cbd
CENTRE FOR BIODIVERSITY DYNAMICS

Annual Report 2021

Norwegian Centre of Excellence

NTNU – Trondheim
Norwegian University of Science and Technology

CBD IN SHORT

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

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

TABLE OF CONTENTS

COVER PHOTO:
A Copper Chafer (*Protaetia cuprea*) take-off from a hand. Insects are important in the ecosystem and humans depend on them. Insects, on the other side, do not depend on humans. Picture taken in Tafjord i Norddal, Møre og Romsdal. 06 July 2011. Photo: Arnstein Staverløkk

Background photo: © Shutterstock

COMMENTS FROM THE DIRECTOR:

Bernt-Erik Sæther
Director CBD

As was the case for 2020, 2021 was a different kind of year for CBD. Because of the Corona pandemic, strong restrictions on social contacts and all kinds of travel were imposed during long periods of the spring and autumn. Fortunately, the restrictions were eased for a period during summer, enabling researchers at CBD to conduct field work as planned so serious gaps in the time series were avoided.

It is my feeling that the members of CBD, to a large extent, were able keep up with their original plans of progress in this second year of the pandemic. However, the periods with reduced in-person social interactions were challenging, which made it much more difficult and laborious to maintain and develop interactions and networks with other colleagues both locally, nationally and internationally.

As in previous years, 2021 also brought large changes in the staff of the CBD. Seven PhD-students defended their thesis. Two PhD-students and 5 postdocs also started at the center, mainly related to hirings at associated projects.

This year, several researchers at CBD were awarded externally funded projects. Researcher Eivind Undheim received an ERC Starting Grant for the project *Lacewing venom: Linking the molecular and phenotypic evolution of adaptive traits* (VenomEvolvability). Professor Cameron Ghalambor was awarded a Fellesløft-grant for the project *Physiological mechanisms underlying insect community responses to climate change*, which is co-funded by the Research Council of Norway and NTNU. The Research Council of Norway also funded the project *Paleo-genomics to reconstruct the evolutionary responses of endemic high-arctic reindeer to past environmental change* (ColdRein) lead by Michael Martin and the Young Investigator

project *Social dynamics and eco-evolutionary feedbacks in wild populations* to Yimen Araya-Ajoy.

An important milestone for the research at CBD was the launch of the project *Ecosystem Trøndelag*. The aim of this project is to analyse patterns of variation in species diversity along ecological gradients going from the coastal landscape in the west via forested areas around the city of Trondheim to alpine regions close to the Swedish border in the east. Including a wide range of taxa, the central focus of this project is to analyse the relationship between temporal and spatial variation in the turnover rates of species and how these are affected by different environmental covariates. The field work in this project was done in close collaboration with the municipalities in the study areas, which will hopefully facilitate rapid implementation of results into practical management.

In 2021, several researchers at CBD were involved in producing summaries of the results obtained in 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. In this project, CBD was one of three principal nodes (the two others are the Centre for Ecological and Evolutionary Synthesis, University of Oslo, and the Department of Arctic and Marine Biology, UiT Arctic University of Norway). Several of the results were summarized in the *Climate Research Special Issue 35*, in which CBD-researchers were involved in 9 papers. An important contribution of CBD to this project has been the development of models for sustainable exploitation in a fluctuating environment that includes species interactions in space, showing that harvesting can also affect the dynamics of non-harvested species and, hence, strongly affect structures of ecosystems.

The research at CBD is divided into three research areas (RAs): population ecology, evolutionary biology and community dynamics. In 2021, several papers were published on problems located at the intersections between the different RAs and, therefore, used integrated approaches both from ecology and evolution. For example, in a paper published in *American Naturalist*, S. Engen and collaborators used quantitative genetic models to derive predictions about the structure of ecological communities. This paper unifies theory from all three research areas. Similarly, C. Pelabon and collaborators inferred spatiotemporal variation in the strength of selection from some basic environmental variables and showed how responses to selection can be statistically

assessed (two papers published in the journal of *Evolution*). In American Naturalist, Sæther et al. showed that one of the classical concepts in population genetics, Sewall G. Wright's adaptive topography, can be utilized to analyse selection and phenotypic evolution incorporating ecologically realistic assumptions about population dynamics. Another important contribution, published in *Ecology Letters*, was the work by C. Coste and collaborators for how demography affects the familial structure of populations and, thereby, the kinship structure. Variation in the relationship among kin also has important implications for the evolution of social systems and the rate of spread of disease (paper published in *Nature Ecology and Evolution*). This clearly illustrates the importance of including ecologically realistic assumptions in analyses of fundamental biological processes.

The effects of variation in the geographical distribution of abundance of individuals are now a central focus for the research in all three RAs. In 2021, 21 papers were published that included a spatial aspect, ranging from the consequences of immigrations for evolution of local micro-adaptations (Reid et al. in *Evolution Letters*) to age-dependent variation in spatial synchrony of age-classes of marine fishes (Marquez et al. in *Ecology*) and geographical variation in the distribution of tree species in South American forests (Marjakangas et al. in *Plant Ecology*).

In 2021, an important focus in RA1 has continued to be analyses of how individual heterogeneity in demography causes challenges for predicting population responses to changes in the environment (e.g. caused by climate change). Several researchers at CBD have been involved in a network of researchers to develop models and statistical methods to assess the effects of such individual heterogeneities in demography as a follow-up of a Lorentz workshop on *Individual heterogeneity in animals' life histories*: more than meets the eye in Leiden, the Netherlands, February 3-7, 2020. This collaboration has identified and contributed to the solution of several important problems (e.g. by Fay et al. in Methods in *Ecology and Evolution*) that must be addressed before comparative analyses of individual heterogeneity in demography across species with different life histories can be done. Furthermore, a mechanistic understanding of the general decrease in survival and reproduction by age have been the focus of two papers published in the *Proceedings of the National Academy of Sciences USA* by Froy et al. and by Omholt and Kirkwood.
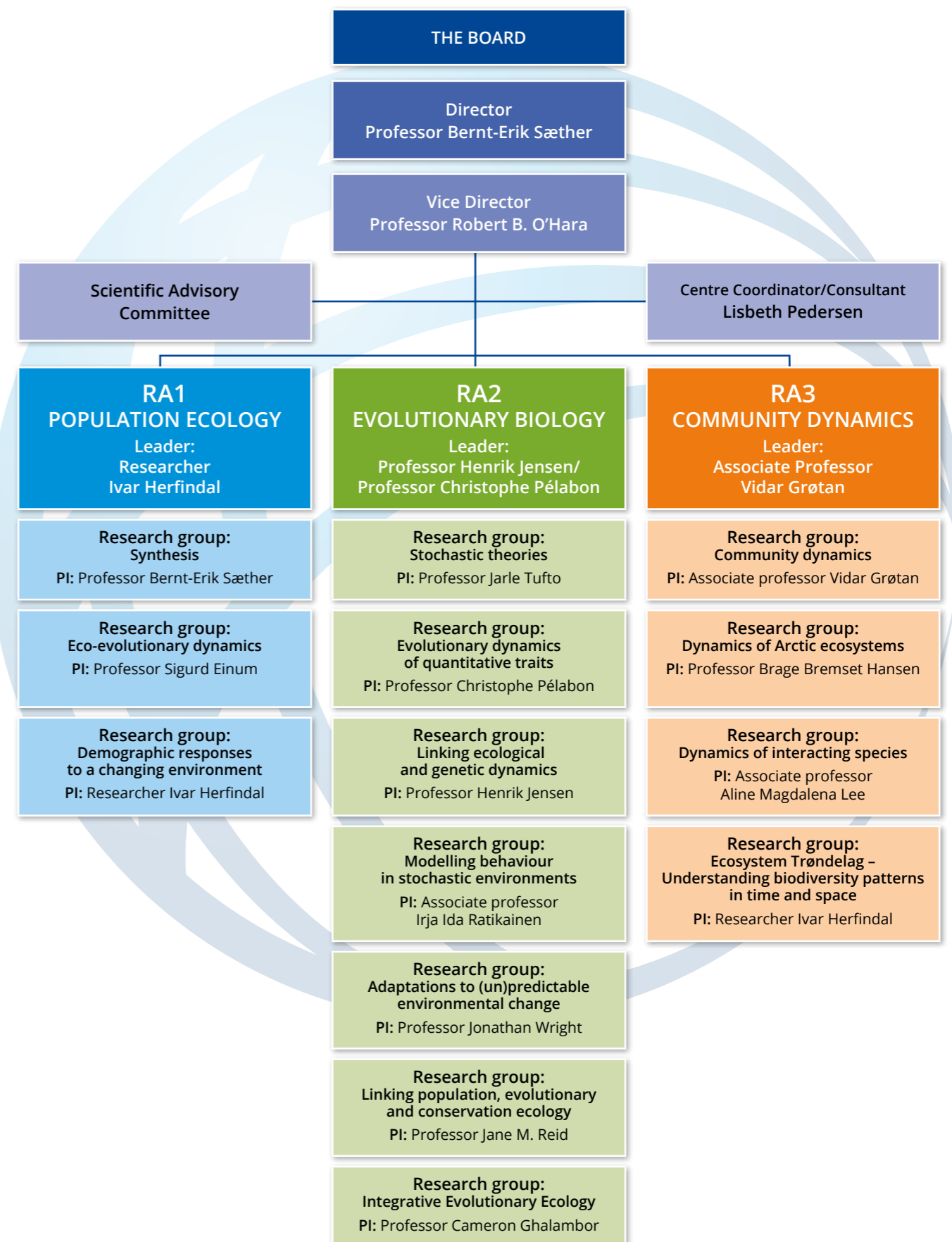
An important milestone was achieved in 2021 by the publication of the book *Demographic Methods across the Tree of Life*, edited by Roberto Salguero-Gomez and Marlène Gamelon (20 % Researcher at CBD). Several of the chapters include methods and approaches developed at CBD and will therefore contribute to making these more widely known and applied. This is illustrated by the fact that 9 researchers at CBD have contributed to 6 chapters in this book.

CBD has also continued to support the work by the Netherlands Institute for Ecology in building up the SPI-Birds database, which is a meta-base that includes a large number of population studies especially of hole-nesting birds across Europe extensively described by Culina et al. in a paper published in the *Journal of Animal Ecology*. Potentially, this provides an excellent possibility for analysing the effects of environmental changes on population processes and species interactions across large geographical areas.

In RA2, a lot of activity has occurred as a continuation of the Center of Advanced Study (CAS) -project *Evolvability: A New and Unifying Concept in Evolutionary Biology?* with professor Thomas F. Hansen, University of Oslo, and professor Christophe Pelabon at NTNU as leaders. An important milestone summarizing the state of art in this field of research was published by the leaders of this project as a review in *Annual Reviews in Ecology*, Evolution and Systematics.

In addition to work involved in the completion of SUSTAIN, a focus in RA3 has been on analyses and modelling of trophic interactions. Analyses have been published on how predator-prey interactions affect the composition of bird communities (Burgas et al. in *Frontiers in Ecology and Evolution*) and how variation in phenology affects producers and consumers differently (Roslin et al. in *Nature Climate Change*). Similarly, in a paper published in *Nature Ecology and Evolution*, Samplonius et al. underlines strongly the importance of broadening the approach for improving our understanding of how phenological changes are likely to affect consumer-producer interaction.

To summarize, the last two years have been a crash-course in how important personal interactions are for making scientific progress. Hopefully, this will be appreciated in the coming years when the working conditions return to normal.

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SCIENTIFIC ACTIVITY

RESEARCH GROUP: SYNTHESIS

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

Aim: *To apply stochastic models to understand processes affecting the dynamics of populations and phenotypes in fluctuating environments.*
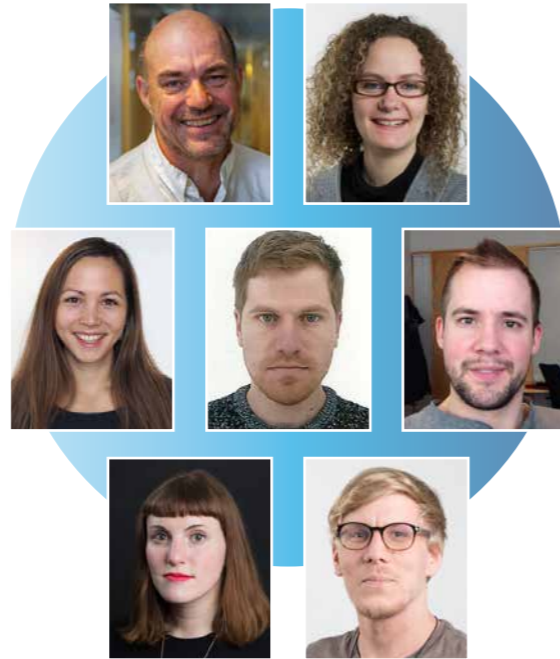
Bernt-Erik Sæther, Marlène Gamelon, Hannah Froy, Rémi Fay,
Thomas Kvalnes, Lara Veylit, Stefan Vriend

MAJOR SCIENTIFIC CONTRIBUTIONS

Evolution in density-regulated populations living in fluctuating environments

An understanding of how expected global changes will affect biological diversity requires models that include changes in the characteristics of populations over time. This variation will affect the rate of evolution of new adaptations to an altered environment. Unfortunately, we lack a theoretical framework which is based on ecologically realistic assumptions to conduct such analyses (Govaert et al. 2019). We have previously provided a general theoretical framework for analyses of phenotypic evolution in fluctuating environments subject to density-regulation (Lande et al. 2009, Engen et al. 2013). A general and surprising conclusion from our analyses is that changes in the mean phenotype of the individuals in the population may strongly affect the strength of selection (Engen et al. 2020). This means that frequency-dependent selection will then potentially influence how fast new adaptations to an altered environment can evolve.

Sæther et al. (Sæther et al. 2021) applied a new evolutionary maximum principle, i.e. **there exists a general quantity, the expected population size, that evolution tends to maximize** (Engen et al. 2020), to calculate the adaptive topography of four different reproductive traits (timing of egg-laying, clutch size, number of fledglings and mean tarsus length) in a population of

the collared flycatcher *Ficedula albicollis* breeding at the island of Gotland in southern Sweden. This enabled us to examine the influence of directional and stabilizing selection acting on these reproductive traits. We found evidence for density-dependent selection, i.e., that those phenotypes with lower fitness at small population sizes were superior close to the carrying capacity, K, compared to those with higher fitness at small population densities. As previously found for the total number of eggs produced per season by great tit females breeding in the forest of Hoge Veluwe in the Netherlands (Fig. 1a), this generated r- and K-selection on date of egg-laying (Fig. 1b) and number of fledglings. This generated an adaptive topography influenced by changing population size; phenotypes favored at low densities were different from those with higher fitness at population sizes close to the carrying capacity, K. In addition, fluctuations in population size induced correlated selection among different reproductive traits (Fig. 1b). Thus, intermediate phenotypes were those that maximized the Malthusian fitness (Fig. 1a), suggesting that r- and K-selection may affect the evolution of reproductive strategies of small temperate passerines towards intermediate trait values. By comparing the actual values of different life history traits with the location of these maxima (Fig. 1b), we were able to evaluate the influence of r- and K-selection on different reproductive traits in this species.
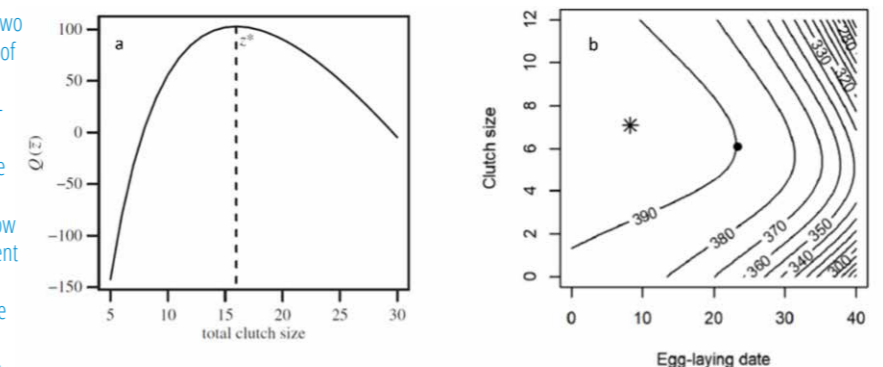
Evolution of the **G**-matrix

The **G**-matrix consists of the additive genetic variance and co-variance among multiple phenotypic traits. Its structure strongly influences the response to selection (Lande 1979), but the processes affecting the structure of the **G**-matrix are poorly understood. This severely restricts our ability to predict phenotypic evolution and rates of ongoing adaptation (Pujol et al. 2018, Shaw 2019). For example, there are remarkably few examples in which micro-evolutionary responses to selection at a given locality have been correctly predicted (Pujol et al. 2018). This becomes even more puzzling considering the many cases in which significant directional selection have been documented on fitness-related traits with heritability significantly greater than zero but without any apparent evolutionary response (Merilä et al. 2001, Pujol et al. 2018). This illustrates two great paradoxes in evolutionary biology: the maintenance of substantial genetic variation in traits assumed to be closely related to differences in fitness and the lack of response in heritable traits subject to relative strong directional selection.

