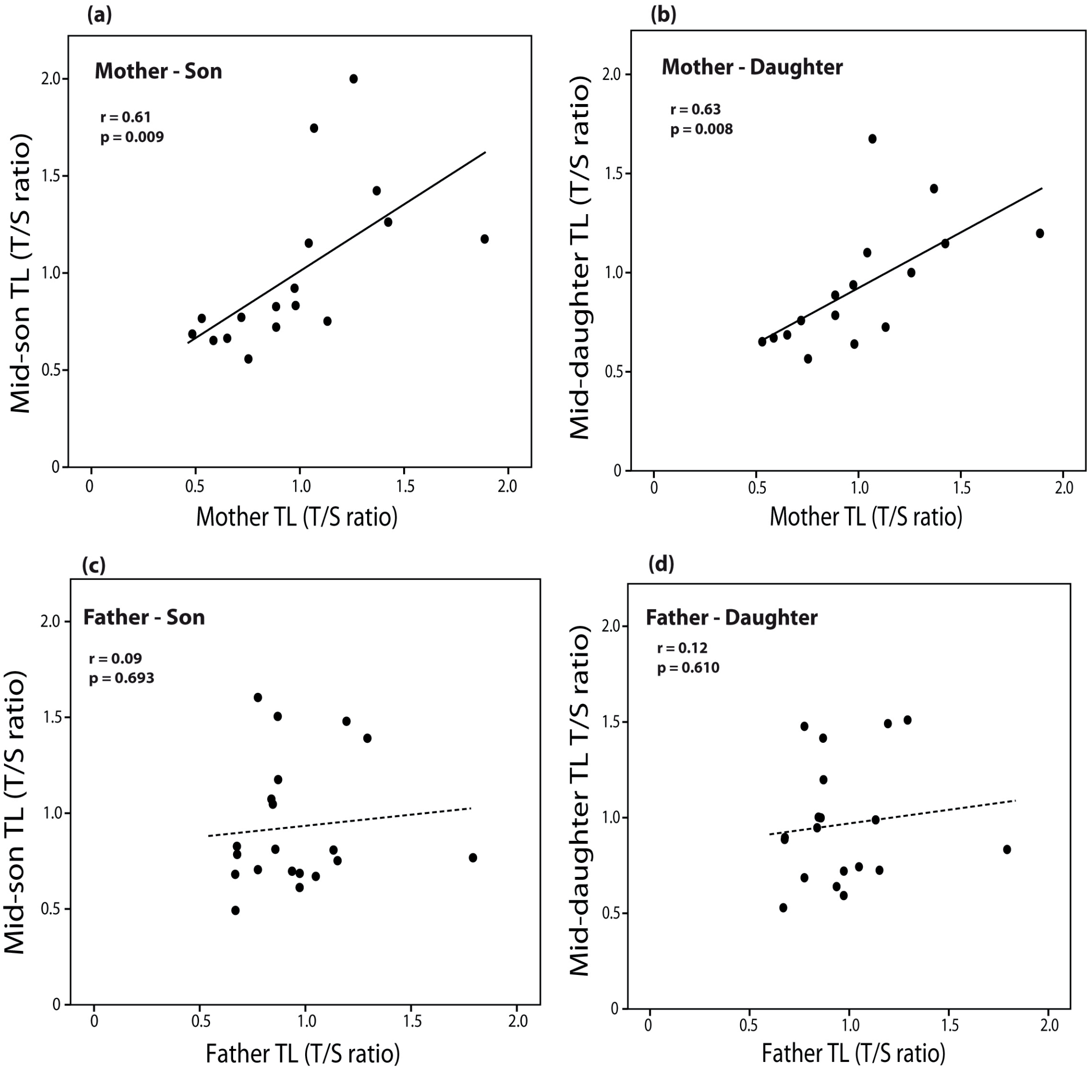

Figure 13. Results from parent-offspring regressions illustrating stronger maternal inheritance of telomere length in great reed warblers. Further analyses using the multigenerational pedigree in an 'animal model' showed that half of the phenotypic variance can be explained by genetic effects and the other half due to non-genetic maternal effects. Figure from Asghar et al. 2015.

