

# Annual Report 2014



# CBD IN SHORT

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

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

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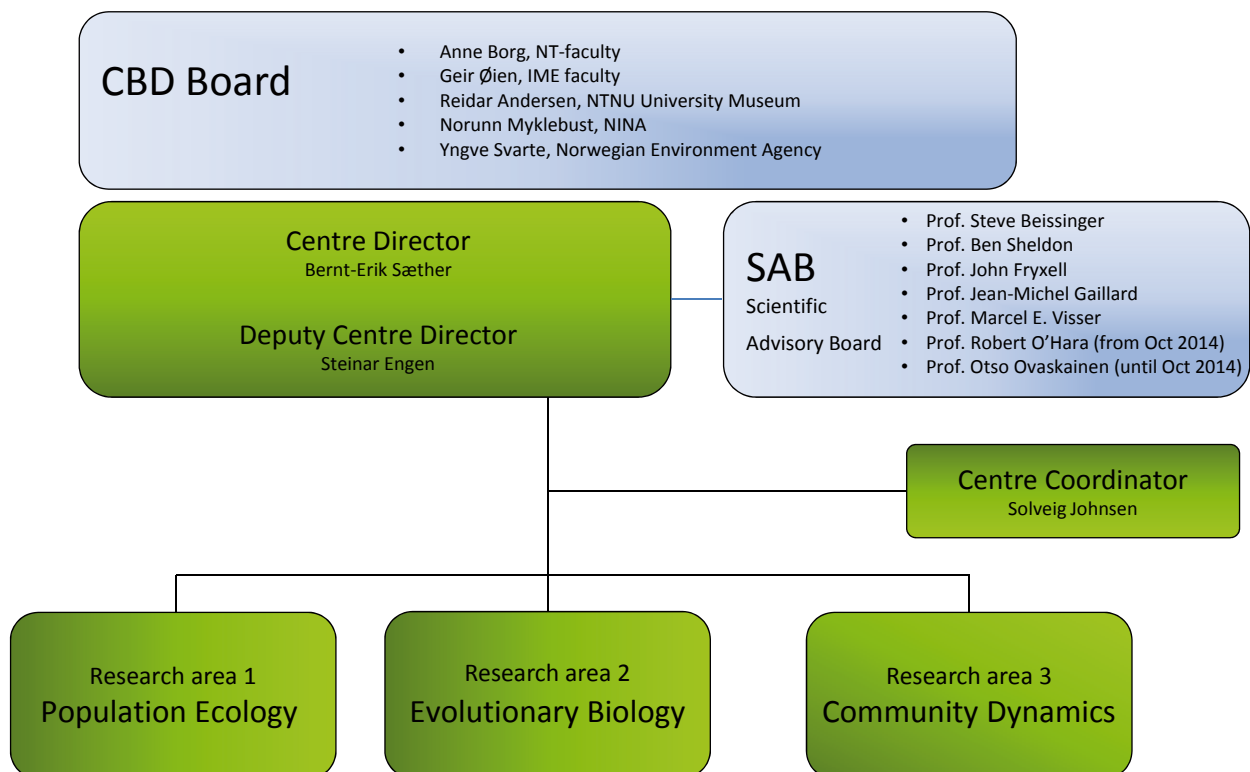
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# 1. MANAGEMENT AND ADMINISTRATION

## MANAGEMENT STRUCTURE

CBD is organized as a separate research centre analogue to a department with Faculty of Natural Science as host faculty. CBD involves collaborations between two partners: NTNU and the Norwegian Institute for Nature Research (NINA). Management of the centre is run by the Centre Director (Sæther) together with the Deputy Centre Director (Engen) and the Centre Coordinator (Johnsen). The organizational structure of the centre is flat. The operational unit of CBD is the research groups belonging to CBD's core members, who are researchers with faculty positions at NTNU or positions as senior researchers at NINA. A Steering board including members from each of the involved faculties at NTNU (including the Museum),

NINA and the Norwegian Environment Agency oversees that activity at CBD is operated according to the project description funded by the Research Council of Norway. A central task for the Steering board is also to promote the collaboration among the different departments and to integrate in CBD relevant research at NINA that can be important for achieving the scientific goal of CBD. The Scientific Advisory Board consisting of 6 internationally leading scientists contributes to develop a strategy for the scientific development of the centre, facilitating the leadership to achieve the scientific aims. SAB is also heavily involved in implementing appropriate means of actions to fulfil the strategy plan and act as external advisors for the management of CBD.



## THE BOARD AND THE SCIENTIFIC ADVISORY BOARD OF CBD



From the left: Geir Øien, Reidar Andersen, John Fryxell, Norunn S. Myklebust, Robert O'Hara, Jean-Michel Gaillard, Marcel E. Visser, Anne Borg, Ben C. Sheldon, Bernt Erik Saether and Steve Beissinger.

## COMMENTS BY THE CHAIR

CENTRE OF BIODIVERSITY DYNAMICS (CBD) is the first and only centre of excellence hosted by Faculty of Natural Science and Technology at NTNU. Topically, the centre is in the core of NTNU's vision "Knowledge for a better world" and the ambition of the faculty to support this vision through its research groups. Excellence in science, manifested by the research accomplishments of CBD, is an integral element of this strategy. Furthermore, CBD is a major backbone of our university strategic

thematic area "Sustainability". For CBD, 2014 has been a year of centre consolidation and outstanding scientific achievements. The progress of this research environment is of great inspiration to our students and scientific personnel. We are foreseeing new highlights from CBD in the years to come.