Engen and Sæther (2021) investigated the simplest generalization of single locus models to quantitative genetics with many loci, assuming simple additive effects on a set of phenotypes and a linear approximation to the fitness function. If a single locus never codes for more than two traits, then additive genetic covariance between two phenotype components always has the opposite sign of the product of their coefficients in the fitness function under no mutation, a pattern that is likely to occur frequently also in more complex models. In our major examples only 1-2 percent of the loci are over-dominant for fitness, but they still account for practically all dominance variance in fitness as well as all contributions to the **G**-matrix. In this model, the additive genetic variance of fitness became practically zero as it should be at stasis according to Fisher's (1930) Fundamental Theorem of Natural Selection. However, traits highly correlated with fitness usually had significant dominance variance. These analyses show that the structure of the **G**-matrix reveals important information about the contribution of different traits to fitness, and that focus should also be directed towards traits with large contribution to eigenvectors of the **G**-matrix with small eigenvalues.

Figure 1. Examples of adaptive topographies in two hole nesting bird species. (a) Intermediate values of the total number of eggs produced maximized the expected population size in a Dutch great tit population (Sæther et al. 2016). (b) Different combinations of date of egg-laying and clutch size maximize the expected population size in the collared flycatcher (Sæther et al. 2021). The solid lines show density-depedent adaptive topographies at different population sizes (numbers), and the solid circle in (b) and the dashed line in (a), respectively, denote the values maximizing evolution, whereas the star indicates the actual mean values in the population.

RECOMMENDED READING:

Engen, S., Y. G. Araya-Ajoy, J. Wright, and B.-E. Sæther. 2020. Phenotypic evolution in stochastic environments: the contribution of frequency- and density-dependent selection. Evolution **74**:1923-1941.

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Sæther, B.-E., S. Engen, L. Gustafsson, V. Grøtan, and S. J. G. Vriend. 2021. Density-dependent adaptive topography in a small passerine bird, the collared flycatcher. American Naturalist **197**:93-110.

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RESEARCH GROUP: ECO-EVOLUTIONARY DYNAMICS

Members in 2020:
PI: Professor Sigurd Einum
Researcher Tim Burton
PhD candidate Astrid Raunsgård
PhD candidate Safa Chaabani
PhD candidate Semona Issa

Tim Burton, Sigurd Einum, Safa Chaabani, Semona Issa
Right: Astrid Raunsgård

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

MAJOR SCIENTIFIC CONTRIBUTIONS

Our activity in 2021 focused on how organisms respond to a broad range of environmental factors including temperature, seasonality, mercury, and parasites. Some of this work asks how different genotypes respond differently to different environmental conditions and, hence, how environmental change can lead to evolutionary responses (Bruijning et al. 2021, Fossen et al. 2021). Other parts ask how different components of fitness are influenced by environmental contaminants under contrasting temperature regimes (Issa et al. 2021) or how environmental conditions may shape optimality of life history traits (Einum et al. 2021). As in previous years, we continue to use the freshwater zooplankton *Daphnia* as our main empirical study system.

In one of these studies, we addressed the commonly observed pattern in aquatic ectotherms whereby adult body size declines with increasing environmental temperature experienced during development (i.e., as a phenotypically plastic response), a pattern known as the temperature-size rule. One influential hypothesis explaining this observation is that the challenge of obtaining

sufficient oxygen to support metabolism becomes greater with increasing body size and, more so, at high temperatures. Yet, previous models based on this hypothesis do not account for phenotypic plasticity in the physiology of organisms that counteract oxygen limitation at high temperature. Einum et al. (2021) modelled the predicted strength of the temperature-size response using previous estimates from our group of how both the oxygen supply and demand is affected by temperature when allowing for phenotypic plasticity in the aquatic ectotherm *Daphnia magna*. These predictions remained highly inconsistent with empirical temperature-size responses, with the prior being close to one order of magnitude stronger than the latter (Fig 1). These results failed to provide quantitative support for the hypothesis that oxygen limitation drives temperature-size clines in aquatic ectotherms. Einum et al. (2021) concluded that future studies into the role of oxygen limitation should address how the strength of the temperature-size response may be shaped by evolution under fluctuating temperature regimes, which may produce different predictions. Furthermore, by demonstrating a pronounced deviation between predicted responses and

empirical observations, this study cautions against using oxygen limitation models to project future size distributions of aquatic ectotherms in response to climate change. This approach has been used to predict dramatic declines in the body size of marine fishes in response to future climate change. For example, Arctic oceans have been projected to show an increase in temperature of 0.2 °C during 2000-2050 and no noticeable change in oxygen content. Yet, maximum body size of fish species currently residing in these waters has been predicted to decline by close to 10% over the same period due to the effect of increased oxygen limitation with warming. This is far from observed temperature-size relationships in aquatic ectotherms which are less than a 1% decline in mass per 0.2 °C increase. We show that even when accounting for phenotypic plastic responses that increase oxygen supply under high temperatures, the predicted slope of the temperature-size relationship remains too steep to describe empirical data well, and it will be highly misleading to employ such simple deterministic models when predicting future changes in ectotherm size distributions.

RECOMMENDED READING:

Bruijning, M., Fossen, E. I. F., Jongejans, E., Vanvelk, H., Raeymaekers, J. A. M., Govaert, L., Brans, K. I., Einum, S., De Meester, L. (2021) Host–parasite dynamics shaped by temperature and genotype: Quantifying the role of underlying vital rates. Functional Ecology, doi.org/10.1111/1365-2435.13966

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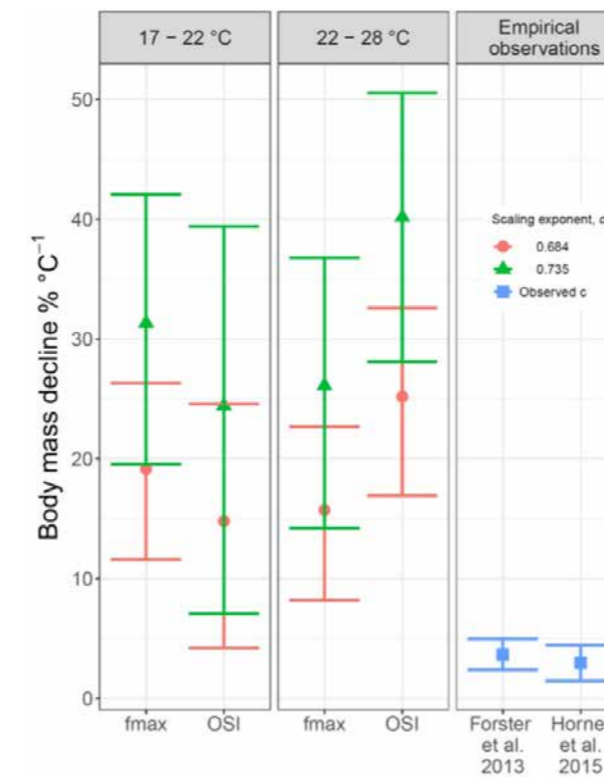
Figure 1. Predicted and observed declines in body mass (BM) of aquatic ectotherms with increasing temperature (temperature-size rule slopes, error bars ± 95% CI). "With plasticity" gives the predicted slopes based on empirical measurements of *fmax*, and "Without plasticity" those based on the oxygen supply index (OSI). Slopes were estimated for two temperature intervals and for the two boundary values of the surface area-body mass scaling exponent *c* (red circles *c* = 0.684, green triangles *c* = 0.735). Values (mean ± 1.96 SE) from two meta-analyses of aquatic ectotherms are given for comparison.

Research group:
Demographic responses to a changing environment

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

Aim: *To understand causes and consequences of spatial and temporal variation in demography*

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

Major scientific contributions

One of the main challenges to obtain a sustainable management of populations and ecosystems is to assess how harvesting, in interaction with climate, affects populations and ecosystems. However, a first step towards such knowledge must be to describe consequences of harvesting alone on population dynamics and demography. The Vega moose population has been studied for decades with such a purpose as a collaboration between NINA and CBD. Results from this unique study system have revealed that harvesting affects population demography in several ways. In addition to the more obvious direct consequences on survival and recruitment rates, there are more subtle effects that also can play a major role for population dynamics and evolutionary processes (Herfindal et al. 2022a).

The spatial scale of population co-fluctuations, also known as spatial population synchrony, is important, for instance, for extinction risk and how to implement spatially explicit harvesting strategies. Several factors can affect spatial population synchrony, but spatial autocorrelation in environmental variation has been suggested as the main driver. An apparent general pattern is that the spatial autocorrelation in environmental conditions, such as temperature, is highest in terrestrial and marine systems as compared to limnic or coastal ecosystems (Herfindal et al. 2022c). A compilation of studies on plant and animal populations in different ecosystems confirmed the importance of environmental autocorrelation on population synchrony (Herfindal et al. 2022b). However, it is also evident that climate change may alter the scaling of population synchrony if there is spatial heterogeneity in how climate change affects local populations (Herfindal et al. 2022b).

Climate change affects both thermal and cryptic environments for wildlife populations, which poses challenges for species that are polymorphic in colouration or change coloration seasonally. Arctic foxes in the mountains of Norway are interesting because they are both polymorphic in coloration, with white, blue and a rare sand coloured morph, and alternate between summer and winter pelage. One of the puzzling features of the restoration program in Norway is that the frequency of the blue morph foxes has been increasing among wild-born foxes compared to the proportion released from the captive population. The demographic performance of the different colour morphs was examined in an 11-year population study. Blue morph foxes had higher breeding propensity and survival under natural conditions (Di Bernardi et al. 2021). Moreover, there was an interaction between demographic performance and environmental conditions, where blue morph juveniles tended to have higher survival than white morph individuals during cold winters. The demographic differences do not appear to be related to benefits of camouflage or thermoregulation but may be due to intrinsic differences in physiology associated with the colour morphs, such as the stress response, immune function or reproductive behaviour.

The current warming of the oceans has been shown to have detrimental effects for a number of species. Most demographic time series are too short to study the effects of climate on

wildlife in the classical sense of meteorological patterns over at least 30 years. However, Hansen et al. (2021) analysed a harvest time series of Atlantic puffins (*Fratercula arctica*) that goes back as far as 1880. It originates in the world's largest puffin colony, in southwest Iceland, which has recently experienced a strong decline. By estimating an annual chick production index for 128 years, Hansen et al. (2021) found prolonged periods of strong correlations between local sea surface temperature (SST) and chick production. The sign of decennial correlations switched three times during this period, where the phases of strong negative correlations between puffin productivity and SST correspond to the early 20th century Arctic warming period and to the most recent decades. Most of the variation (72%) in chick production was explained by a model in which productivity peaks at an SST of 7.1 °C, clearly rejecting the assumption of a linear relationship. There is also evidence supporting non-stationarity. The SST at which production peaked has increased by 0.24 °C during the 20th century, although the increase in average SST during the same period has been more than three times faster. This indicates that the population's decline is at least partially caused by the increasing SST around Iceland.
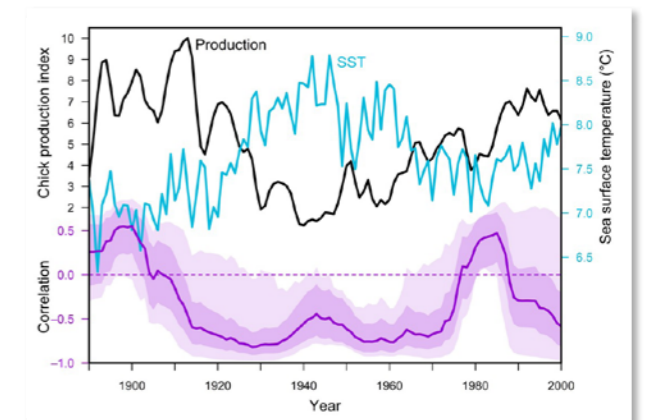
Roads and traffic constitute a more direct effect of human activities on animals. To quantify negative and positive effects of roads on bird species richness, Kroeger et al. conducted comprehensive meta-analyses. Specifically, they tested how the relationship between roads and bird richness varies when considering road type, habitat characteristics and feeding guild association. Overall, bird richness was similar in road habitats compared to nonroad habitats, but impacts of roads on bird richness are highly context dependent. Bird richness was lowered by road presence in areas with denser tree cover but did not differ according to road type. Richness differences between habitats with and without roads further depended on the primary diet of species. For example, the richness of omnivores was positively affected by road presence. However, further research should explicitly test for differences in species composition and abundance to try and disentangle contexts where a road will have negative effects and where it will not.

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Di Bernardi, C., Thierry, A.-M., Eide, N.E., Bowler, D.E., Rød-Eriksen, L., Blumentrath, S., Tietgen, L., Sandercock, B.K., Flagstad, Ø., and Landa, A. 2021. Fitness and fur colouration: Testing the camouflage and thermoregulation hypotheses in an Arctic mammal. Journal of Animal Ecology, **90**, 1328–1340.

Hansen, E.S., Sandvik, H., Erikstad, K.E., Yoccoz, N.G., Anker-Nilssen, T., Bader, J., Descamps, S., Hodges, K., Mesquita, M.D.S., Reiertsen, T.K., and Varpe, Ø. 2021. Centennial relationships between ocean temperature and Atlantic puffin production reveal shifting decennial trends. Global Change Biology, **27**, 3753–3764.

Herfindal, I., Lee, A.M., Hamel, S., Solberg, E.J., and Sæther, B.-E. 2022a. Demographic consequences of harvesting: a case study from a small and isolated moose population. Climate Research, **86**, 53-64.

Herfindal, I., Lee, A.M., Marquez, J.F., Le Moullec, M., Peeters, B., Hansen, B.B., Henden, J.-A., and Sæther, B.-E. 2022b. Environmental effects on spatial population dynamics and synchrony: lessons from northern ecosystems. Climate Research, **86**, 113–123.

Herfindal, I., Aanes, S., Benestad, R.E., Finstad, A.G., Salthaug, A., Stenseth, N.C., and Sæther, B.-E. 2022c. Spatiotemporal variation in climatic conditions across ecosystems. Climate Research, **86**, 9-19.

Kroeger, S.B., Hanslin, H.M., Lennartsson, T., D'Amico, M., Kollmann, J., Fischer, C., Albertsen, E., and Speed, J.D.M. 2022. Impacts of roads on bird species richness: A meta-analysis considering road types, habitats and feeding guilds. The Science of the Total Environment, **812**, 151478.

Shaftel, R., Rinella, D.J., Kwon, E., Brown, S.C., Gates, H.R., Kendall, S., Lank, D.B., Liebezeit, J.R., Payer, D.C., Rausch, J., Saalfeld, S.T., Sandercock, B.K., Smith, P.A., Ward, D.H., and Lanctot, R.B. 2021. Predictors of invertebrate biomass and rate of advancement of invertebrate phenology across eight sites in the North American Arctic. Polar Biology, **44**, 237–257.

Figure 1. Puffin chick production peaked at a sea surface temperature of 7.09°C. The shaded area indicates the 95% confidence interval

Figure 2. Puffin chick production (black) and annual mean sea surface temperature (blue). Their correlations (purple) are estimated from 31-year sliding windows. Shaded areas are 95% confidence intervals with (light) and without (dark) correction for temporal autocorrelation

Research Area 1 POPULATION ECOLOGY

Research Area 1 POPULATION ECOLOGY

Research group: Theoretical and statistical modelling

Current group members:
PI: Professor Jarle Tufto / Professor Steinar Engen

Aim: *To develop stochastic theoretical models and statistical methods for estimating parameters of such models to understand ecological and evolutionary processes involving different forms of environmental and demographic stochasticity.*

Steinar Engen, Jarle Tufto

Major scientific contributions

Statistical models are used to represent imperfect knowledge about physical processes in all the sciences. This includes models of the dynamics of biological diversity. All such models involve unknown model parameters that must be inferred from observed data. Two major paradigms for statistical inference are classical frequentist statistics on the one hand and Bayesian statistics on the other. Within the Bayesian paradigm, probabilities are used to represent subjective beliefs about the model parameters. In contrast to the frequentist paradigm, coherent statistical inference is then, in principle, straightforward, consisting of updating these beliefs via Bayes theorem which leads to a posterior distribution representing degree of belief in different parameter values conditional on the observed data.

In situations where little prior knowledge about unknown parameter values exists, it is generally acknowledged that fully objective choices of priors are not always possible. However, in many applied settings, principles such as shift or scale invariance can be invoked to construct "objective" priors best representing prior ignorance of the parameter values. Such invariance principles often lead to priors with infinite total mass, for example, a uniform density on the whole real number line. Such probability distribution thus violates generally accepted probability axioms and are hence referred to as improper distributions. Still, such priors are routinely used in practice. In some cases, typically when the data is sparse, such improper priors can lead to the posterior distribution also becoming improper.

In Taraldsen, Tufto & Lindqvist (2021) we present an axiomatic foundation of statistics building on previous work by Rényi (1955), replacing the axioms of Kolmogorov (1933). This framework of statistics accommodates both improper priors and improper posteriors, and we prove the existence of a

unique prior to posterior transformation, also in cases where the observed data has infinite prior marginal probability (when the marginal prior probability distribution of the data is not sigma-finite). We also discuss a method, first used by Tufto et. al. (2012, Appendix S4), for sampling from an improper posterior distribution via Markov chain Monte Carlo, something which is usually deemed meaningless elsewhere in the literature (see e.g., Gelfand & Sahu, 1999).