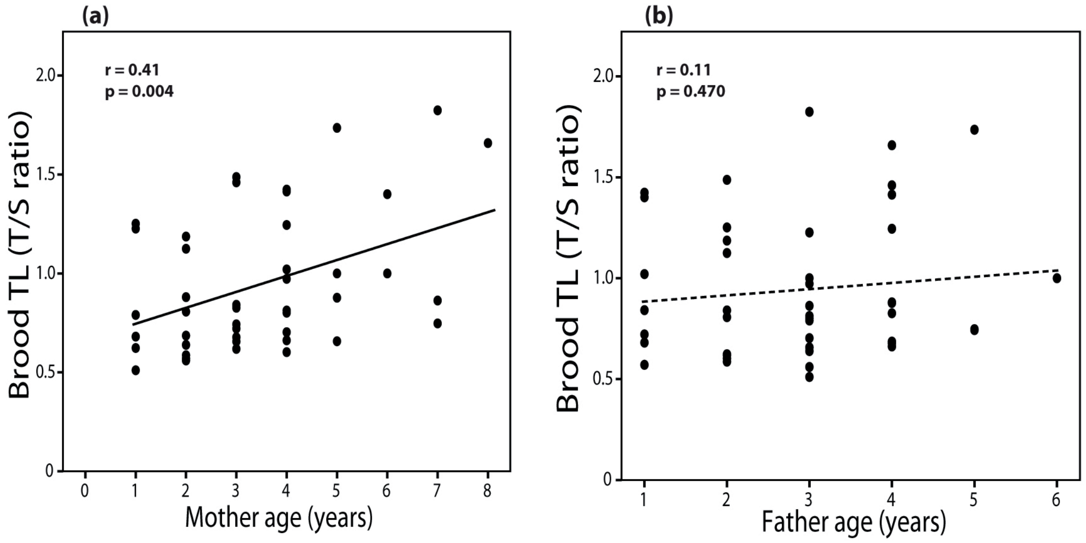

Figure 14. Figure showing the positive relationship between brood mean telomere length (brood TL) and the mother's age in great reed warblers. Offspring of older mothers get longer telomeres, while no relationship was found with father age. Figure from Asghar et al. 2015.

uniqueness of this study is that we were able to measure telomere length both in offspring and parents as nestlings (9 days old) in the birds' natural environment. This resulted in a pedigree of 203 unique individuals connected with a complex network of fully confirmed dams, sires, full- and halfsibs, grandparents and other more distant relatives. We used qPCR to measure the telomere lengths from blood samples and a combination of parent-offspring regressions and 'animal model' to distinguish between genetic and non-genetic effects.

Our main finding was that mothers, but not fathers, influence their offspring's telomere length through non-genetic effects (Fig. 13). First of all, older females produce offspring with longer telomeres (Fig. 14). Interestingly, in several studies on mammals including humans, the opposite pattern has been found, where paternal effects influenced the length of the telomere. Until now, this pattern was thought to be explained by the fact that female ova are produced early in life and don't experience more cell divisions, which should prevent the female's aging to affect the telomere lengths in her ova. This explanation is however refuted by our study on wild birds, and other hypotheses need to be tested. Among potential explanations is that telomerase, which is an enzyme that can counteract telomere shortening, is more active in older female's ovaries.

Furthermore, we identified a non-genetic maternal effect on telomere length. This type of effect could be explained by regulation of antibodies or hormones in the egg yolk, but needs further investigation.

Finally, we could show that in addition to these non-genetic effects, about half of the phenotypic variance has a genetic basis in our great reed warbler population. This suggests that telomere length is a trait that could potentially evolve if selection acts upon it.

Concluding remarks

By applying two long term study systems from two wild passerine species we have contributed with findings which may illuminate our understanding of the functional role of telomere dynamics in shaping life history traits. The great reed warbler study from Lake Kvismaren in Central Sweden revealed that telomere length is a highly heritable trait which is a prerequisite for being significant in evolutionary processes. The genetic correlations between telomere length and body size has yet to be investigated in house sparrows. However, the negative association between body size and telomere length found in the artificial selection study at Leka in northern Norway may reveal evidence for a functional mechanism that could underpin a trade-off between individual size and longevity within species.

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RESEARCH AREA 3: COMMUNITY DYNAMICS

The aim of RA3 is to analyse how community dynamics in time and space of different taxa along ecological gradients are affected by environmental stochasticity

Questions

- Does heterogeneity among species in population dynamics in general represent a significant component of the dynamics of communities?
- How does similarity in community structure differ in time and space with the number of species in the community?

Achievements

- Methods are developed that enable identification of networks of species-to-species associations at different spatial scales.

CBD, COMMUNITY DYNAMICS AREA

Nerea Abrego

One of the cutting-edge challenges in community ecology lies on the development of mechanistic and predictive statistical models that allow for disentangling the contributions of different assembly processes in shaping ecological communities. Joint-species distribution models that utilize latent variable structures provide promising opportunities in this context (see discussion in Warton et al. 2015). The main focus at the Community Dynamics research area is in developing a general joint-species distribution modelling framework which can be flexibly adapted to different types of the data, and used to answer several types of fundamental and applied questions in community ecology.