Rather than dismissing Bayesian inference in cases where the posterior distribution becomes improper, we argue that improper posteriors are no more unacceptable than improper priors. In practical terms, an improper posterior playing the role of the prior in subsequent studies only means that more and perhaps a different type of data should be collected.

RECOMMENDED READING:

Gelfand, A. E., & Sahu, S. K. (1999). Identifiability, improper priors, and gibbs sampling for generalized linear models. Journal of the American Statistical Association, **94**(445), 247–253

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Rényi, A. (1955). On a new axiomatic theory of probability. Acta Mathematica Academiae Scientiarum Hungarica, **6**(3), 285–335

Taraldsen, G., Tufto, J., Lindqvist, B.H. (2021) Improper priors and improper posteriors. Scandinavian Journal of Statistics, https://doi.org/10.1111/sjos.12550

Tufto, J., Lande, R., Ringsby, T.-H., Engen, S., Saether, B.-E., Walla, T. R., & DeVries, P. J. (2012). Estimating Brownian motion dispersal rate, longevity and population density from spatially explicit mark-recapture data on tropical butterflies. The Journal of Animal Ecology, **81**(4), 756–769.

Research Group: Evolutionary dynamics of quantitative traits
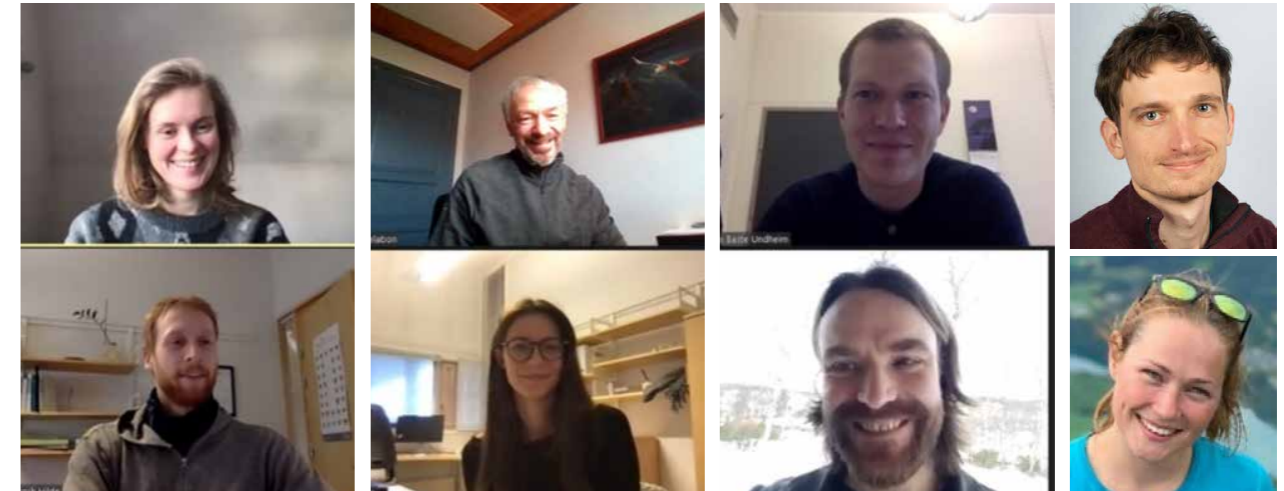
Agnes Holstad, Christophe Pélabon, Eivind Undheim, Yann Czorlich, Christoffer H Hilde, Salomé Bourg, Geir H Bolstad og Anna Andreassen

Current group members:
PI: Professor Christophe Pélabon
Researcher Eivind Undheim
Researcher Geir H. Bolstad (NINA)
Postdoc Salomé Bourg
Postdoc Yann Czorlich (NINA)
PhD candidate Agnes Holstad
PhD candidate Anna Andreassen
PhD candidate Christoffer H Hilde

**Aim:** *Understand the evolutionary dynamics of complex traits*

The group is testing predictive models for the evolutionary dynamics of multivariate quantitative traits, focusing particularly on the evolutionary consequences of specific genetic architectures. Using both experimental and comparative approaches, the group aims at operationalizing measures of the evolutionary potential, or evolvability. These last years, the group has collaborated with F. Jutfelt from the physiology group at the Institute of Biology (NTNU) to study the evolutionary potential of thermal performance traits.

Major scientific contributions

One of the major achievements of the group in 2021 is the publication in Evolution of a study on the predictability of artificial selection studies. We present a simple equation for the error variance of the prediction due to the combined effects of genetic drift and uncertainty in genetic parameters in multivariate characters. Using our own artificial selection experiment on floral traits of the *Dalechampia* blossom, we show how sampling effects may dominate the uncertainty during early generations making it difficult to predict selection responses over few generations, especially for correlated traits.

A second achievement concerns a study on the measurement and interpretation of fluctuating selection in the wild. Fluctuating selection, spatially or temporally, has been suggested as an important mechanism maintaining genetic variation. Estimating selection is particularly difficult, however, and it often remains unclear whether patterns of variation in the selection gradients estimated in wild populations truly reflect fluctuating selection or simply result from measurement error. In a second paper published by the group in *Evolution* in 2021, we combined phenotypic selection studies repeated over several years within and among populations of *Dalechampia scandens* in Mexico and Costa Rica and showed the importance of accounting for the ecological context for interpreting spatial and temporal variation in selection gradients. More specifically, we showed that despite being estimated with large uncertainties, pollinator-mediated selection gradients on blossom traits often changed in response to changes in the pollinator assemblage, the changes in selection
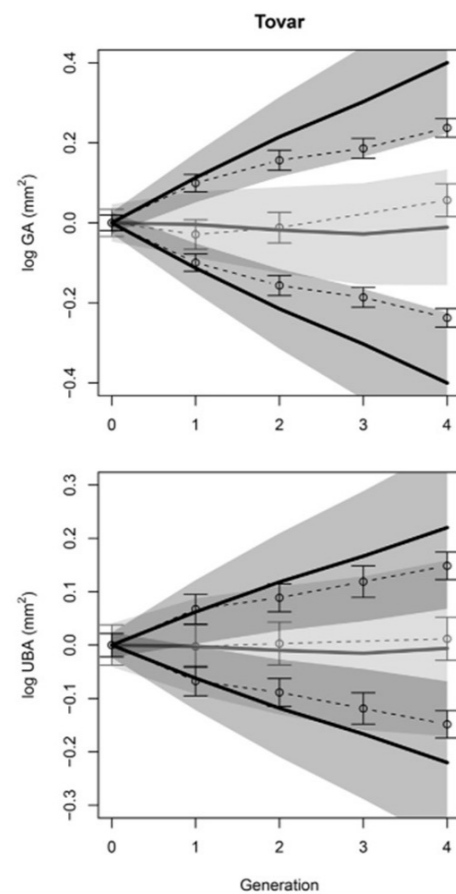
Figure 1: Observed and predicted response to selection on two traits of the *Dalechampia* blossom. The responses are shown for gland area (GA), which is the selected trait, and bract area (UBA), which is the correlated trait. Observed responses centred on the mean of the up- and down-selected lines in trait means (±2SE) are given as the dotted lines. The predicted responses with their prediction intervals (±2SE) are represented by the black lines and shaded area. Control lines are reported in grey with their prediction intervals in light grey.

gradient being specific to the function of the traits. These results thus illustrate how consideration of trait function and ecological context can facilitate both the detection and the causal understanding of spatiotemporal variation in natural selection.

Another important achievement is the review written by Thomas Hansen (UiO) and Christophe Pélabon on the concept of evolvability in evolutionary quantitative genetics. This review describes the history of the evolvability concept within the field of quantitative genetics. This review shows that the idea of evolvability, that is, the generation and the presence of heritable variation, has been associated with the field of quantitative genetics since its inception with the work of Galton. It then summarizes the theoretical and empirical research on evolvability in quantitative genetics of the past 40 years. It particularly shows how new operational measures of evolvability, such as mean-scaled evolvability for univariate traits and conditional evolvability for multivariate traits, have open new possibilities for understanding variation in evolutionary potential and assess the potential constraining effect of low evolvability on macroevolutionary patterns.

RECOMMENDED READING:

Albersten E, ØH Opedal, GH Bolstad, R Pérez-Barrales, TF Hansen, C Pélabon, WS Armbruster. 2020. Using ecological context to interpret spatiotemporal variation in natural selection. Evolution **75**: 294–309.

Hansen, T. F., and C. Pélabon. 2021. Evolvability: a quantitative genetics perspective. Annual Review of Ecology, Evolution, and Systematics **52**: 153-175.

Pélabon, C., E. Albertsen, A. Le Rouzic, C. Firmat, G. H. Bolstad, W. S. Armbruster, and T. F. Hansen. 2021. Quantitative assessment of observed vs. predicted responses to selection. Evolution **75**: 2217-2236.

Pélabon, C., S. D. Côté, M. Festa-Bianchet, J.M. Gaillard, M. Garel, J.F. Lemaître, A. Loison, M. Tidière, and C. Toïgo. 2021. Effects of population density on static allometry between horn length and body mass in mountain ungulates. Oikos **130**: 2161-2169.

Research group: Linking ecological and genetic dynamics

Current group members:
PI: Professor Henrik Jensen
Professor Ingelin Steinsland
Professor Michael D. Martin
Professor Stig W. Omholt
Associate Professor Arild Husby
Associate Professor Stefanie Muff
Associate Professor Thor Harald Ringsby
Researcher Ingerid J. Hagen (NINA)
Postdoc Debora Goedert
Postdoc Laurène Lecaudey
PhD candidate Anne Catriona Mehlhoop
PhD candidate Corne de Groot
    (Ludwig-Maximilians-Universität München)
PhD candidate Dilan Saatoglu
PhD candidate Fabian Kellner
PhD candidate Gabriel David (Uppsala University)
PhD candidate Hamish A. Burnett
PhD candidate Janne C. Hetle Aspheim
PhD candidate John McAuley (University of Edinburgh)
PhD candidate Lasse Frost Eriksen
PhD candidate Michael Le Pepke
PhD candidate Ronja Kiviö
PhD candidate Rori Wijnhorst
    (Ludwig-Maximilians-Universität München)
PhD candidate Sarah Lundregan
PhD candidate Thazin Htay
PhD candidate Vanessa Bieker
PhD candidate Ådne M. Nafstad
Engineer Henrik Pärn
Engineer Oskar Speilberg
Sr. Engineer Peter S. Ranke

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 inter-actions. 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 timescales. 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
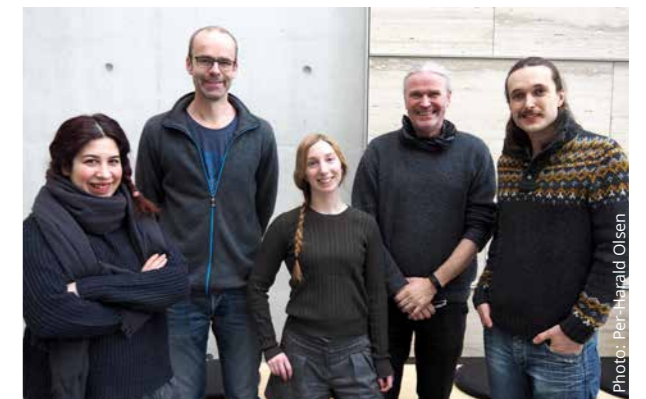
Dilan Saatoglu, Henrik Jensen, Sarah Lundregan, Thor Harald Ringsby, Michael P. Pedersen

studied natural vertebrate metapopulations, including house sparrows, reindeer, 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 along with the results from our studies are not only needed to parameterize and test models developed by ourselves and other RGs at CBD but are also particularly attractive for scientists who wish to use our unique data in national and international collaborative projects that test hypotheses and answer questions in various fields in biology.

MAJOR SCIENTIFIC CONTRIBUTIONS

## Spatial structure and dispersal dynamics

Dispersal may have profound consequences for the evolutionary and ecological dynamics of spatially structured populations. Inter-population exchange of individuals influences the rate of local adaptation, the strength of selection, and the genetic structure of a metapopulation. Dispersal may also affect the risk of local extinctions, reduce the strength of density dependence, increase population densities and increase spatial synchrony in local population fluctuations. Identifying dispersers and their natal populations is often impossible or very difficult in natural populations. We used genome-wide 200K Single Nucleotide Polymorphism data and our novel genetic assignment approach (BONE, network-based estimation) to identify the dispersers in a house sparrow (Passer domesticus) metapopulation and compared these results with extensive capture-mark-recapture information from the same system. Our results showed that assignment accuracy and disperser identification was high even at low levels of genetic differentiation and increased with the proportion of a population that had been sampled. Thus, dispersal studies integrating both ecological and genetic data provide robust assessments of the dispersal patterns in natural populations. Next, we examined how emigration and immigration of house sparrows in the metapopulation were affected by spatial and temporal variation in population size, inter-island distance, local demography and habitat characteristics. Our results showed that emigration and immigration occurred mostly between nearby islands, and island populations with farm and non-farm habitat types received more immigrants when their mean sizes were large. However, there was proportionally and numerically less emigration and immigration involving farm habitat islands, as compared to non-farm habitat islands. Furthermore, emigration in response to spatial differences in mean population size differed between the habitat types: the proportion and number of emigrants was positively related to temporal increases in recruit production on farm islands but not on non-farm islands. The spatial structure of this metapopulation is therefore best described by a spatially explicit model in which the exchange of individuals within each habitat type is strongly affected by the degree of geographical isolation, population size and recruit production. However, these relationships differed between the two habitat types; non-farm islands showing similarities to a mainland-island model type of structure, whereas farm islands showed features more associated with source–sink or balanced dispersal models. Such differential dispersal dynamics between habitat types are expected to have important consequences for the ecological and evolutionary dynamics.

The genetic architecture and fitness-consequences of fur colour variation

Genome-wide association studies provide good opportunities for studying the genetic basis of adaptive traits in wild populations. We used high-density single nucleotide polymorphism and individual fitness data from a wild non-model species, the Arctic fox (Vulpes lagopus). Using a whole-genome approach, we identified the MC1R gene as the sole causal gene underlying the white and blue fur colour morphs that occur in Scandinavian populations of this species. Furthermore, we showed the adaptive importance of fur colour genotypes through measures of individual fitness that link ecological and evolutionary processes. We found a tendency for blue foxes that are heterozygous at the fur colour locus to have higher fitness than homozygous white foxes. The effect of genotype on fitness was independent of winter duration but varied with prey availability, with the strongest effect in years of increasing rodent populations. MC1R is located in a genomic region with high gene density, and this means there is potential for indirect selection through linkage and pleiotropy. Our study shows that whole-genome analyses can be successfully applied to wild species and identify major effect genes underlying adaptive traits. Furthermore, we show how this approach can be used to identify knowledge gaps in our understanding of interactions between ecology and evolution.
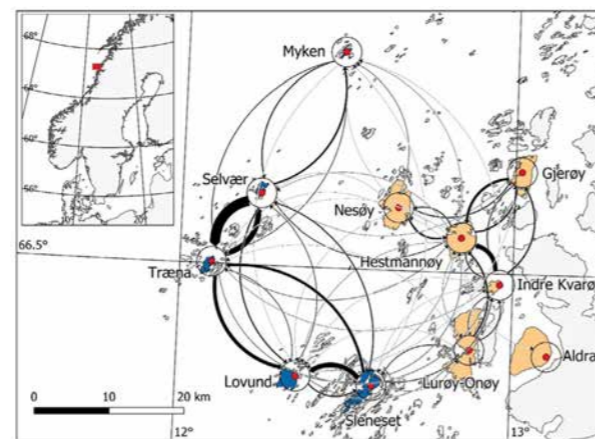
Figure 1. Map showing the house sparrow metapopulation study area. The islands with names are the main study islands in the metapopulation. Two habitat types exist in the metapopulation based on whether islands have farms ("farm islands," closest to the islands) or only gardens and small villages ("non-farm islands," further from the mainland). The arrows show inter-island dispersal events in the period 1993-2014 based on extensive capture-mark-recapture data of individuals ringed as nestlings or recently fledged juveniles (N=2192). The arrow thickness represents the total number of emigrants and immigrants over the whole study period, and the arrowhead shows the direction of dispersal.
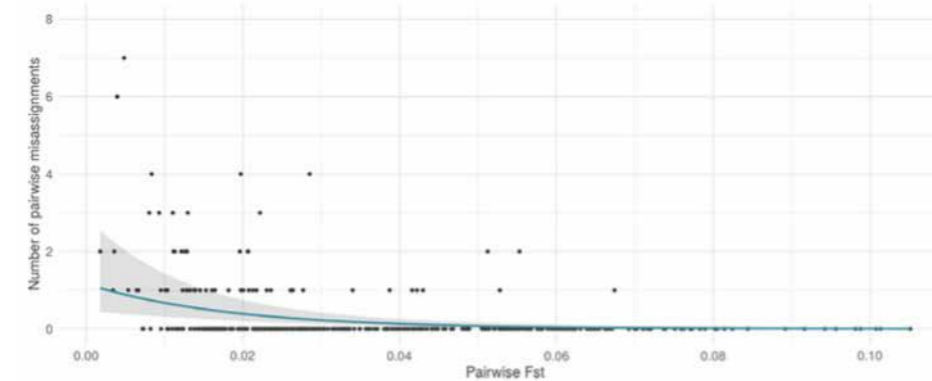

Figure 2. Relationship between the annual number of genetically misassigned recruits and FST for each population pair in an insular house sparrow metapopulation (N=1645 recruits and 414 population pair-years). For genetic assignment and we used genome-wide 200K SNP data and our novel genetic assignment approach (BONE). These assignments were compared with extensive capture-mark-recapture information from the same system, and the line shows the predicted values for the number of pairwise misassignments with its 95% confidence interval in grey.

The statistical language of evidence

In a recent publication in the journal Trends in Ecology and Evolution, we discuss the topic of statistical significance testing. Despite much criticism, black-or-white null-hypothesis significance testing with an arbitrary P-value cutoff still is the standard way to report scientific findings. In a small literature review, we found that much of the current research in ecology and evolution is still disregarding the warnings and frequently relies on binary decisions based on P-values to report statistical significance. While the P-value itself is a sound mathematical concept that does not have to be banned when used correctly, we should stop using the term 'statistical significance' and replace it with a gradual notion of evidence. One obstacle to progress is likely a lack of knowledge about suitable alternatives. Based on previous suggestions made in other fields (e.g., medical statistics), we suggest replacing significance testing with a language of evidence that allows for a more nuanced approach to communicate scientific findings. Evidence-based language is a simple and intuitive alternative to statistical significance testing that anyone can start using immediately. To facilitate the change, we provide both generic
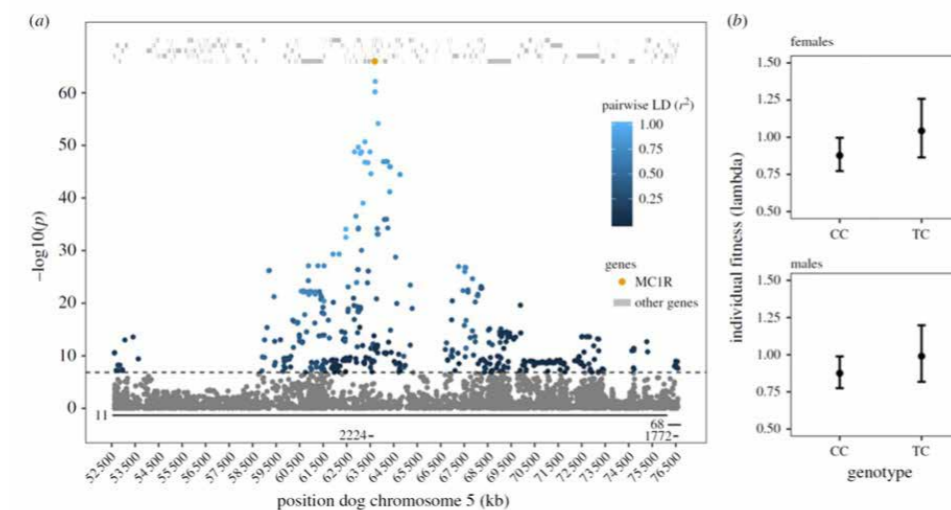
Figure 3. (a) Plot showing BLAST determined dog chromosome 5 locations of 486 SNPs significant in GWAS of fur colour in Arctic fox (N=681 individuals, N=359218 SNPs). The horizontal lines above the x-axis and the corresponding numbers show how the different Arctic fox scaffolds BLAST to dog chromosome 5. On the y-axis, significance values of the SNPs in the GWAS are shown on a negative log scale. Pairwise linkage disequilibrium (LD, r2) between top SNP AX177333963 and the other significant SNPs is shown by the blue colour gradient. All dog genes in the region are shown as grey lines at the top. The position of putative causal gene MC1R is shown with an orange dot (note that the y-axis values do not apply for genes). The dashed horizontal line shows the significance threshold after Bonferroni correction of the GWAS. (b) Predicted individual fitness (lambda) of the Arctic fox fur colour morph genotypes CC (white) and TC (blue) in females (top) and males (bottom). Whiskers represent 95% confidence intervals of predicted values. Predictions are based on additive GLMMs with genotype as predictor variable and year and subpopulation as random factors.

and real examples for rewriting results sections in research papers accordingly. Language of evidence is not only consistent with suggestions from other fields but also with the reporting standards of international research networks, such as the Intergovernmental Panel on Climate Change. Instead of re-inventing the wheel, we think that ecology and evolution might benefit from adopting some of the 'good practices' that existed for a long time.

The paper was published online November 2021 and has sparked vigorous discussions both on social media (Twitter), blog posts and emails. We also received three letters via the editorial system of TREE, one to which we responded in February and two more which will be replied to spring 2022.

Selection to reduce risk of dying affects aging

Every animal is exposed to a number of abiotic and biotic risk factors causing mortality. Several of these risk factors are intimately associated with the act of energy acquisition and, as such, with the amount of reserve the organism has available from this acquisition for overcoming temporary distress. We developed a fresh perspective on the evolution of aging which focuses on optimizing an individual's exposure to mortality risk across the course of life. A significant source of risk is associated with acquiring the energy necessary for all functions of life. In particular, a considerable fraction of lifetime energy acquisition is used for somatic maintenance. We show how reduction of mortality risk through restrained allocation to somatic maintenance may enhance lifetime fitness but result in

aging. Our results are discussed in relation to current theories of the evolution of aging, where we anticipate it will help to illuminate the debate about the mechanisms underlying aging in the wild and the nature and roles of trade-offs.

READING:

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Omholt, S. W., and Kirkwood, T. B. L. 2021. Aging as a consequence of selection to reduce the environmental risk of dying. Proceedings of the National Academy of Sciences of the United States of America, **118**, e2102088118,

Ranke, P. S., Araya-Ajoy, Y. G., Ringsby, T. H., Pärn, H., Rønning, B., Jensen, H., Wright, J. and Sæther, B.-E. 2021. Spatial structure and dispersal dynamics in a house sparrow metapopulation. Journal of Animal Ecology **90**: 2767-2781.

Saatoglu, D., Niskanen, A. K., Kuismin, M., Ranke, P. S., Hagen, I. J., Araya-Ajoy, Y. G., Kvalnes, T., Pärn, H., Rønning, B., Ringsby, T. H., Sæther, B.-E., Husby, A., Sillanpää, M. J., and Jensen, H. 2021. Dispersal in a house sparrow metapopulation: An integrative case study of genetic assignment calibrated with ecological data and pedigree information. Molecular Ecology **30**: 4740-4756.

Tietgen, L., Hagen, I. J., Kleven, O., Di Bernardi, C., Kvalnes, T., Norén, K., Hasselgren, M., Wallén, J. F., Angerbjörn, A., Landa, A., Eide, N. E., Flagstad, Ø., and Jensen, H. 2021. Fur colour in the Arctic fox: genetic architecture and consequences for fitness. Proceedings of the Royal Society B **288**: 20211452.
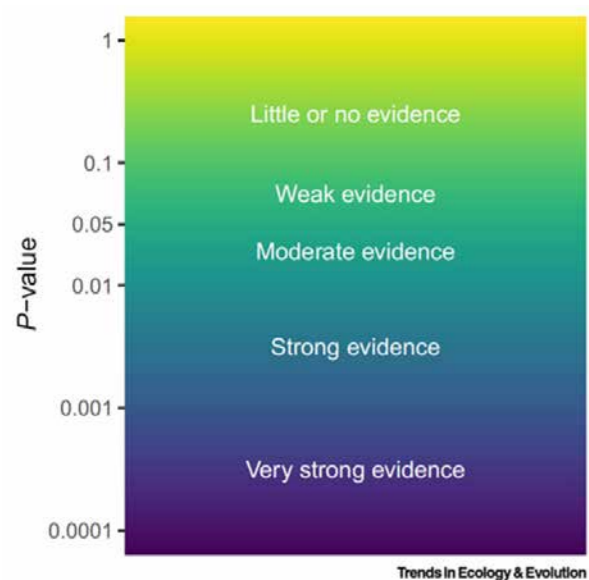
Figure 4. Suggested ranges to approximately translate the P-value into the language of evidence. The boundaries should not be understood as hard thresholds.

RESEARCH GROUP:
MODELLING BEHAVIOUR IN STOCHASTIC ENVIRONMENTS

Current group members:
PI: Associate professor Irja Ida Ratikainen
Guest researcher Martin I. Lind
Postdoc Ivain Martinossi

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

Martin Lind, Irja Ida Ratikainen
Right: Ivain Martinossi

MAJOR SCIENTIFIC CONTRIBUTIONS

We have continued to contribute to RA2 through research on how phenotypic plasticity will be selected for or against in the long term. Reversible plasticity allows organisms to make repeated adjustments to their phenotype throughout their lives but may also be costly and therefore assumed to be less strong than perfect in many environments. In a paper published in Journal of Evolutionary Biology (Haaland et. al. 2021), we show through modelling that greater investment in this type of plasticity can be favoured due to effects of bet-hedging (reduction in fitness variance). This is because stronger plasticity will allow the organism to avoid very poor performance in most environments and therefore strong negative effects on fitness. We show that this effect is more important for organisms living in environments with higher spatial autocorrelation (coarser environmental "grain") and fewer interactions with the relevant environment (e.g fast life histories). This could, for example, add to our understanding of why birds that breed fewer times can have more plastic egg laying dates.

RECOMMENDED READING:

Haaland, T.R., Wright, J. and Ratikainen, I.I. 2021. Individual reversible plasticity as a genotype-level bet-hedging strategy. Journal of Evolutionary Biology **34** (7) 1022-1033 doi: 10.1111/jeb.13788

RESEARCH GROUP: ADAPTATIONS TO (UN)PREDICTABLE ENVIRONMENTAL CHANGE

Current group members:
PI: Professor Jonathan Wright
Researcher Yimen Araya-Ajoy
Postdoc Joel Pick
PhD candidate Mette Finnøen
PhD candidate Myranda Murray

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

Jonathan Wright,
Mette Helene Finnøen,
Yimen Araya-Ajoy

Right: Myranda Murray, Joel Pick

This research group contributes to the research program of CBD primarily in Research Area 2. A variety of approaches are applied: from the development of mathematical models and wider conceptual frameworks to detailed life-history and behavioural studies on vertebrates in the field and laboratory. Environmental variation is becoming more frequent and unpredictable as a consequence of anthropogenic change, yet we currently lack the tools to evaluate the extent to which organisms can adapt to this phenomenon. Adaptations to predictable short-term environmental variation should favour reversible or irreversible (developmental) plasticity, whilst unpredictable long-term environmental variation will favour bet-hedging and adaptive tracking. A fundamental challenge here is in defining such adaptive phenomena for phenotypes that vary hierarchically among species, populations, genotypes and individuals, and also within individuals for repeatedly expressed labile phenotypic traits (behaviour, physiology and morphology). To address this challenge, we combine approaches from behavioural ecology and quantitative genetics using statistical models and the concept of the reaction norm to explore phenotypic variation among individuals alongside within-individual plasticity in labile and social 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

## 1 Recovery, body mass and buoyancy: foraging dive cycles in the European shag

Foraging dives in birds and mammals involve complex physiological and behavioural adaptations to cope with the breaks in normal respiration. Optimal dive strategies should maximize the proportion of time spent under water actively foraging versus the time spent on the surface. Oxygen loading and carbon dioxide dumping carried out on the surface could involve recovery from the consequences of the last dive and/or preparation in anticipation of the next dive depth and duration. However, few studies have properly explored the causal pattern of effects within such dive cycles, which is crucial prior to any assessment of optimal dive strategies. Using time depth recorders and global positioning system loggers, we recorded over 42,000 dives by 39 pairs of male and female European shags, (*Phalacrocorax aristotelis*). V-shaped dives involved a straight descent and ascent, presumably reflecting an unsuccessful search for prey. U-shaped dives involved a descent followed by horizontal movement followed by an ascent, presumably reflecting active hunting pursuit of pelagic prey. Males were larger than females, but we were unable to distinguish between sex effects and the nonlinear effects of body mass on dive behaviour.

Path analysis showed that within-individual dive-to-dive variation in surface times can best be explained as recovery from the previous dive. As expected in a pelagic hunter with unpredictable dive durations, there was no evidence of anticipatory prep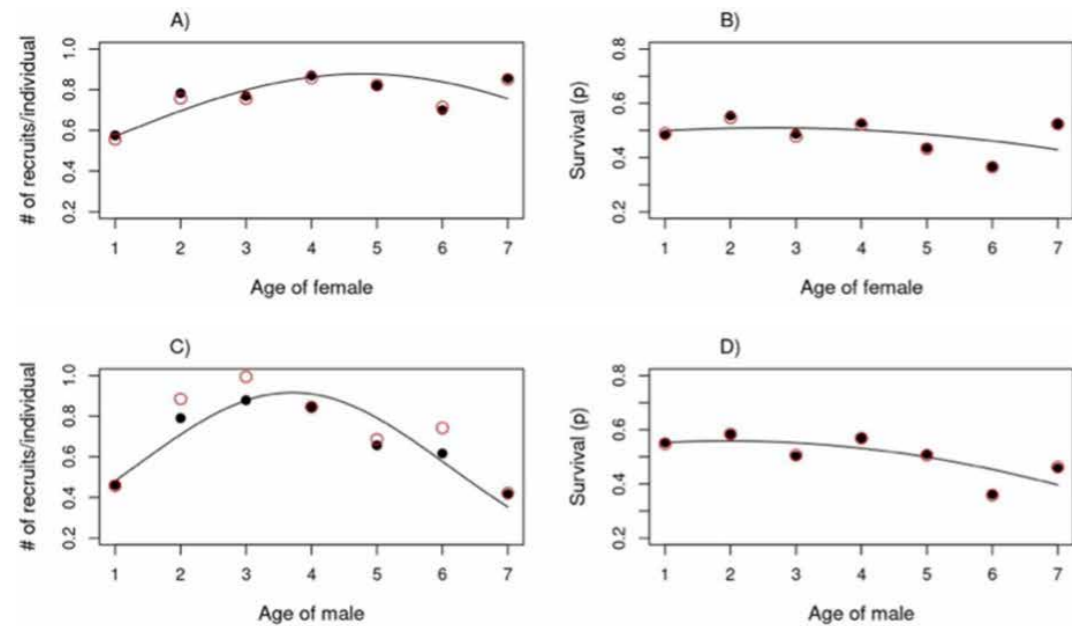aration of oxygen stores in predive surface durations. Among-individual variation in dives showed that body mass directly affected descent durations, but individual variation in all other dive and surface durations was driven by variation in descent duration, suggesting a critical role for dive depth in overcoming body mass-dependent effects of hydrodynamic/wave drag and buoyancy. Our analyses test for the first time certain critical assumptions for studies assessing optimal dive strategies in birds and mammals, thereby revealing new details and avenues for research concerning adaptive diving behaviour.

2 Individual variation in generation time reveals density regulation as a driver of pace-of-life

Generation time determines the pace of key demographic and evolutionary processes. Quantified as the weighted mean age at reproduction, it can be studied as a life-history trait that varies within and among populations and may thus evolve in response to ecological conditions. We combined quantitative genetic analyses with age- and density-dependent models to study generation time variation in a house sparrow (*Passer domesticus*) metapopulation. Generation time was heritable, and males had longer generation times than females. Individuals with longer generation times had greater lifetime reproductive success but not a greater than expected population growth rate. Density regulation acted on recruit production, suggesting that longer generation times should be favoured when populations are closer to carrying capacity. Furthermore, generation times were shorter when populations were growing and longer when populations were closer to equilibrium or declining. These
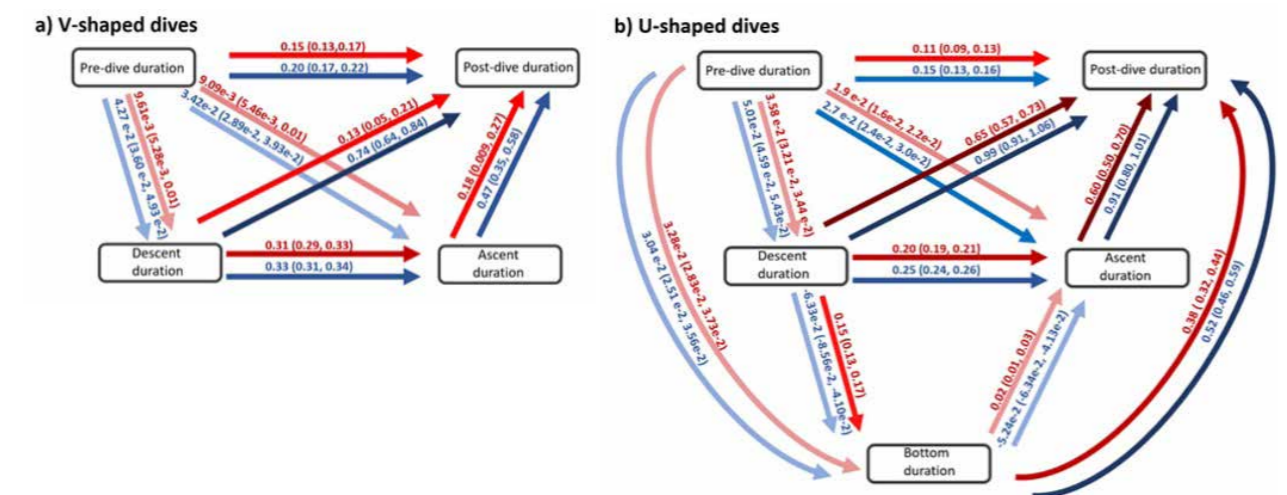
Figure 1. Path diagram summarizing the strength and direction of cause-and-effect relationships during dive cycles using the within-individual variation in the within individual mean-centred dive parameters. Results are shown for (a) sampling V-shaped dives and (b) active foraging U-shaped dives (see main text for details). All parameters were mean centred. The strength of effect sizes (± 95% CIs) are indicated as darkness of colours (lightest=NS, light=1.00e-4–0.04, mid=0.05–0.25, mid-dark=0.25–0.55, dark=0.55–1.50), shown for females (red) and males (blue).