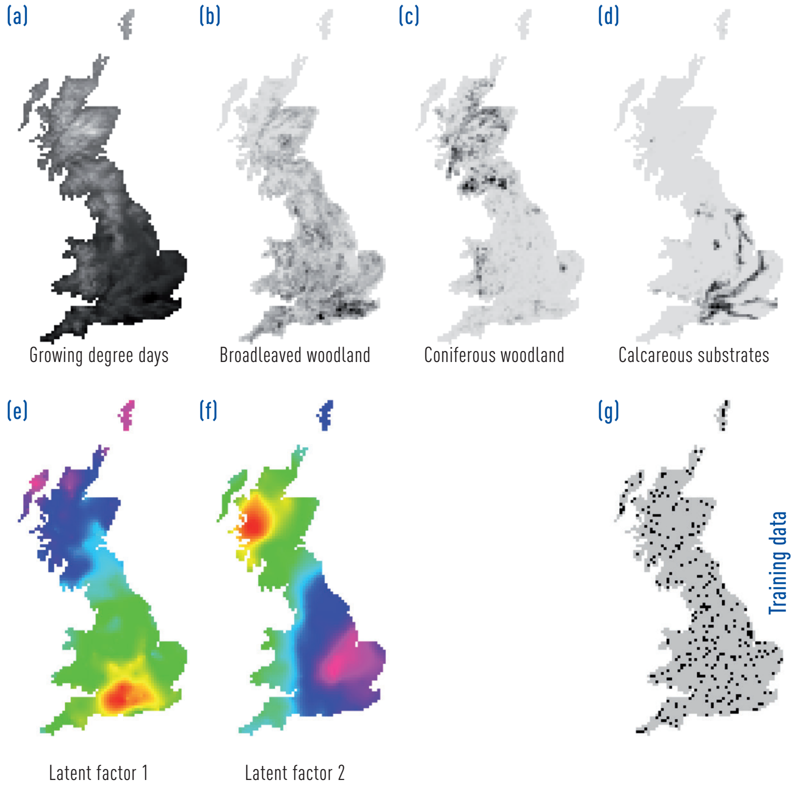

Figure 15. Measured environmental covariates and model-identified latent factor used to model a butterfly community from UK. The upper panels show the measured covariates 1–4: the number of growing degree days above 5 degrees (a), and the fraction of each grid cell consisting of broadleaved woodland (b), coniferous woodland (c) and calcareous substrates (d). The lower line of panels shows the two most dominant latent factors (i.e. hidden environmental covariates) identified by the model: latent factor 1 (e) and latent factor 2 (f). The black squares in panel g show the 300 randomly selected 10 km × 10 km grid cells that were used to parameterize the model. The remaining 2309 (shown by grey) were used to test the predictive performance of the model.

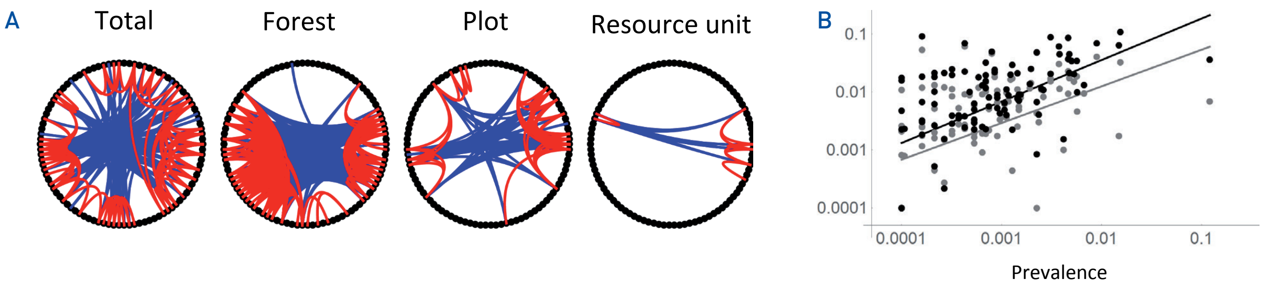

Figure 16. Panel A shows the species-to-species fungal associations detected at different spatial levels. Species are shown by the black dots, and species pairs are connected by a red (respectively, blue) line if they showed a positive (respectively, negative) association with at least 95% posterior probability. In order to visualize network structure, the species were ordered circularly based on the angle derived from two leading eigenvectors of the correlation matrix. Panel B shows the predictive powers of the models based on environmental covariates and occurrences of the other species. The dots show the species specific Tjur R2 values and the lines the linear regressions. The colours indicate whether the predictions are based on environmental variables only (Prediction 1; grey) or on environmental variables and the occurrences of all other species (Prediction 2; black).

One major step was the development of a spatially structured joint species distribution model provided by Ovaskainen and collaborators in a paper published in *Methods in Ecology and Evolution*. The main novelty of this approach is the use of spatially structured latent factors, which makes it possible to capture the effects of missing covariates, the effects of biotic interactions or the combination of these two. The computational and statistical efficiency of the approach arises from that there generally is far fewer latent factors than there are species. This is because all species are modelled with the help of a shared set of latent factors, each species having its own loading for each latent factor. If the latent factors were known covariates, the loadings would simply correspond to regression coefficients which could be estimated using standard techniques. However, it is often the case that species distributions are partly determined by unknown or unmeasurable covariates, or by biotic interactions. These 'hidden covariates' are here accounted for by the latent factors, and as they are not known a priori, they must be estimated (Fig. 15). Informally, the latent factors, and their spatial scales, are estimated so that they explain as much as possible of the variation in the distributions of all the species simultaneously. In addition, the number of latent factors is estimated, with the aim of including a sufficient number of latent factors to allow the model to capture as much of the biologically relevant variation as possible, but to avoid overfitting and thus the inclusion of latent factors that model noise rather than signal. It was also demostrated demonstrated that the inclusion of spatially structured latent factors greatly improved the model's predictive power for locations that were not present in the training data.