Research Area 2 EVOLUTIONARY BIOLOGY

Research Area 2 EVOLUTIONARY BIOLOGY

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Figure 2. Age-dependent reproduction and survival. Black solid circles represent the survival probability for each age class. Black lines represent the predicted values of a model assuming that the age-dependent patterns of survival and reproduction can be modelled using a quadratic function. Red circles are the estimates of a model treating age as a categorical variable. Ages of more than 7 years only represented 0.38% of the data, and so are combined into the category of 7 years for the categorical analyses and the plot.

results support classic theory predicting that density regulation is an important driver of the pace of life-history strategies.

Density regulation is a ubiquitous process in natural populations and has been a key component of early life-history models. However, few empirical studies of life-history variation have focused on density-dependent effects on the mean age of reproduction. By combining multi-level analyses of the mean age at reproduction along with models of age- and density-dependent survival and reproduction, we provide various lines of evidence supporting classic life-history theory predicting that density dependence is a key determinant in shaping the pace of life-history strategies. Because generation time determines the speed of evolutionary responses to selection, a detailed understanding of the eco-evolutionary dynamics of the mean age at reproduction may provide important insights for predicting whether organisms will be able to adapt to current rates of environmental change.

RECOMMENDED READING:

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Araya-Ajoy, Y.G., Niskanen, A., Ranke, P.S., Kvalnes, T., Rønning, B., Jensen, H., Ringsby, T.H., Sæther, B.-E. & Wright, J. (2021) Variation in generation time reveals density regulation as an important driver of individual pace of life in a bird metapopulation. *Ecol. Lett.* **24**, 2077-2087.

RESEARCH GROUP:
LINKING POPULATION, EVOLUTIONARY AND CONSERVATION ECOLOGY

Current group members:
PI: Professor Jane Margaret Reid
Postdoc Debora Goedert
Postdoc Jennifer Morinay
Postdoc Paul Acker
PhD candidate Anders Poulsen-Charmouh
    (University of Aberdeen)
PhD candidate Lisa Dickel
PhD candidate Max Tschol (University of Aberdeen)
PhD candidate Sarah Fenn (University of Aberdeen)
Field technician Tim Morley (University of Aberdeen)

Aim: *To understand how population and evolutionary dynamics can affect each other and to apply such understanding to help manage and conserve wild populations.*

Jane M. Reid, Debora Goedert, Jennifer Morinay
Paul Acker, Anders Poulsen-Charmouh, Lisa Dickel
Max Tschol, Sarah Fenn, Tim Morley

MAJOR SCIENTIFIC CONTRIBUTIONS

Our objectives require new theoretical and empirical understanding of how movements (including both dispersal and reversible seasonal migration) can vary and affect survival and reproduction in the context of environmental variation and change. During 2021, we made progress on multiple projects that span these areas despite considerable ongoing challenges with working environments and fieldwork opportunities due to pandemic restrictions. Our approaches include sophisticated analyses of multi-year datasets alongside conceptual, theoretical and analytical developments.

Occurrence and impacts of dispersal in structured populations

We used exceptional long-term data from free-living song sparrows (Melospiza melodia) to examine how incoming immigrants alter patterns of genetic variation and fitness and, hence, the progress of evolution (Figure 1). We showed that immigrants import genes that decrease local juvenile survival and, hence, maintain local additive genetic variation in the face of directional selection. Natural immigration thereby constrains the course of adaptive evolution (Reid et al. 2021, Evolution Letters). Lisa Dickel then led work to examine the properties and impacts of immigrants. We used relatively high-density microsatellite data to show that immigrants that arrived in the

study population over recent decades are effectively outbred and typically unrelated to existing natives and to each other (Dickel et al. 2021, Molecular Ecology, congratulations to Lisa on her excellent first paper!).

These results allowed us to set out some hypotheses regarding expected fitness of offspring and grand-offspring of immigrants, given the potential for heterosis and epistatic breakdown. Lisa is now testing these hypotheses using the song sparrow data, with some fascinating initial results that we will finalise in 2022. Deb Goedert (working jointly with Henrik Jensen's group) undertook a major literature review to look for previous estimates of heterosis and epistatic breakdown in wild populations. There seem to be very few estimates for structured populations outside the contexts of genetic rescue or hybridisation. Hence, we plan to use both the song sparrow and house sparrow systems to quantify such effects and evaluate the impacts of natural immigration in 2022.

Meanwhile, PhD students Max Tschol and Anders Paulsen and lead collaborator Dr Greta Bocedi (University of Aberdeen) used individual-based simulation models to show how population structure and dispersal can shape the dynamics of sexual selection (Tschol et al. 2021, Evolution) and potentially substantially increase the time to extinction of highly inbred local populations.

Occurrence and impacts of seasonal migration: selection and plasticity

Despite the pandemic conditions, the major fieldwork achievement in 2021 was to advance the effort to quantify individual expression of seasonal migration versus year-round residence in our study system of European shags. Now in the 12th year of fieldwork, we did better than ever, with >20,000 field resightings of ringed individuals collected in winter 2020-2021. This was substantially due to heroic efforts by Tim Morley. After the efforts with the multi-year data collection, the full potential of the dataset is now becoming clear.

In collaboration with colleagues at UK Centre for Ecology & Hydrology, Paul Acker built and analysed some clever full-annual-cycle multi-event models to estimate probabilities of reproductive outcomes given individuals' winter locations. We showed that episodes of winter survival selection on seasonal migration versus residence that we already documented (Acker et al. 2021, Journal of Animal Ecology) can be reinforced by selection through subsequent reproductive success. This system therefore provides a notable example of how selection can strongly fluctuate (i.e. change direction) between years (Acker et al. 2021, Proceedings of the Royal Society B). Paul subsequently further developed these models to quantify within-individual variation in seasonal migration versus residence, both within and between years, and associated selection. This work also led us to review general properties of phenotypic plasticity and selection that can arise in discrete threshold traits (Reid & Acker 2021, Evolution).

We were very happy to be joined by Jennifer Morinay, who started her Marie Curie postdoctoral fellowship at CBD in September. Jennifer will look at relationships between seasonal migration, dispersal, and social information in the European shag system. Initial analyses already showed some intriguing associations between seasonal migration and the occurrence of small-scale breeding dispersal between consecutive years.

We look forward to being joined in 2022 by Thomas Haaland who will return to CBD to start a postdoctoral project on theoretical eco-evolutionary dynamics and by PhD candidate Cassandra Ugland and a further postdoctoral researcher who will quantify early-life phenotypic and genetic variation and selection on migration using data on juvenile movements and survival in our European shag system.

Application to conservation policy

Much research in population and evolutionary ecology is justified by the broad ambition that resulting understanding will, in future, inform effective population management. Yet, given the current challenges facing biodiversity, it is important that translation happens sooner rather than later.

Accordingly, Sarah Fenn (University of Aberdeen) and our colleagues used a decade of intensive ring-resighting data from the protected red-billed chough (*Pyrrhocorax pyrrhocorax*) in Scotland to show that a programme of supplementary feeding has successfully increased first-year survival probability, but only in some years (Fenn et al. 2021, Journal of Applied Ecology). These analyses contributed to the decision to further extend the supplementary feeding programme, at least until more sustainable forms of management can finally be introduced. We wrote a review paper to summarise how our long-term research has shaped conservation policy and also fed back to advance fundamental understanding (Reid et al. 2021, Journal of Animal Ecology). Jane was also appointed to the NatureScot (i.e. Scottish Government agency) Scientific Advisory Committee, with responsibility for overseeing development and quality of science-based policy for biodiversity and environment in Scotland.

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Tschol, M, **Reid, JM**, Bocedi, G. (2021) Spatial population structure promotes coevolution of costly female preference and male display. *Evolution* online. https://doi.org/10.1111/evo.14426

Current group members:
PI: Professor Cameron Ghalambor
PhD candidate Rebecca Cheek (Colorado State University)

Aim: *T*o understand how individual level responses to environmental variation influence adaptive evolutionary change.

Cameron Ghalambor, Rebecca Cheek

MAJOR SCIENTIFIC CONTRIBUTIONS

The objectives of our group are to understand the behavioural and physiological mechanisms employed by individuals to cope with environmental change and how these plastic responses facilitate or constrain adaptive evolution. We work on a diversity of organisms, including fish, birds, and insects. Current projects include understanding 1) how trade-offs between physiological tolerance and biotic interactions shape species distributions, 2) the mechanisms that drive and maintain microgeographic adaptation, and 3) the drivers of physiological diversity and the implications for vulnerability to climate change. In the past year we were fortunate to receive a new interdisciplinary "Fellesløft" grant from the Norwegian Research Council. This project is in collaboration with CBD members, Irja Ratikainen, Bob O'Hara, and Russ Lande, as well as Torbjørn Ekrem and Frode Ødegaard from the NTNU University Museum. We will be working with an international team of researchers to better understand the drivers of latitudinal variation in insect physiology and develop models to better predict vulnerability to changing climatic conditions.

RECOMMENDED READING:

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Shah, A. A., Woods, H.A., Havird, J.C., Encalada, A.C., Flecker, A.S., Funk, W.C., Guayasamin, J., Kondratieff, B. C., Poff, N. L, Thomas, S.A., Zamudio, K.R., and C. K. Ghalambor. 2021. Temperature-dependence of metabolic rate in tropical and temperate aquatic insects: support for the Climate Variability Hypothesis in mayflies but not stoneflies. *Global Change Biology*. **27**: 297-311.

Potter, T., Bassar, R.D., Bentzen, P., Ruell, E.W., Torres-Dowdall, J., Handelsman, C,A, Ghalambor, C.K., Travis, J., Reznick, D.N., and T. Coulson. 2021. Environmental change, if unaccounted, prevents detection of cryptic evolution in a wild population. *American Naturalist*. **197**: 29-46.

Research group: Community Dynamics

Current group members:
PI: Associate professor Vidar Grøtan
Professor Anders Gravbrøt Finstad
Professor Bob O'Hara
Professor Otso Ovaskainen
Researcher Knut Anders Hovstad (NBIC)
Researcher Ola Diserud (NINA)
Postdoc Christophe Coste
Postdoc Emily Grace Simmonds
Postdoc Hanna Fried-Petersen
PhD candidate Bert van der Veen
PhD candidate Caitlin Mandeville
PhD candidate Ellen Claire Martin
PhD candidate Kwaku Adjei
PhD candidate Lisa Sandal
PhD candidate Philip Mostert
PhD candidate Tanja Petersen
PhD candidate Wouter Koch
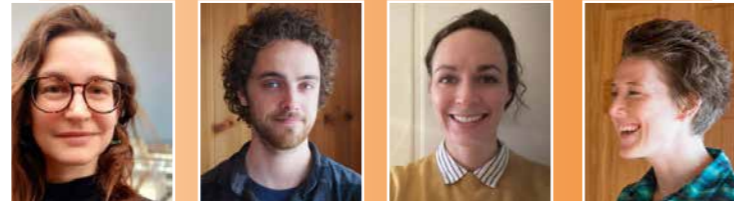
Aim: *To examine how community dynamics in time and space of different taxa along ecological gradients are affected by environmental stochasticity.*

UPPER PICTURE: Tanja Petersen, Lisa Sandal, Anders Gravbrøt Finstad, Bob O'Hara, Emily Grace Simmonds, Vidar Grøtan

RIGHT: Christophe Coste, Otso Ovaskainen, Ola Diserud, Knut Anders Hovstad / Hanna Fried-Petersen, Bert van der Veen, Ellen Claire Martin, Caitlin Mandeville / Kwaku Adjei, Wouter Koch, Philip Mostert

Major scientific contributions

The number of species, the relative abundance of species as well as which species are present in the community varies in space and time. One of the key topics addressed by community ecology is understanding the mechanisms and processes contributing to variation in community composition. Although it is possible to construct rather successful "pattern-fitting" models of community dynamics by assuming that all species have identical characteristics (neutral models), an improved understanding of community dynamics and species coexistence involves understanding mechanisms and processes involved in creating and maintaining variation among species in their responses to the environment. This year we can present a smorgasbord of studies that in various ways contributes towards improved understanding of community dynamics.

The Centre of Biodiversity Dynamics aims to work across traditional boundaries of evolution, population dynamics and community dynamics by '... *applying a theoretical framework developed to analyse dynamics of populations of single species in fluctuating environments to also include temporal and spatial variation in genetic composition within populations and in structure of communities and ecosystems at a higher organismic level'* (CBD midterm report, 2017).

The study we present next represents an extremely important fulfilment on this key aim:
An evolutionary and ecological community model for distributi-on of phenotypes and abundances among competing species

Factors affecting the coexistence of competing species have received a great deal of attention by ecologists for nearly a century. Still, how different processes such as interspecific competition affect local coexistence of ecologically similar species and, hence, influence the structure of communities is poorly understood. A major reason for this is that extrapolation of results from models of pairwise interactions between species to networks of interacting species has proved challenging. Furthermore, most models used in community ecology do not include realistic assumptions about factors affecting intraspecific variation, for example, with respect to abundance or distribution of phenotypes. Finally, many community models are purely ecological, which prevents analyses of the consequences of phenotypic evolution for the structure of the communities.

In Engen et al. (2021), we proposed a model for the organization of communities that includes ecologically realistic assumptions about inter- and intraspecific dynamics and evolution based on general quantitative genetics theory for generating packing of species in the phenotypic space. We included ecologically realistic assumptions, such as density dependence and stochastic fluctuations in the environment and analysed how evolution caused by r- and K-selection will affect the packing of species in the phenotypic space as well as the species abundance distribution.

We developed a model based on a generalization of the concept of r- and K-selection applied to a system of an arbitrary number of competing species with the degree of interspecific competition expressed by the generalization of the Lotka-Volterra model. The dynamics of each species are determined by parameters given by their vital rates, which in turn are functions of the phenotype of each individual expressed as a vector of traits of an arbitrary number of dimensions. In addition to including intraspecific r- and K-selection, the model generates character displacement by embedding interspecific competition coefficients that decrease as the phenotypes of species become more different. The model includes competition coefficients that are not symmetric for pairs of species, which is required for a realistic description of the dynamics of interspecific competition. Finally, the model is stochastic and can be used to study the effects of fluctuations in the environment on the degree of character displacement as well as how variation in the population dynamics affects the species abundance distribution. Since the species end up with a distribution of traits among them, the abundance models are, in general, heterogeneous, with the degree of heterogeneity depending on consumer-resource interactions and environ-mental stochasticity as well as the evolutionary response to phenotypic selection.

The overall model is very general and provides an opportunity to test effects and implications of various sets of assumptions and parameters. To increase the transparency, we have illustrated some key general relationships between phenotypic evolution and community structure based on several simplifying assumptions.

Two general conclusions appear from our analyses:

1) The species tend to distribute themselves surprisingly stably within the phenotypic space, often approximately uniformly on the surface of a d-dimensional sphere.
Evolution of mean species-specific traits is affected by fluctuations in population size of all species. Mean phenotypes of the species in the community are distributed approximately uniformly on the surface of a multidimensional sphere. This is the expected strategy for optimal reduction of competition by phenotypic divergence so that the species, on average, deviate as much as possible from each other while still having growth rates large enough to avoid extinction. Thus, our model provides an extension of previous ecological models of species packing that did not include evolution. Similarly, most evolutionary models for interspecific coevolution of traits based on consumer-resource or predator-prey models have been deterministic, ignoring stochastic fluctuations in the environment. Environmental stochasticity generates selection that deviates species slightly from this surface, but, still, the variance in the distribution of the phenotypes will be far less than expected from a random species packing.

2) Species interactions as well as the potential for niche differentiation also affect another important characteristic of community structure, the species abundance distribution. In general, the model produces a shape of the distributions of log abundances that is skewed to the left, which is typical of most natural communities. A general pattern that appears is that increased resource diversity increases the number of species in the community and reduces the variance in log abundance. A similar effect occurs if environmental stochasticity is reduced.
This model of community evolution provides a theoretical framework that predicts a relationship between the structure of the phenotypic space and the form of species abundance distributions that can be compared against time series of variation in community structure. The general model structure provides rich opportunities to test effects and implications of various sets of assumptions and parameters and will likely provide the foundation for several studies in the years to come.