In another paper published in *Methods in Ecology and Evolution*, Ovaskainen et al. developed a statistical method that also utilizes joint-species distribution models with a latent variable parameterization, but instead of a spatially explicit approach, they considered a spatially hierarchical study design. With the method, it is possible to identify large networks of species-to-species associations at different spatial scales (Fig. 16A). They then modelled the occurrences of 100 wood-inhabiting fungal species using a joint species distribution model, which accounts for the influences of the measured covariates (such as decay stage and size of the resource units), for random variation in species occurrence (at resource unit, plot and forest levels), as well as for species-to-species associations (negative and positive). In this paper, it was also illustrated how latent variables models can be used to infer associative networks at various spatial scales (Fig. 16A). This demonstrates how one can generate improved predictions for a focal species by utilizing information on the occurrences of the other species – which methodology we plan to utilize to bring a statistical aspect to the selection of indicator species (Fig. 16B).

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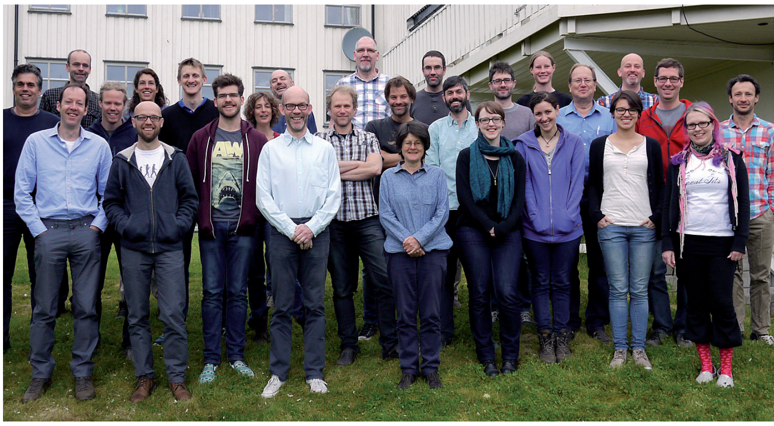
3. WORKSHOPS IN 2015

WILD ANIMAL GENOMICS MEETING 2015

A workshop on the use of genomics techniques in natural populations was held June 23rd-25th in Selbu, a small village 40 km east of Trondheim, Norway. The workshop was organized by Arild Husby (University of Helsinki) and Henrik Jensen (CBD) and was funded by grants from the Norwegian Research Council and CBD.

29 researchers from 9 countries across Europe and North-America attended the workshop. Participants ranged from PhD-students to well established, and internationally leading researchers within the field. The shared interest of all participants and the main focus of the discussion was how we best can make use of the recent development of genomics techniques to answer key questions in ecology, genetics, conservation and evolution of natural populations.

There was large diversity in the topics of the talks, which were both theoretical and empirical. Many focused on the identification of genes underlying ecologically important traits, and how their discovery can help us understand ecological and evolutionary dynamics in natural populations. Another set of talks aimed at how we can detect signs of selection in nature by using genomic data. In addition, there were a number of talks that focused on related topics such as inbreeding depression, recombination rates, epigenetics, and genomics of speciation. The empirical study systems ranged from insects to birds and mammals, and included both natural and experimental populations.



From the left: Marcel Visser, Joseph Hoffman, Henrik Jensen, Petri Kemppainen, Jon Slate, Anne Charmantier, Doug Speed, Toby Fountain, Christina Grossen, Sæther, Hans Ellegren, Bengt Hansson, Jacob Höglund, Patrik Nosil, Josephine Pemberton, Marty Kardos, Rowan Barrett, Susan Johnston, Arild Husby, Eryn McFarlane, Jisca Huisman, Leif Andersson, Luisa Pallares, Kees van Oers, Jocelyn Poissant, Veronika Laine, Charles Perriere (not present when picture was taken: Bilal Ashraf and Ingerid Hagen).

Participants mainly presented work in progress. Combined with the informal atmosphere at the workshop this resulted in many fruitful discussions. Hopefully, this will contribute to the role that use of genomics techniques will play in increasing our understanding of fundamental processes in natural populations.

In between talks and discussions there was also time for a hike to the top of Bringen, a nearby mountain at 1041 meters above sea level. Among other bird species, Golden Eagle and Ptarmigan were spotted on the hike.

MEETING OF THE GROUP "GENETIC ARCHITECTURE" FOUNDED BY A NFR GRANT AURORA 2015

The group "Genetic architecture" was established to reinforce collaborations between teams in France and Norway working on the themes of genetic architecture and the Genotype-Phenotype map.

We aimed at exchanging knowledge and specific skills in data analyses and theoretical developments, and starting new collaborative projects. This group involved 10 senior scientists, PhDs and post-doc from two French research centers (CNRS Gif s/Yvette and INRA Bordeaux) and two Norwegian universities (University of Oslo and NTNU). The first meeting of the group took place at the CBD in Trondheim early March 2015. During the first day, the different groups, via their PhD's or post-docs, presented their current research activities. These ranged from estimating selection on extremely long lived organisms such as oak trees, to artificial selection on fish or plants and modeling the effect of various genetic architectures on genes network in order to infer properties of the genotype-phenotype map. The next days were used to plan future research. During the spring and summer, PhD students visited the different institutions for various period of time; Elena Albertsen from CBD traveled to Gif S/Yvette and the CBD has welcomed Clementine Renneville from the CNRS. The closing meeting for the project took place early November 2015 in Bordeaux where we worked on ongoing projects and planned future collaborative work.

Experimental fields to study quantitative genetics of trees at the INRA Bordeaux where the second meeting of the Genetic Architecture group took place early November 2015.

CBD-IMPRS Workshop on Statistical Approaches to Multivariate Phenotypes, 11-16th January 2015

Ten PhD students and four staff from the CBD visited The Max Planck Institute for Ornithology (MPIO) located in Seewiesen, near Munich, for a practical workshop on these advanced statistical techniques.

The workshop was organised by Prof Jonathan Wright (CBD) and Dr Niels Dingemanse (MPIO, Munich), and lectures and practical sessions were also provided by Dr Alastair Wilson (Exeter, UK), Prof Dirk Metzel (Munich), Dr Ned Dochtermann (North Dakota, USA), Dr Geir H. Bolstad (CBD, NINA) and Yimen Araya-Ajoy (MPIO) on different aspects of understanding and analysing of multivariate phenotypic data (e.g. MCMCglmm, SEM).

The workshop generated lots of interesting and illuminating discussions, mostly around the technical aspects of these analyses in R. More than half of the workshop was allocated to practical use of these statistics by the students themselves and their presentations of the results generated and their newly acquired knowledge.

Prof. Jonathan Wright

Eager participants.
From the right: Peter Sjolte Ranke, Håkon Holand, Erlend I. Fossen, Irja Ratikainen, Stine Svalheim Rasmussen. Ane Marlene Myhre standing in the front.

Mitigation Measures of Human Induced Impacts on Marine Ecosystems, September 16th 2015

The workshop on "Mitigation measures of human induced impacts on marine ecosystems" organized by the CBD-members Olivia Langhamer and Petra Rodewald was held September 16th at IBI.

It was a rather small, but very interesting and constructive workshop where 15 researchers from different institutions in Norway (NTNU with IBI and Ind. Ecology, NINA, NIVA), from KVA in Sweden and from Melbourne University in Australia gathered. Other participants were from the industry PE Reefs and from Lister community. In that way the workshop contained a broad variation of presentations within both research topics and applications at the Norwegian, Swedish and Australian coasts, with several examples and future plans for effective marine habitat designs as enhancement tools. There were many possibilities for interesting and fruitful discussions on e.g. effective reef designs for different purposes and localities in temperate waters, anthropogenic impacts, lobster and fish behavior, data collection, and habitat mapping. Future scientific collaboration plans have been established with an agreement on a proposal-writing about marine habitat enhancement and its effects on the coastal environment. Additionally, collaboration with the coastal industry will be arranged since they plan to create new working places in a community (Flekkefjord) that is heavily affected by the oil crack. This workshop was organized in connection to a visiting PhD student from Melbourne University and we are grateful to the CBD for supporting it!

Photo: Olivia Langhamer

4. INTERNATIONAL COLLABORATION

During 2015 the international collaboration between employees at the CBD and researchers abroad has been extensive. This has resulted in the regular presence of short-term visitors at the centre, resulting in that more than 50 % of the CBD seminars was given by such guests. Two researchers stayed for longer periods: professor Subash Lele, University of Edmonton, Canada (January 5-July 2) and dr. Katja Räsänen, Institute of Integrative Biology, ETH-Zurich, Switzerland (January 12-June 30).

Much of the collaboration from the previous year was also followed up in 2015. This involves in RA1 the collaborations with professor T. Coulson, Department of Zoology, University of Oxford, UK. in constructing the data base of individual-based demographic data of birds and mammals, involving a large number of researchers from many parts of the world. Furthermore, the research on the trophic interactions in Arctic ecosystems involving researchers in United Kingdom and USA was also continued. In Research Area 2 the research collaborations between researchers at CBD and prof. Marcel E. Visser, Netherlands Institute of Ecology, Wageningen, The Netherlands, ass. professor Niels Dingemans, Max Planck Institute for Ornithology, Seewisen, Germany and dr. Luis-Miguel Chevin, CEFE, CNRS, Montepellier, France were further expanded in 2015.