Model-based ordination for species with unequal niche widths

Communities that are surveyed along environmental gradients provide unique insight into the ecological niche of species. The ecological niche is reflected in a species' distribution, so that the species' range limits reflect its ability to tolerate environmental conditions less than optimal. A species' tolerance is synonymous with niche width, so that species with different tolerances occupy different locations on the specialist–generalist spectrum.

Contemporary multivariate statistical methods at best assume that species have the same ability to tolerate deviations from
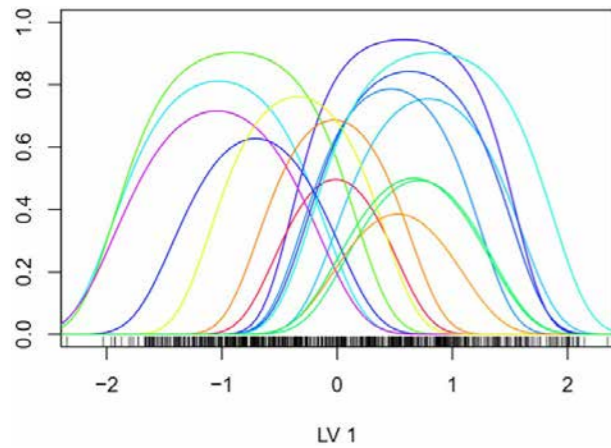
Figure Estimated quadratic curves for some of the Swiss alpine plants included in the study. Each curve represents the niche of a species, where e. g. high and wide curves represent generalist species with a high probability of occurrence, and low narrow curves represent specialist species with a low probability to occur.

their optimal environmental conditions. Van der Veen et al. (2021) developed a new method that instead allows to estimate tolerances for species separately. The new model formulation includes a quadratic term that allows to fully estimate species niches, so that not only tolerances, but also the optima and maxima of species niches can be estimated explicitly and separately for different niche axes. Explicitly estimating these three parameters gives unique insight into reasons for species rarity, whether it is due to low abundance or probability of occurrence (maxima), a high degree of habitat specialization (tolerance) or unsuitable observed environmental conditions (optima).

Species interactions, environmental gradients and body size shape population niche width

Competition for shared resources is commonly assumed to restrict population-level niche width of coexisting species. However, the identity and abundance of coexisting species, the prevailing environmental conditions, and the individual body size may shape the effects of interspecific interactions on species' niche width. Eloranta et al. (2021) studied the effects of interspecific and intraspecific interactions, lake area and altitude, and fish body size on the trophic niche width and resource use of a generalist predator, the littoral-dwelling large, sparsely rakered morph of European whitefish using stable isotope, diet and survey fishing data from 14 subarctic lakes along an environmental gradient in northern Norway. We demonstrated that intermediate intensity of interspecific interactions may broaden species' niche width, whereas strong competition for limited resources and high predation risk may suppress niche width in less productive environments. Acknowledging potential humped-shaped relationships between population niche width and interspecific interactions can help us understand species' responses to environmental disturbance (e.g. climate change and species invasions) as well as the driving forces of niche specialization.

Co-occurrences of tropical trees: disentangling abiotic and biotic forces

Species co-occurrences in local communities can arise independent or dependent on species' niches. However, the role of niche-dependent processes has not been thoroughly deciphered when generalized to biogeographical scales, probably due to combined shortcomings of data and methodology. Marjakangas et al. (2021) explored the influence of environmental filtering and limiting similarity, as well as biogeographical processes that relate to the assembly of species' communities and co-occurrences of tropical trees in eastern South America. Generally, the influence of environmental filtering exceeded that of limiting similarity in shaping species' co-occurrences. Contrary to what was expected from assuming limiting similarity, phylogenetic relatedness or functional similarity did not limit tree co-occurrences.

Temperature effects on the temporal dynamics of a subarctic invertebrate community

Climate warming is predicted to have major impacts on the structure of terrestrial communities, particularly in high latitude ecosystems where growing seasons are short. Higher temperatures may dampen seasonal dynamics in community composition as a consequence of earlier snowmelt, with potentially cascading effects across all levels of biological organisation. Robinson et al. examined changes in community assembly and structure along a natural soil temperature gradient in the Hengill geothermal valley, Iceland. Sample collection over several time points within a season allowed us to assess whether temperature alters temporal variance in terrestrial communities and compositional turnover. We found that seasonal fluctuations in species richness, diversity and evenness were dampened as soil temperature increased, whereas invertebrate biomass varied more. Body mass was found to be a good predictor of species occurrence, with smaller species found at higher soil temperatures and emerging earlier in the season. Our results indicate that climate warming will likely dampen the seasonal turnover of community structure that is characteristic of high latitude invertebrate communities.

Modelling temperature-driven changes in species associations across freshwater communities

Perrin et al used a large-scale presence–absence dataset of freshwater fish from lakes across the Fennoscandian region to estimate the effect of temperature on species associations. We identified a trend of negative associations between species tolerant of cold waters and those tolerant of warmer waters, as well as positive associations between several more warm-tolerant species, with these associations often shifting depending on local temperatures. Results confirmed that freshwater ecosystems can expect to see a large-scale shift towards communities dominated by more warm-tolerant species.

Phenological shifts of abiotic events, producers, and consumers across a continent

Ongoing climate change can shift organism phenology in ways that vary depending on species, habitats and climate factors studied. To probe for large-scale patterns in associated phenological change, Roslin et al used over 70000 records from six decades of systematic monitoring across the former Soviet Union. Among 110 phenological events related to plants, birds, insects, amphibians and fungi, we found a mosaic of change, defying simple predictions of earlier springs, later autumns and stronger changes at higher latitudes and elevations. Site mean temperature emerged as a strong predictor of local phenology, but the magnitude and direction of change varied with trophic level and the relative timing of an event. Beyond temperature-associated variation, we uncovered high variation among both sites and years, with some sites being characterized by disproportionately long seasons and others by short ones. Our findings emphasize concerns regarding ecosystem integrity and highlight the difficulty of predicting climate change outcomes.

Biodiversity dynamics in urban areas under changing land-uses

Urbanization is increasing worldwide, but urban expansion inevitably happens at the cost of other ecosystems and understanding how this will affect biodiversity is crucial. Tanja Kofod Petersen's PhD thesis "Biodiversity dynamics in urban areas under changing land-uses" showed that biodiversity data (GBIF data on species occurrences and distributions) from Norway and Trondheim were greatly skewed regarding species- and conservation groups and their geographic distributions. Land-cover and land-cover related variables determined number- and distribution of species in an urban-rural context: threatened species were generally found in habitats with low human pressure, whereas alien species richness was mainly determined by the initial introduction site. Disturbance-tolerant plant species adapted for rapid resource acquisition were found in urban areas, compared to stress-tolerant species outside of the city. Furthermore, results suggested that as land-cover changes, bird communities will become less diverse – in particular, we will lose forest- and wetland specialists, and be left with generalists. To favor native biodiversity in future urban development, an overall recommendation is to minimize the conversion of vulnerable habitats as much as possible and to monitor urban areas closely to mitigate the introduction and spread of alien species.

Ecological dependencies make remote reef fish communities most vulnerable to coral loss

Ecosystems face both local hazards, such as over-exploitation, and global hazards, such as climate change. Since the impact of local hazards attenuates with distance from humans, local extinction risk should decrease with remoteness, making faraway areas safe havens for biodiversity. Strona et al. (2012) studied

reef fish communities across the globe and did, however, find the opposite pattern: there was an increased risk of fish species loss with increasing remoteness. Isolation and reduced anthropogenic disturbance may increase ecological specialization in remote communities and, hence, their vulnerability to secondary effects of diversity loss propagating through networks of interacting species. Thus, increased risk of species loss could be explained by an increase in fish-coral dependency with the distance of coral reefs from human settlements as well as far-reaching impacts of global hazards. Hotspots of fish risk from fish-coral dependency are distinct from those caused by direct human impacts, increasing the number of risk hotspots by ~30% globally.

RECOMMENDED READING:

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Engen, Steinar; Grøtan, Vidar; Sæther, Bernt-Erik; Coste, Christophe. (2021) An evolutionary and ecological community model for distribution of phenotypes and abundances among competing species. *The American Naturalist*. vol. **198** (1).

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Robinson, Sinikka I.; Mikola, Juha; Ovaskainen, Otso; O'Gorman, Eoin J.. (2021) Temperature effects on the temporal dynamics of a subarctic invertebrate community. *Journal of Animal Ecology*. vol. **90** (5).

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Research group: Dynamics of Arctic ecosystems

Current group members:
PI: Professor Brage Bremset Hansen (NTNU and NINA)
Researcher Vebjørn Veiberg (NINA)
Postdoc Bart Peeters
Postdoc Mathilde Le Moullec
PhD candidate Laura Bartra Cabré

Aim: *Our research applies demographic modelling and multi-species stochastic approaches to understand how environmental change, harvest and trophic interactions influence population and community dynamics, as well as eco-evolutionary dynamics, in time and space.*

Bart Peeters, Mathilde Le Moullec, Brage Bremset Hansen
Laura Bartra Cabré, Laura Bartra Cabré

Major scientific contributions

Current projects

Our main current project is INSYNC (FRIPRO, RCN 2018-2022), which aims to use novel field-experimental approaches and demographic time-series analyses to explore how climate drivers of key ecosystem components shape spatiotemporal dynamics of the tundra community in Svalbard. Collaborators include Univ. Aberdeen, Univ. Groningen, Univ. Iceland, CNRS Montpellier, Norwegian Meteorological Institute, the Univ. Centre in Svalbard (UNIS), the Norwegian University of Life Sciences (NMBU), and the Norwegian Institute for Nature Research (NINA). Recently, we have expanded *INSYNC* towards understanding the evolutionary impacts of climate change, harvest, and extinction-colonization events in wild Svalbard reindeer. We are also heavily involved in project *ColdRein* (FRIPRO, RCN 2021-2025, NTNU Dept. Natural History), where we combine ancient and modern genomics to explore the evolutionary paths to this isolated, endemic subspecies.

Interactions between harvest and climate change

We are particularly interested in understanding and predicting how impacts of different natural and anthropogenic drivers interact. For instance, climate change effects and loss of landscape connectivity may interact with other drivers of ecological and evolutionary dynamics, such as harvest. In Peeters et al. (2022, Ecology Letters), we used an existing Integrated Population Model and empirical parameterization of density-dependent climate effects to simulate reindeer population dynamics under different scenarios of harvest and rain-on-snow, the main driver of population fluctuations. We showed that, because weather effects on vital rates are strongly density-dependent, low to moderate harvest levels before winter may dampen population fluctuations and reduce the probability of population crashes, as well as the probability of extirpation following extreme weather events. We also demonstrated that such climate-density interactions are more common than previously acknowledged in (resource-limited) northern ungulates, and simple generic population models show that the dampening effects of harvesting can largely be generalized across species, yet they depend on the species' life history traits (Figure 1).

The current level of harvest of Svalbard reindeer is very low, and the management policy is that it should have negligible impacts on population dynamics and structure. The official (and questionable) strategy to achieve this is to keep harvest low and try "shoot through" the population. In another paper (Peeters et al. 2021) published in the Climate Research special issue for the SUSTAIN project, we combine harvest data with population monitoring data to demonstrate that this conservative strategy is far from being achieved. A strong bias towards specific age-sex groups in the harvest offtake results from a combination of hunters' preferences and a non-flexible quota allocation system. As further reviewed in Lee et al. (2022, Climate Research), demographic effects of such biased harvest may be strong locally (due to spatial aggregation of the harvest effort) and in years following extreme weather events.

Figure 1 (Peeters et al. 2022, *Ecology Letters*): Proportional harvesting reduces population fluctuations and quasi-extinction risk. Effects of proportional harvesting (blue = 0, red = 0.25) on (a, b) the distribution in population growth rates (r_t) as a function of population density (N_t/K) and multiplicative environmental variance (shaded areas), and (c, d) simulated population trajectories for the (a, c) Ricker and (b, d) Beverton-Holt models with parameters β_0 = 1.0, K =100, γ_∞ = 0.22. (e) Probabilities of quasi-extinction (increasing $P(N<K/5)$ indicated by the blue-to-red gradient) are shown for the Ricker model with multiplicative environmental variance and increasing harvest proportions (left = 0, center = 0.1, right = 0.2), maximum growth rates (β_0, x-axis) and variance in growth rate (y-axis, shown for populations at their carrying capacity (K) in the absence of harvesting, Var[$r_t | N_t=K$]$_{noharvest}$).
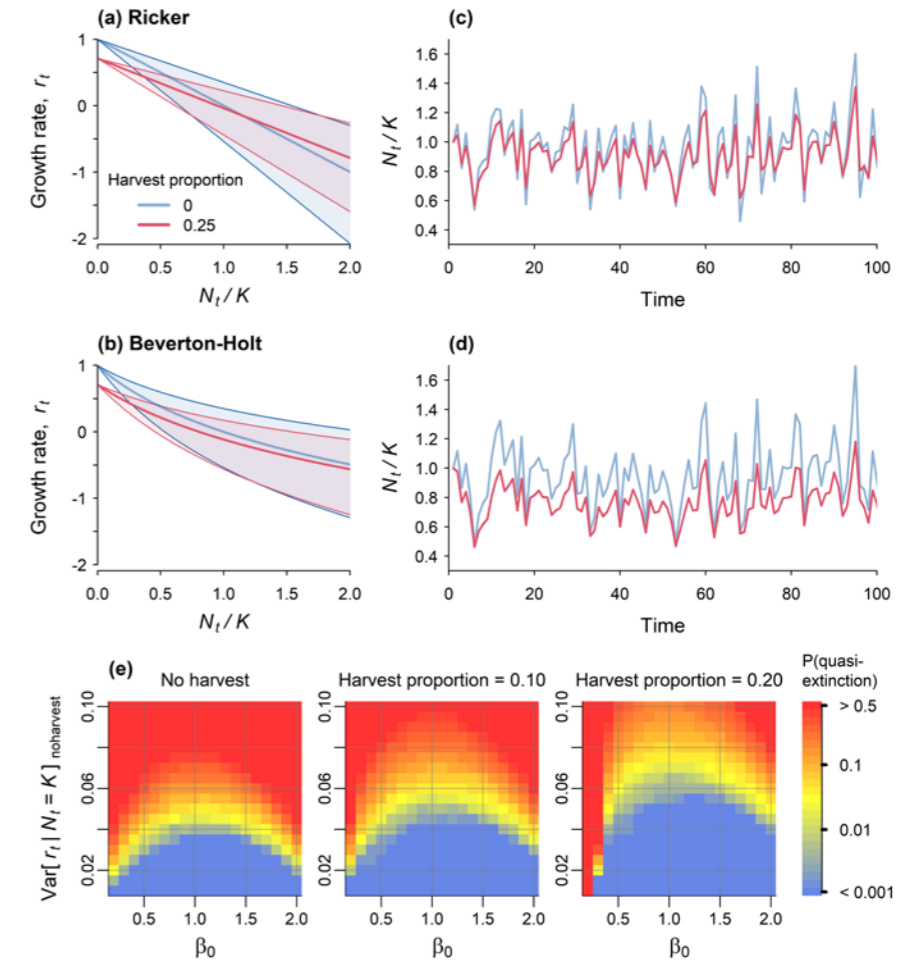
Spatial population synchrony

We have recently been focusing on how weather events, climate change, and harvest impact larger-scale patterns of population dynamics, such as the level and scaling of spatial population synchrony (reviewed in Lee et al. 2022 and Herfindal et al. 2022, Climate Research). One question that arises from empirical and theoretical papers is whether changes in, for example, environmental stochasticity will cause changing patterns of synchrony and how this will vary between ecosystems and life histories. These are key topics of current MSc and PhD projects. In August, we arranged a two-day in-person methodological workshop at Teveltunet, Meråker, where people from different CBD research areas and departments tried to disentangle the pros and cons of different methods to assess changes in synchrony. Population modelling and simulation exercises at this workshop showed that some commonly used methods often fail to (or erroneously) detect temporal changes in spatial population synchrony, which led us to propose a new and, apparently, improved method (Le Moullec et al. (2021).

RECOMMENDED READING:

Herfindal I, Lee AM, Marquez JF, Le Moullec M, Peeters B, Hansen BB, Henden JA and Sæther B-E (2022) Environmental effects on spatial population dynamics and synchrony – lessons from northern ecosystems. *Climate Research* **86**:113-123.

Le Moullec M, Acker P, Grøtan V, Lee AM, Herfindal I, O'Hara B, Martin EC, Peeters B, Bjørkås R, Reid JM, Ringsby TH, Sæther B-E and Hansen BB (2021). How can we assess temporal changes in population synchrony? Annual Meeting of the British Ecological Society (see poster here).

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Peeters B, Pedersen ÅØ, Veiberg V and Hansen BB (2021). Hunting quotas, selectivity and stochastic population dynamics challenge the management of wild reindeer. *Climate Research* **86**:93-111.