In 2015 a more extensive collaboration between researchers at CBD and professor Francisco Cao from Out of Equilibrium Dynamics Group of the Universidad Complutese de Madrid, Spain was established. The aim of this collaboration is to develop models for the dynamics of interacting species in a fluctuating environment and how these interactions are affected by harvesting. Graduate student Javier Jarillo spent the period January 30 – May 7 at CBD to work on these problems. This joint venture will be central for providing the expected contribution from CBD to fulfil the goal of the SUSTAIN-project.

The interactions with the Metapopulation Research Group at the University of Helsinki were further strengthened in 2015. This involves shared positions (professor Ovaskainen in 50 % and associate professor Arild Husby in 20 % at CBD). This resulted in a joint project funded by NFR in 2015 under the leadership of A. Husby.

Members of CBD have during the period 1.7.2013-31.12.2014 made 36 appearances at congresses, conferences or workshops abroad. In addition, CBD organized three international workshops in Trondheim (see p. 23-27). In addition, a conference where graduate students and postdocs particularly aimed at the SAB was held at Trondheim January 19-20 2015.

5. POPULAR SCIENCE

Several of the research projects at CBD recieved attention by the media. Articles presenting the work in all of the three large field projects operated by CBD at the coast of Helgeland in northern Norway (house sparrows, water voles and moose) appeared in regional newspapers and local broadcasts.

In international media, CBD's research on climate impact on the terrestrial ecosystem in Svalbard adrew attention . This included radio interviews in Yale Climate Connections (a podcast for 200 US radio channels) and a news report from the Arctic Frontiers Conference held in Tromsø (national radio channel P4). CBD was also central in a news story by Arctic Deeply (News Deeply, US) on the extreme warm spell covering most of the Arctic around new year, and its potential implications for wildlife such as the reindeer. Furthermore, results from the remote sensing work of the interdisciplinary REINCLIM project on climate-plant-reindeer dynamics in Svalbard were extensively covered by NASA and chosen as "image of the day".

Other results obtained at CBD have caught some attention from the media in 2015. The paper on color change in Dalechampia blossom published by Pélabon et al. in Functional Ecology had some echoes in the Dutch journal Bioniews where the multiple function and the complexity of the transformed Dalechampia leaves were extensively commented. Bolstad et al.'s paper in Proceedings of the national Academy of Science of the United States of America dealing with the evolvability of the allometric slope has also received attention, first in the journal PNAS itself (Harrisson 2015, http://www.pnas.org/content/112/44/13426.extract) but also in the Norwegian popular science journal Gemini (http://gemini.no/2015/09/flueavl-kaster-lys-over-100-ar-gammel-biologigate/) as well as in Phy.org (http://phys.org/news/2015-09-fruit-flies-century-old-biological.html).

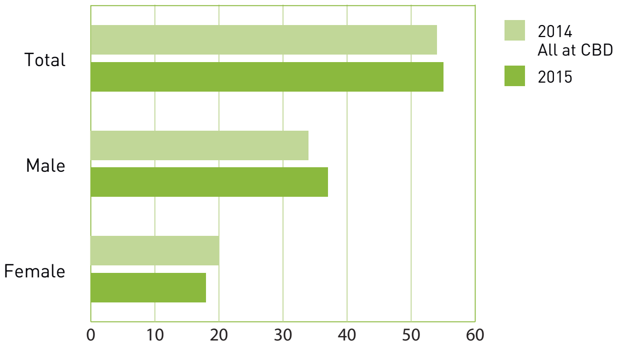
6. GENDER EQUALITY

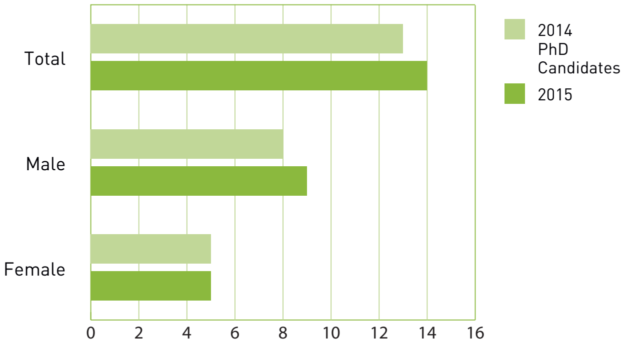
Two female professors (Gunilla Rosenqvist and Ingelin Steinsland) were actively involved in the CBD. This means that there is a strong male-bias in the sex-composition among the core members of the CBD. At the end of 2015 48 % of the Ph.D students and postdocs were female.