Peeters B, Grøtan V, Gamelon M, Veiberg V, Lee AM, Fryxell JM, Albon SD, Sæther B-E, Engen S, Loe LE and Hansen BB (2022). Harvesting can stabilize population fluctuations and buffer the impacts of extreme climatic events. *Ecology Letters* **00**:1-13.

Research Area 3 COMMUNITY DYNAMICS

Research Area 3 COMMUNITY DYNAMICS

RESEARCH GROUP: DYNAMICS OF INTERACTING SPECIES

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

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.

Marie Vestergaard Henriksen, Aline Magdalena Lee, Elena Albertsen, Ragnhild Bjørkås, Jonatan Fredricson Marquez

Figure 1. Some main pathways discussed in Lee et al. 2022 through which spatial patterns (blue), species interactions (red), and density dependence (purple) alter harvesting effects on population dynamics, synchrony and resilience to environmental fluctuations. Arrows between boxes show effects of the factor or process in one box on the other. Arrows aimed at other arrows show how factors or processes modify the effects represented by the receiving arrows. Labels on arrows describe mechanisms through which the effects represented by the arrows function.

MAJOR SCIENTIFIC CONTRIBUTIONS

Population responses to harvesting in fluctuating environments – effects of interspecific interactions and spatial patterns

Achieving sustainable harvesting of natural populations depends on our ability to predict population responses to combined effects of harvesting and environmental fluctuations while accounting for other internal and external factors that influence population dynamics in time and space. We published a review on recent research showing how interspecific interactions and spatial patterns can influence population responses to harvesting in fluctuating environments, highlighting several pathways through which harvesting can, often inadvertently, influence the dynamics and resilience to environmental fluctuations of both harvested and surrounding non-harvested populations and species (Figure 1). We discussed how knowledge of these pathways can be used to increase the sustainability of harvesting (Lee et al. 2022). Additionally, we wrote an opinion piece with suggestions for how to develop optimal harvesting strategies in the face of species interactions and climate change (Lee & Sæther 2022).

Effects of local density regulation and temperature on spatial synchrony in a marine fish community

The degree of spatial synchrony in the density dynamics of populations is often determined by multiple processes that both synchronize and desynchronize. To better understand how populations are spatially synchronized, how changes in environmental condition might alter synchrony patterns, and how differences among species could impact whole communities, we need to disentangle the relative effects of individual processes. Therefore, we studied the spatial density synchrony of several fish populations found in the Barents Sea and measured the effects that sea bottom temperature and density regulation had on the observed synchrony patterns. Temperature was found to synchronize density dynamics, as expected from the Moran effect. However, the synchronizing effects of temperature differed among the species. On the other hand, density regulation, which is expected to have a more localized effect, was found to desynchronize density dynamics. While the effects of temperature and density regulation on synchrony were relatively weak, they were consistent across species. Still, it is evident that additional

processes, such as species interactions, lagged environmental effects, population structure or harvesting pressure, also have important effects on the synchrony patterns of these populations. Given the changing climatic trends observed globally, and direct and indirect effects that intense harvesting pressure have on many populations, it is important that future research continue to disentangle the effects of individual processes regulating synchrony within natural communities.

Improving the establishment of grasslands for pollination

Semi-natural grasslands are biodiversity hotspots and core habitats for pollinators because of their high diversity of flower resources. With the global decline in pollinators, these habitats have become increasingly important. Unfortunately, semi-natural grasslands are now regarded as threatened in Europe. To counteract the effects of this loss of habitat on pollinators, new habitats are being established using seeds from flowering plant species commonly found in semi-natural grasslands. However, establishment may be problematic if the seeds are not adapted to the local conditions. At NIBIO, seeds collected from populations across the country (Nordland, Østlandet, Vestlandet, Sørlandet, Innlandet, Midt-Norge) are being grown in Southern Norway to produce region-specific seed mixtures. At these production facilities, we are comparing

flowering phenology, pollination, and seed production of populations from the different regions of seven different species. We do this to better understand the importance of regional adaptation when establishing new grasslands rich in floral resources. Our preliminary findings show that, for some species, flowering phenology and seed production varies greatly among populations. These findings suggest that certain species are more strongly adapted to regional conditions which will be important for their successful establishment and survival in new semi-natural habitats and thus for our ability to improve conditions for pollinators.
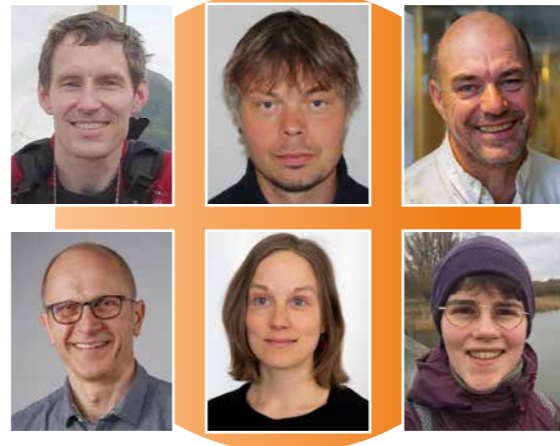
RECOMMENDED READING:

Marquez JF, Sæther BE, Aanes S, Engen S, Salthaug A, Lee, AM (2021) Age-dependent patterns of spatial autocorrelation in fish populations. *Ecology*, **102**(12):e03523

Lee AM, Jarillo J, Peeters B, Hansen BB, Cao-García FJ, Sæther BE, Engen S (2022) Population responses to harvesting in fluctuating environments. *Climate Research*, **86**:79-91

Lee AM & Sæther BE (2022) Optimal harvesting in a changing climate. *Climate Research*, **86**:21-27

Herfindal I, Lee AM, Marquez JF, Le Moullec M, Peeters B, Hansen BB, Henden JA, Sæther BE (2022) Environmental effects on spatial population dynamics and synchrony – lessons from northern ecosystems. *Climate Research*, **86**:113-123

Research Area 3 COMMUNITY DYNAMICS

Research group: Ecosystem Trøndelag – Understanding biodiversity patterns in time and space

Current group members:
PI: Researcher Ivar Herfindal
Professor Anders Gravbrøt Finstad
Professor Bernt-Erik Sæther
Professor Torbjørn Ekrem
Postdoc Anna Norberg
PhD candidate Angeline Bruls

Aim: *To understand how environmental and anthropogenic factors affect patterns of biodiversity at different spatial and temporal scales*

This research group is a newly formed assemblage of people from different research groups that are involved in the research program called "Ecosystem Trøndelag".

Ivar Herfindal, Anders Gravbrøt Finstad, Bernt-Erik Sæther, Torbjørn Ekrem, Anna Norberg, Angeline Bruls

Major scientific contributions

Ecosystem Trøndelag was launched as a strategic research programme at CBD, with the aim to increase our understanding of how human impacts on nature, and in particular land use changes, affect patterns of biodiversity in time and scale. Because nature is so diverse, even within a rather small region as Trøndelag, three focal study areas along environmental gradients from coast to inland were chosen: Ørland, Trondheim and Malvik, and Røros (Fig. 1). The activity the first year was primarily planning and carrying out field work. In each of the three study areas, sample locations were distributed in important nature types that experience high pressure from human activities. At each location, we did vegetation mapping, breeding bird surveys, and insect sampling. This provided an impressive amount of data that now is being identified and analysed using a combination of state-of-the-art techniques within biodiversity analyses. Fieldwork will be repeated in 2022 following the same procedures but with more sample locations.

The project has benefited greatly from a close collaboration with experts at NINA, in particular Jens Åström, Oddvar Hansen and Arnstein Staverløkk on insect collection and identification and Lise Tingstad for vegetation mapping. Ecosystem Trøndelag also has close collaboration with local people in the three study areas that have provided invaluable help in planning and carrying out the field work. Audun Eriksen (Ørland Våtmarkssenter), Tom Roger Østerås (Birdlife Norway) and Martin Røsan (Birdlife Norway) have been instrumental for the bird surveys. Audun Eriksen, Anne-Marit Helmersen
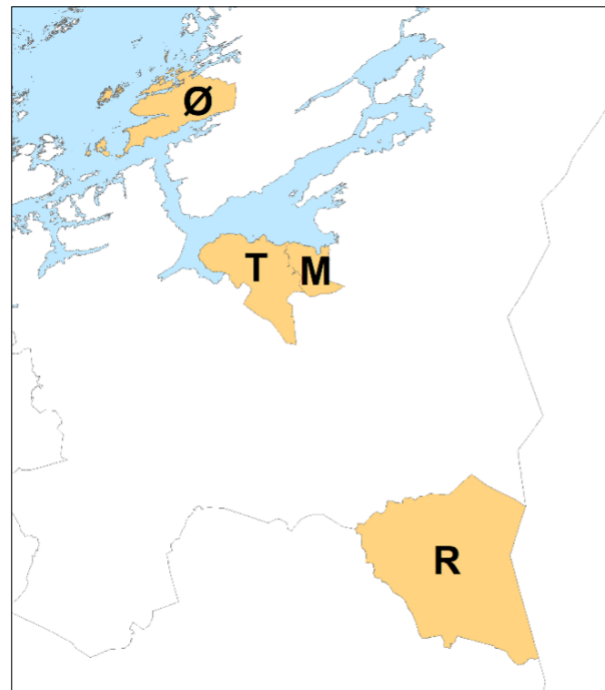
Figure 1. The three study areas in Ecosystem Trøndelag: Ørland (Ø), Trondheim and Malvik (T and M) and Røros (R).

(Ørland Våtmarkssenter) and Marit Østby Nilsen (Fjelldriv) have also done an impressive job collecting insect samples from the traps.

Figure 2. Malaise traps in a forest stand in Ørland municipality in Trøndelag.

Figure 3. The setup for insect capture: A combination of window traps and a malaise trap
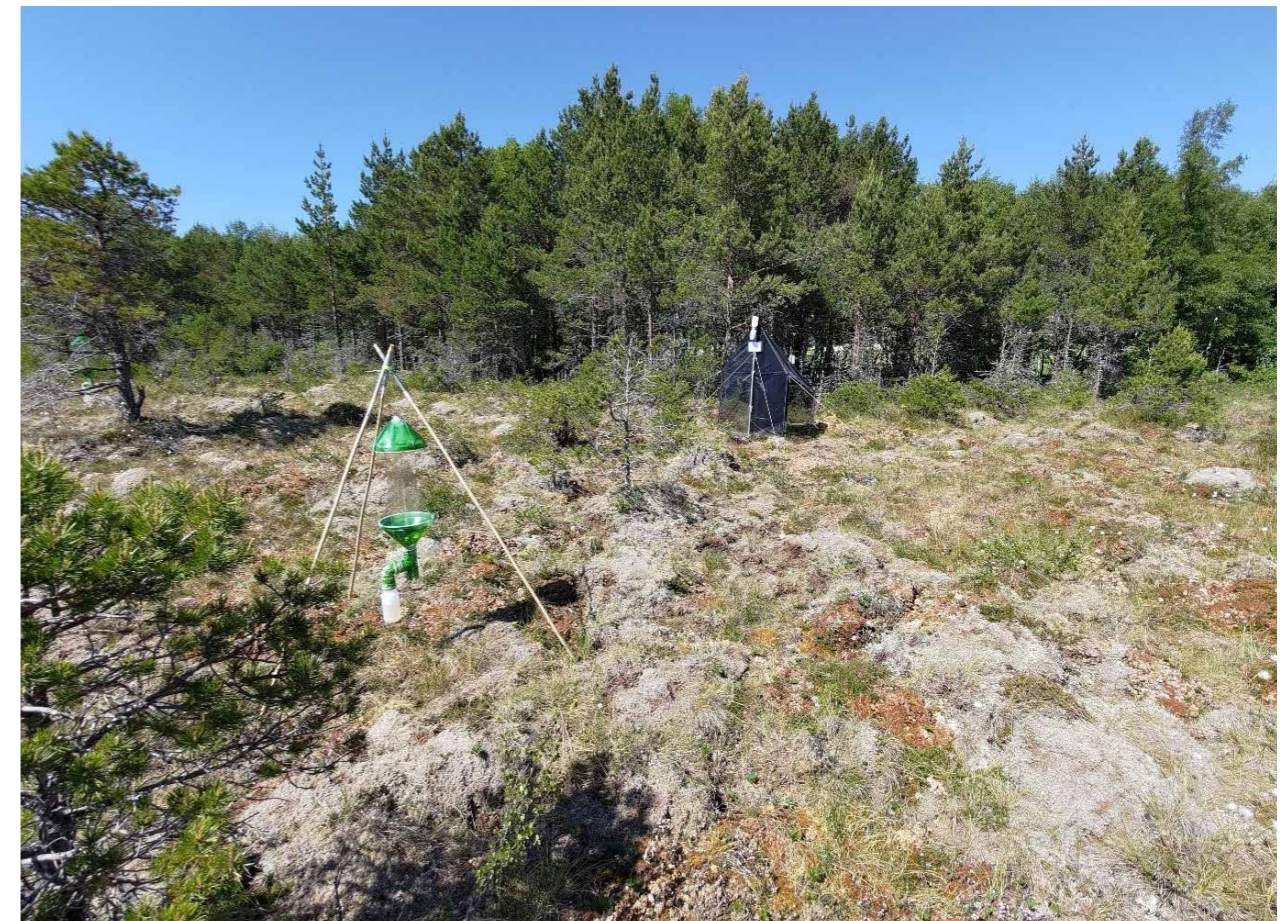
NEW AT NTNU

NAME: Angeline Bruls
START DATE: March 2021
POSITION: PhD candidate

Feeling like the Netherlands were a bit too tidy, flat, and warm, I wanted to move up north after my MSc at Wageningen University. I'd spent several semesters at the University Centre in Svalbard, but although I loved the ruthless arctic wilderness, I am happy I ended up at the CBD in Trondheim! Going for hikes and skiing trips is a bit more relaxing when you don't have to worry about polar bears…

I started my PhD on diversity patterns in Trøndelag's freshwater communities in March 2021 with a seemingly endless period of home office. After working from my parents' house, trains, friends' kitchen tables, and temporary sublets, I was delighted to finally move to Trondheim during the summer. I finally got to meet the people of CBD, and it felt like my PhD was really getting started! If this pandemic has taught me one thing, it is that in-person communication is invaluable, both when it comes

to discussing the details of my work with my supervisors, as well as creating a good work environment with my peers and colleagues. In the years to come, I look forward to learning more about freshwater ecology, community dynamics, cross-country skiing, and all the other wonders CBD and Trondheim have on offer.

NAME: Debora Goedert
START DATE: January 2021
POSITION: Postdoc

I started a sparrow-ninja postdoc track at CBD in 2021, working with Henrik, Jane, and many others on a project to investigate ecological and evolutionary implications of immigrants to small populations. In particular, I'm looking at that by investigating the effects of the immigrants' genetic variation on the fitness of their offspring. Although seemingly very different, this project relates a lot to various topics I worked with in the past, in particular some of my population and quantitative genetics work with wood frogs (ask me about my frog!). This project also brings me back to working with birds after 10 years of wandering in the lands of fish, lizards, frogs, and insects!

Like many others that started during a covid lockdown, I am still getting to know people in the department, but I am grateful for the many smiley and kind faces I have gotten to know so far! NTNU has been a welcoming and fun place to work, and it has been extremely exciting to listen and learn from so many talented and engaging colleagues and visitors. I look forward to more years here! I am also still getting to know Trondheim, but worry not, that's something I hope to remedy soon!

NAME: Philip Stanley Mostert
START DATE: March 2021
POSITION: PhD candidate

I grew up in the city of Johannesburg in South Africa but spent the last five years studying statistics in the quirky city of Grahamstown. After graduation, I wanted to apply the theoretical skills I learned to something significant, and so found myself a career in science in a city I knew nothing about prior to applying. After spending eight months working online at home due to travel restrictions (*on the bright side, it meant that I got to skip the harsh Norwegian winter and travel abroad during

the temperate summer), I traveled to Trondheim armed with well over two kilograms of rooibos tea, which I later learned was commercially available practically everywhere. Despite starting a new discipline completely online and moving to a strange and foreign location amid a global pandemic, I have found life easy in Trondheim thanks to the boundless support of coworkers and fellow CBD members. More so, I have found a love for Norwegian culture and their outdoors and truly understand the meaning of the word "hyggelig" after experiencing my first white winter.

NAME: Hannah Fried-Petersen
START DATE: October 2021
POSITION: Postdoc

The latitude of Philadelphia, USA is ~39° N. From there I began my academic journey north. First stop: Master's degree in Munich, Germany (~48° N) to work on invasive species in the Danube River. Next stop: Uppsala, Sweden (~59° N) for a PhD on stability and resilience of invertebrate communities in Swedish lakes and streams. Current stop: beautiful Trondheim, Norway (~63° N) for a postdoc. I am really enjoying all that this latitude has to offer and I am very grateful to have the opportunity to work at CBD, which is pushing boundaries and forming synergies in so many areas.

Broadly, I am a community ecologist interested in ecological stability, resilience, and biomonitoring. My past research has focused on studying long-term and spatially extensive community changes using compositional and trait-based analyses of freshwater invertebrate communities. At CBD, I explore methods for modeling multi-species population fluctuations, helping to bridge the gap between population and community dynamics.