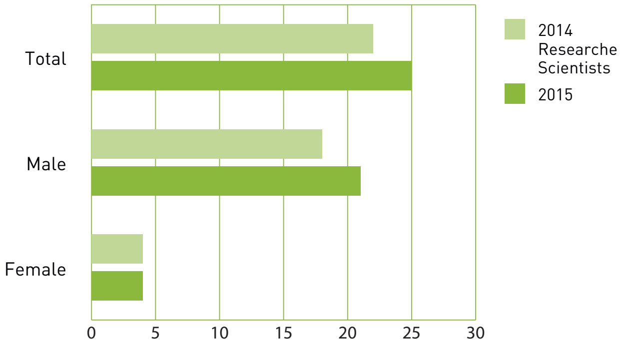
It is a central focus for the leadership of CBD to increase the recruitment of females to positions at all levels because we strongly believe that a balanced sex-ratio generates an environment that will facilitate excellence in research. CBD will facilitate such foreign visits by maintaining long-term collaboration with those research groups where visitors can soon obtain the logistics necessary e.g. for housing, childcare and schooling. We hope this will facilitate future recruitment of females to senior positions at CBD.

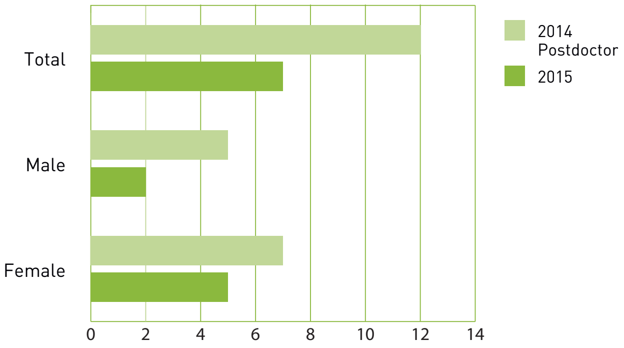
At the end of 2015 the overall female involementent in the centre were 36%.
Of our young researchers -Postdocs and Ph.Ds 48% are female

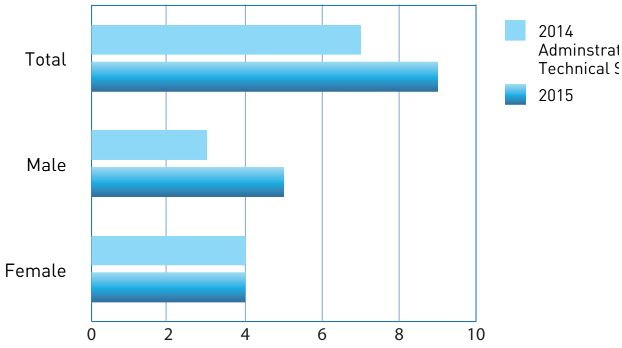
GENDER DISTRIBUTION







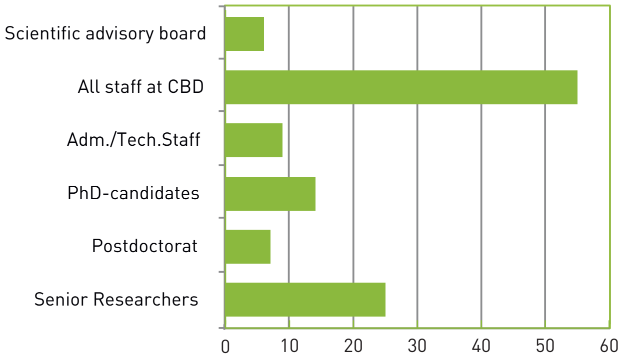




7. KEY FIGURES

Key numbers in CBD 2014	2015	2014	2013
Staff			
Senior Researchers	25	26	22
Postdoctorat	7	12	10
PhD-candidates	14	13	12
Adm./Tech Staff	9	7	3
All staff at CBD	55	58	47
Scientific advisory Board	6	6	6
Results			
Journals	60	58	40
Anthologies		11	25
Reports		5	11
Media attentions	>30	12	42
Books/chapters	2	2	
Costs and funding			
Operational Costs	18 316	17 989	8 689
Funding NINA	500	500	500
NFR	13 010	6 899	558
NTNU	4 806	10 590	7 631

OVERVIEW ALL PERSONELL AT CBD IN 2015



Appendix 1 – CBD members

CBD Board

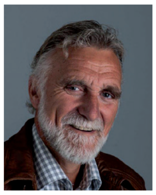

Bernt-Erik Sæther
Director


Steinar Engen
Deputy Director


Solveig Johnsen
Centre Coordinator


Anne Borg
Decan NT-Faculty
Chair Board


Geir Øien
Professor
Decan IME-faculty


Reidar Andersen
Director
NTNU University Museum


Jorunn Myklebust
Director
NINA


Yngve Svarte
Managing Director
Norwegian Environment Agency

SAB Scientific Advisory Board

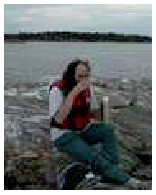

Steve Beissinger
Professor
Department of Environmental Science, Policy & Management
University of California
Berkely, USA