NEW AT NTNU

NAME: Jennifer Morinay
START DATE: September 2021
POSITION: Postdoc

I moved to Trondheim at the end of August. Having to make a transition from a postdoc in Italy, with warmth, good wine, and splendid food, to another postdoc in Norway is not an easy process, I have to confess. Yet, the wet and cold weather in Trondheim also revealed beautiful nature and outdoor experiences which I very much enjoy. Afterall, I really like cold environments, as testified by my time spent in Sweden and Antarctica. So this dispersal event up north was for me an opportunity to reconnect with this and also pursue my work on (sea)bird behaviors.

Importantly, I am Breton (before being French), and I am very much attached to my native region with a peaceful life by the sea. Trondheim now also offers me this sea-related life which I will fully experience for my first spring and summer here. I also very much like crafting in my free time, and I am thrilled to have found happy crafters here at CBD to share our interests!

For more scientific considerations, I am a behavioral and evolutionary ecologist with research interests spanning social learning, personality, habitat selection, and movement ecology.

My current research interests lie in understanding the evolution and origin of individual differences when making informed decisions. During my PhD at the Universities of Lyon (France) and Uppsala (Sweden), I worked on the flycatcher-titmice system from Gotland Island (Baltic Sea), studying sources of individual differences in heterospecific social learning and, in particular, how this behavior depends on individual experience, personality, and cognitive abilities. During my postdoc at ISPRA (Italy), I collaborated with animal movement ecologists to investigate the use of social information for foraging decisions in colonial breeders in two colonial bird species (a raptor, the lesser kestrel, and a seabird, the Scopoli shearwater). I am now a lucky MSCA fellow at CBD for two years. More specifically, I am studying how seasonal migration can have carry-over effects onto breeding dispersal and how both these decisions could be mediated by social bonds between individuals.

My time here at CBD will be full of interactions and exchanges, nourished by the talent of the evolutionary researchers here and my contribution to a behavioral investigation of habitat selection decisions.

NAME: Joel Pick
START DATE: May 2021
POSITION: Postdoc

I'm a postdoctoral researcher, currently working in the group of Prof. Jon Wright. Generally, my work focuses on social interactions and predominantly on the causes and consequence of variation in parental investment in birds. I am also interested in statistical methodology, such as mixed effects (or hierarchical) models, quantitative genetic models and meta-analysis. In my current position I am working to develop tools for simulating data from mixed effects models for both education and research.

NAME: Ivain Martinossi
START DATE: September 2021
POSITION: Postdoc

CLOSER TO THE SEA

I joined the CBD as a Post Doc in September 2021, after spending most of my academic life at the University of Uppsala, in Sweden. I see myself as an evolutionary biologist with a strong interest in sexual selection and its interactions with ecological factors. In other words, I am fascinated by how males and females evolve their morphologies and interacting behaviors, and how environmental conditions interplay with these complex phenomena.

In my past projects I have dissected the action of natural selection on males and females by replicating evolution in the lab, with beetles, and on the chips of my computer, with models. With my current project I have found the perfect next step: I will study sexual selection in the wild. To do this, I will have to get wet and dive to collect data on populations of fish along the coast of Norway. Diving is my passion and that is why the move to Trondheim was an obvious decision for me. The city itself is very much turned towards the sea, and the sight of the fjord reminds me of that every day.

What's more, I get to join the CBD, clearly one of the best environments for an evolutionary ecologist such as myself, alive with scientific discussions and hosts to some of the best names in the field. I am looking forward to my stay here, and I feel that I will learn a lot while getting to do what I love: science and diving.

WORKSHOPS AND CONFERENCES 2021

GJÆREVOLL CENTRE WORKSHOP

The Gjærevoll Centre is a new initiative put forward by NTNU and NINA with the overall goal of promoting environmental sustainability and biodiversity.

The centre aims to foster research, education, and scientific outreach by becoming a hub for collaborations between all stakeholder groups, from science to government, society, business, and agriculture. To develop this vision further, a workshop was organized on the 1st of November 2021, in Trondheim. The workshop received overwhelming interest from a variety of departments at NTNU and external organizations, bringing the Gjærevoll Centre one step closer to a reality.

The Gjærevoll Centre workshop included talks from institutions such as SINTEF, NINA, NIBIO, and from departments at NTNU ranging from biology, to geography, sociology, engineering, economics, history, mathematics, architecture, and the natural history museum. After the talks, the attendees were divided into smaller groups where they discussed three main questions related to the research, education and outreach goals of the centre: (1) What would be the primary added value of the centre compared to what already exists? (2) What activities should be prioritized to ensure this added value? (3) What structure should the centre have to ensure inclusiveness across all disciplines?

The more than 25 departments and institutions participating shared ideas and expertise about potential paths forward, and all agreed that the centre was a great initiative that could not have come at a better time. Similarly, all agreed that great emphasis should be put on education and external communication, because research is not sufficient to lead the green transition. After the workshop, the members leading the creation of the Gjærevoll Centre will analyse and assess all the input collected and define the major goals, structure and funding plan.

SPATIAL POPULATION SYNCHRONY WORKSHOP

CBD has focused a lot of research towards understanding spatial population synchrony and its causes and consequences. One remaining issue is to better understand, theoretically and empirically, how temporal changes in the environment, such as through climate warming, can impact the level and scaling of synchrony.

On 11-13 August, we arranged an in-person methodological workshop at Teveltunet, Meråker, where 14 people from different CBD research areas and departments tried to disentangle pros and cons of a set of methods used to assess changes in synchrony over time. The workshop was funded by a CBD seed grant. Population modelling and simulation exercises at this workshop showed that some commonly used methods often fail to (or erroneously) detect temporal changes in spatial population synchrony, which led us to propose a new and, apparently, improved method. The workshop results contribute to MSc and PhD projects and were presented at the annual meeting of the British Ecological Society. Several papers are expected to result from what appeared a highly successful workshop. In person!

NATIONAL AND INTERNATIONAL COLLABORATION
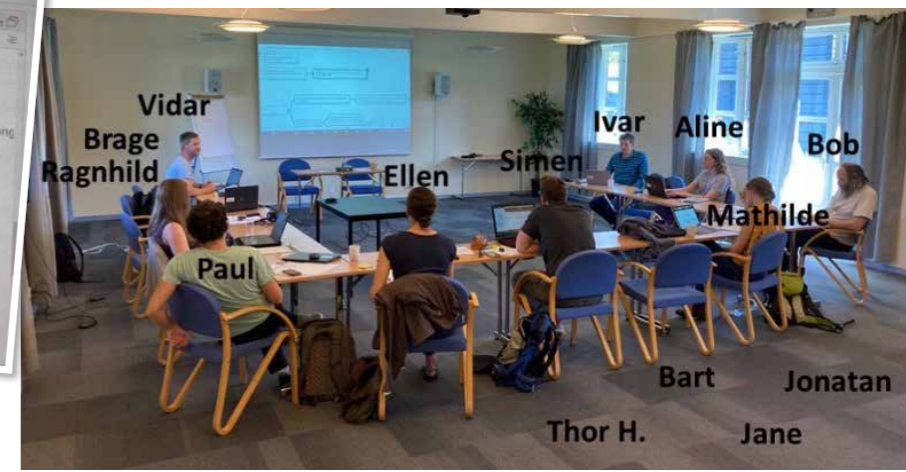
CBD SEMINAR AT LEIRFLATEN GÅRD

On August 24th, CBD came together at Lerflaten Gård in Trondheim to kick off the academic year with good food, fun activities and cutting-edge science.

The day was dismally rainy outside, but the atmosphere in the converted barn was cozy and welcoming. After a tasty lunch, Bernt-Erik introduced the presentation session and the talks got underway.

We heard from Michael Le Pepke and Thor Harald about *Telomers and Insects* followed by a talk titled *Estimating quantitative genetic parameters in wild admixed populations using genomic data* by Kenneth Aase and Steffi Muff. Next we heard from Remi Fay and his talk titled *Quantifying fixed individual heterogeneity in demographic parameters*. The session was wrapped up by Henrik Jensen presenting about *Applications for the new PacBio HiFi genome assembly and long-read sequencing of ancient and novel lineages of* Passer domesticus *in the Nordic region*.

Bernt-Erik returned to the stage and summarized the last year and what he envisioned for the year ahead. Everyone enjoyed a farm tour and some outdoor activities before dinner, and we all left newly inspired for the year ahead.

For a large part of 2021, the possibility for international travel was severely restricted due to the pandemic. This made it impossible to meet in person with most of our international collaborators, including the Scientific Advisory Committee. Still, most of the ongoing scientific interactions were possible to maintain through virtual platforms.

The collaboration initiated at the Lorentz Center workshop on Individual Heterogeneity in Animal's Life Histories – More than Meets the Eye, organized by Sandra Hamel, Stephanie Jenouvrier, Martijn van de Pol and Bernt-Erik Sæther in Leiden in 2020, was continued in 2021. A central aim was to provide a comprehensive overview of the relative importance of both observed and unobserved heterogeneity in life-history variation for a group of species that are situated along the slow-fast continuum of life history variation. This collaboration has already resulted in several submitted and published papers.

Under the leadership of professor Thomas F. Hansen, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, and professor Christophe Pelabon, CBD, several of the researchers involved in the Center of Advanced Study (CAS) for the project Evolvability: A New and Unifying Concept in Evolutionary Biology at the Norwegian Academy of Science and Letters in Oslo in the academic year of 2019/2020 have, by an extensive use of virtual platforms, continued their collaborations after the life of the center. This has also resulted in several papers, including some perspective rich reviews which are likely to have a huge impact on the future development of this field of research.

The involvement by CBD in the SPI-Birds Network and Database located at the Netherlands Institute of Ecology (NIOO) in Wageningen, the Netherlands was continued in 2021. The network connects researchers working on studies of populations of individual birds. A central focus has been to provide a platform to find and access available datasets.

Living Norway Ecological Data Network (https://livingnorway. no/) is a Norwegian network led by the Norwegian Institute for Nature Research that aims to facilitate open, reproducible and transparent sharing, use and reuse of ecological data to the benefit of society and science. CBD is an active partner in Living Norway. In order to facilitate reproducible ecological synthesis, Living Norway has launched a portal covering Norwegian Ecological data (https://data.livingnorway.no/) as well as R packages and tools for data sharing and re-use. This, as well as standards, routines and data flow used by Living Norway is based upon infrastructure facilitated by the Global Biodiversity Information Facility (https://www.gbif.org/). CBD personnel have also been very active in GBIF through long standing involvement in the Science Committee of GBIF, and from 2022, NTNU is also a partner in the national Norwegian GBIF node consortium.

Members of CBD have also been heavily involved in other collaborations with researchers from several Norwegian universities and applied research institutions. Many of these interactions were established through the large integrated project Sustainable management of renewable resources in a fluctuating environment: an integrated approach across ecosystems (SUSTAIN) and were continued in 2021.

An important step of practical implementation of results obtained by CBD was the establishment of the project Ecosystem Trøndelag, which involves collaboration between landowners and municipalities to analyse factors affecting temporal and spatial variation in species diversity within a specific region (Trøndelag). CBD is also involved in several related projected funded by the Norwegian Environment Agency to develop methods and principles for managing biological diversity at different organismic levels.

POPULAR SCIENCE

Outreach and popular dissemination from CBD occur through very different channels.

For instance, Aline Lee and Irja Ratikainen are scientifically responsible for nearly 200 articles in the Norwegian online encyclopaedia (snl.no) in the categories population dynamics, species interactions, ecology and behavioural ecology and the articles have been read more than 300 000 times in 2021. Lee and Ratikainen have also visited more than 10 classes in upper secondary schools as part of NTNUs version of Skype a scientist (Forsker på skjerm) talking about why some populations go extinct faster than others and what animals do when the climate is changing.

The realisation that much of the research at CBD has important relevance for how we manage our nature has led to several initiatives for participating in the public debate about biodiversity and the biodiversity crisis. Anders Finstad, Bernt-Erik Sæther and Ivar Herfindal have had several feature articles on this topic in regional and national media such as Adressa, Nationen and NRK.no. For instance, Sæther wrote a feature article about how Norway's increasing destruction of bogs and wetland affect our traditional cloudberry dessert on Christmas, which was published in NRK.no. This got very high attention and triggered several interviews with Sæther on regional and national media. Similarly, Brage Bremset Hansen and Vebjørn Veiberg's feature article in Svalbardposten about parasites on the Svalbard reindeer drew much attention.

The high societal relevance of the research also got attention from the Norwegian Sci-Tech news (gemini.no). Both Tanja Pedersen and Wouter Koch were interviewed about their PhD work on urban ecology and citizen science data, respectively. Ivar Herfindal was also interviewed about the research project "nature-based solutions for land use transitions towards more sustainable societies" that was funded by the NTNU Sustainability call. Bernt-Erik Sæther was invited to present results from the Sustain project at the national conference "Forskning i Friluft".

At a very different angle, Mathilde le Moullec, Lara Veylit and Christophe Coste participated in a scientific outreach on gender equality in science for the French TV program FR2. The film team visited NTNU and interviewed researchers both at CBD and other departments, as well as students and the Pro-Rector about recruitment initiatives that are helping to close the gender gap.

Ytring

Jul uten multekrem

Snart må vi finne oss en ny desserttradisjon på julaften.

Bernt- Erik Sæther
Professor i populasjonsøkologi ved Institutt for Biologi og direktør for Senter for biodiversitetsdynamikk ved NTNU

Publisert 19. des. 2021 kl. 22:29

Når vi setter oss til bords på julaften vil én av fem innta multekrem som dessert. Det kan det snart være slutt på, skriver professor Bernt-Erik Sæther.
FOTO: LISE ÅSERUD / NTB

Facsimile of the feature article by Bernt-Erik Sæther at NRK.no. Read the full text here: https://www.nrk.no/ytring/jul-uten-multekrem-1.15713770

CBD and research groups are active at several social media channels. For instance, the house sparrow project became very popular on instagram by sharing videos from fieldwork. This way of communicating science will become more important in the future, and CBD will take actions to be in front of this development.

PhD-dissertations

Seven PhD candidates defended their thesis at CBD in 2021:

January 22nd	**Sam Perrin** *"Freshwater fish community responses to climate change and invasive species"*	
Opponents:	Professor Colin Bean, University of Glasgow, UK	
	Associate Professor Damaris Zurell, Universität Postdam, Germany	

February 19th	**Lara Veylit** *"Causes and consequences of body growth variation in hunted wild boar populations"*
Opponents:	Assistant Professor Lise M. Aubry, Colorado State University, USA
	Professor Atle Mysterud, University of Oslo, Norway

March 2nd	**Semona Issa** *"Combined effects of environmental variation and pollution on zooplankton life history and population dynamics"*
Opponents:	Associate Professor Åsa Berglund, Umeå University, Sweden
	Associate Professor Linda Weiss, Ruhr Universitat, Germany

March 19th	**Vanessa Bieker** *"Using historical herbarium specimens to elucidate the evolutionary genomics of plant invasion"*
Opponents:	Senior Lecturer Alexander Papadopolus, Bangor University, UK
	Postdoctoral researcher Jill K. Olofsson, University of Copenhagen, Denmark

April 9th	**Tanja Kofod Petersen** *"Biodiversity dynamics in urban areas under changing land-uses"*
Opponents:	Researcher Jonathan Renoir, Université de Picardie Jules Verne, France
	Professor Olav Skarpaas, University of Oslo, Norway

October 29th	**Christoffer Høyvik Hilde** *"Demographic buffering of vital rates in age-structured populations"*
Opponents:	Professor Yvonne Buckley, Trinity college, Dublin, Ireland
	Senior Lecturer Dylan Childs, University of Sheffield, UK.

December 17th	**Michael Pepke Pedersen** *"The ecological and evolutionary role of telomere length in house sparrows"*
Opponents:	Professor David S. Richardson, Norwich Research Park, UK
	Associate Professor Britt J Heidinger, North Dakota State University, USA

KEY FIGURES 2021

Gender equality

At CBD there continues to be a predomination of females in the earlier stages of a scientific career. In order to ease the transition from postdoc to faculty, CBD, in collaboration with the Department of Biology, offered female researchers the possibility to allocate a portion of their time to undergraduate teaching. Hopefully, the success of earlier career females at CBD in competing internationally for attractive positions in research or for permanent faculty positions at Norwegian universities will also motivate young women for a career in science.

The Department of Biology has an Equal Opportunities Committee which includes two members of CBD.

Key Figures

Key numbers in CBD	2021	
	F	M
Professors/Associate professors	5	18
Researchers	3	15
Postdocs	12	8
PhD candidates	25	16
Technical staff		4
Administration	2	
All staff at CBD	47	61
Total	108	
Scientific Advisory Board	1	5

Costs and funding	KNOK
Cost	
Salary and indir. cost	37 904
Other operating cost	11 674
Sum cost	49 578
Funding	
NFR	5 144
Other funding	500
NTNU	27 070
Sum funding	32 714
Funding associated projects	15 572

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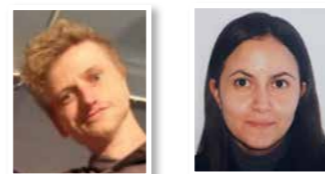
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