Ben C. Sheldon
Professor
Edward Grey Institute
Dept of Zoology
University of Oxford,
United Kingdom


John Fryxell
Department of Integrative Biology
University of Guelph,
Canada


Jean-Michel Gaillard
Professor
Directeur de Recherche, Research Unit 'Biométrie et Biologie Evolutive',
CNRS, University of Lyon, France


Marcel E. Visser
Head of Department
Animal Ecology
Netherlands Institute of Ecology (NIOO-KNAW),
The Netherlands


Robert O'Hara
Professor
Biodiversity and Climate Research Centre
Frankfurt am Main,
Germany
SAB member

PhD Students


Ane Marlene Myhre
PhD IBI


Elena Albertsen
PhD CBD

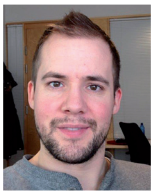

Erlend Fossen
PhD IBI


Mathilde Le Moullec
PhD IBI


Peter Skjolte Ranke
PhD CBD


Endre-Grüner Ofstad
PhD CBD


Stine Svalheim Markussen
PhD IBI


Thomas Kvalnes
PhD IBI


Øystein Nordeide Kielland
PhD IBI


Øystein Hjorthol Opedal
PhD IBI


Emma-Liina Marjakangas
PhD


Thomas Haaland
PhD


Bart Peeters
PhD

PostDocs


Maja Tarka
PostDoc
CBD


Marlène Gamelon
PostDoc
IBI


Nerea Abrego
PostDoc
CBD


Olivia Langhammer
PostDoc
IBI


Erik Blystad Solbu
PostDoc
CBD

Researchers


Anna Marie Holand
Researcher
CBD


Brage Bremseth Hansen
Researcher
CBD


Hanno Sandvik
Researcher
CBD


Håkon Holand
Researcher
CBD


Ingerid Julie Hagen
Researcher
CBD


Bernt Rønning
Engineer
CBD


Petri Kemppainen
Researcher
IBI


Tim Burton
Researcher
IBI


Irja Ida Ratikainen
Researcher
CBD


Ivar Herfindal
Researcher
CBD

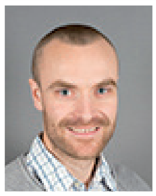
Researchers at NINA


Ola Diserud
Sr. Researcher
NINA


Erling Johan Solberg
Sr. Researcher
NINA


Bram van Moorter
Researcher
NINA


Manuela Panzacchi
Researcher
NINA


Geir Hysing Bolstad
Researcher II
NINA

Professors / Associate Professors


Christophe Pélabon
Professor
IBI


Gunilla Rosenqvist
Professor
IBI


Otso Ovaskainen
Professor (50%)
IME


Arild Husby
Ass. Professor (20%)
CBD


Sigurd Einum
Professor
IBI


Jonathan Wright
Professor
IBI


Ingelin Steinsland
Professor
IME


Thor Harald Rinsby
Ass Professor
IBI

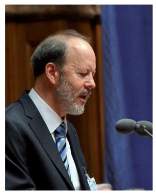

Vidar Grøtan
Ass. Professor
IBI


Jarle Tufto
Professor
IME


Henrik Jensen
Ass. Professor
IBI


Anders Gravbrøt Finstad
Ass. Professor
NTNU University Museum


Stig William Omholt
Professor
Division Director
Faculty of Medicine

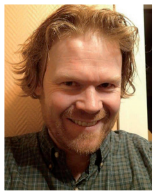

Russel Lande
Professor
IBI
(20 %)

Tech Staff


Varvara Iaschcenko
Engineer
IBI


Linn-Karina Selvik
Engineer
IBI


Anna Båtnes Solvang
Engineer
IBI


Henrik Pärn
Engineer
CBD

APPENDIX 2: SCIENTIFIC PRODUCTION CBD 2015

Abrego N., Bässler C., Christensen M., & Heilmann-Clausen J. 2015. Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biological Conservation* **191**: 469-477.

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Daphnia magna is one of the model organisms that are being used at CBD to study responses to environmental change, with particular emphasis on eco-evolutionary effects of temperature. Photo: Varvara Yashchenko.

Photo: Brage Bremset Hansen

A freshly caught and marked female Svalbard reindeer, held by one of the many MSc students linked to CBD's research projects in Svalbard.

Svalbard reindeer face future winters with less sea-ice yet more ice covering their food plants. An age-structured population model was recently published in *Oikos* (Lee et al. 2015) and is now being used as a tool to predict climate change effects.

Photo: Brage Bremset Hansen

Photo: Mathilde Le Moullec

"You hold, I measure". CBD research activity in high Arctic Svalbard is depending on collaboration with NPI, NINA, NMBU, UNIS as well as several international institutions.

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Front page photo: *Euglossa dilemma* and *Dalechampia scandens* Photo Øystein H. Opedal

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