**Anne Borg**  
Decan, NT-Faculty  
Chair Board



## SUMMARY OF MAIN ACTIVITIES

CENTRE OF BIODIVERSITY DYNAMICS (CBD) opened on July 1 2013. The main focus for the activity during the first 1.5 year of activity has been to establish a research environment in which multi-disciplinary research collaboration is encouraged, in particular bridging the gap between biology, mathematics and statistics. This has been achieved by running weekly lunch- seminars, organizing seminars and workshops on problems attracting both biologists and people with a mathematical focus as well as facilitating establishment of informal meeting areas. The areas provided by NTNU located in the eastern part of the Natural Science Building have been instrumental for facilitating such interactions.

In 2013 CBD included 13 core members (permanent staff) at NTNU (9 professors/associate professors) at the Department of Biology, Faculty for Natural sciences and Technology, 3 professors at Department of Mathematical Sciences, Faculty of Information Technology, Mathematics and Electrical Engineering and 1 professor at the University Museum) and 4 core members at NINA. In addition, 6 persons were employed as researchers on externally financed projects. In 2014 2 of those were hired as associate professors at the Department of Biology and were then included as core members of the CBD. The core members are involved in teaching and in supervising of MSc- and PhD-students and are together with the steering board instrumental for coordinating and integrating the work at CBD with the activities of the institutions involved.

An important challenge in this first period of CBD has been to recruit new staff to the centre. Our strategy has been to search for people internationally, resulting in the hiring of Otso Ovaskainen as professor (60 % position) and core member of the CBD, 2 French post docs and 1 PhD-student. By the end of 2014 13 PhD-students and 12 post docs were employed by CBD.

Much of the scientific focus during these first years of CBD has directed towards problems in evolutionary biology (Research Area 2). For instance, the opening conference of the centre October 14-16 2013 focused on themes such as phenotypic evolution, estimating of selection in fluctuating environments, the importance of genetic drift and evolutionary rescue in changing environments. The talks on this conference were given by specially invited lecturers, members of the Scientific Advisory Board and researchers at CBD.

Another workshop in evolutionary biology entitled 'Evolution in Stochastic Environments' was organized

in January 13-15th 2014 by the core member Jonathan Wright. This workshop was aimed at understanding the effects of unpredictable spatial and temporal environmental variation on evolution (i.e. in the context of variable population dynamics), and more specifically the nature of adaptive responses to such environmental stochasticity.

The workshop involved lectures and discussion sessions provided by Prof Philip Crowley (Kentucky, USA), Dr Aviv Brokman (Kentucky, USA), Prof Steinar Engen (CBD), Prof Dustin Rubenstein (Columbia, USA), Dr Irja Ratikainen (CBD), Dr Sean Ehlman (UCDavis, USA) and Prof David Westneat (Kentucky, USA). The workshop generated lots of interesting and illuminating discussions, mostly concerning theoretical issues around bet-hedging and reconciling the various recent models being developed by the participants and others.

Some of the research at CBD in evolutionary biology was presented by three papers in issue of the Philosophical Transaction of the Royal Society entitled "Integrated phenotypes: understanding trait covariation in plants and animals" published in July 2014. In these contributions, it was shown that genetic correlations could represent serious constraints to phenotypic evolution by favoring specific directions of evolution.

A central focus for CBD is to maintain the continuity of field and laboratory studies that are critical for validating models describing dynamical changes in biological diversity. One of the most comprehensive of those is the study of the dynamics of a metapopulation of house sparrows at the coast off Helgeland that has been running on a large number of islands since 1993. An important contribution in 2014 for linking ecological and evolutionary dynamics in this study system was the development of advanced statistical techniques to estimate the effect of genes for observed variation in different types of traits and the availability of new genomics tools for analyzing genetic dynamics in these house sparrow populations. Emphasis was also made on experimental manipulations of key evolutionary processes in house sparrows, such as selection experiments on basal metabolic rates and manipulations of effective population sizes through changes of the social structure.

Another long-term field study at the CBD is the collection of individual based demographic data of the moose



**Bernt-Erik Sæther**  
Director CBD

at island of Vega in northern Norway, which has been running since 1992. An important milestone in this study was that detailed pedigrees of the relatedness among almost all individuals that have been or are still alive on this island became available. This has facilitated detailed analyses of factors affecting the genetic structure and phenotypic selection on different fitness-related characters in this population of moose.

Researchers at CBD have previously documented that expected changes in climate will strongly affect the trophic interactions among vertebrates in high Arctic ecosystems. The study of the dynamics of Svalbard reindeer was continued in 2013 and 2014, especially focusing on a mechanistic understanding of how extreme climate events are likely to affect the dynamics of reindeer populations.

In order to understand how organisms respond to changing environmental conditions a laboratory study system involving ca. 30 genetically unique clones of *Daphnia* (water fleas) collected from the wild was established in 2013. Waterfleas have many characteristics that make them particularly suitable

for such studies, including dependence of one easily manipulated environmental factor, temperature, clonal reproduction and a short generation time. The set-up allows quantification of the genetic variation in phenotypic responses to temperature treatments (i.e. thermal reaction norms) and estimates of population dynamics parameters (growth rate and carrying capacity). This will provide information about the potential for evolutionary changes in reaction norms not only as a response to a change in temperature, but also in response to changes in population density.

In 2013 and 2014 a focus at CBD was to strengthen and further develop links with other research groups both nationally and internationally. As a consequence, researchers at CBD co-published during the first 1.5 years papers that included more than 20 international collaborators.

An appreciation of the research conducted at CBD was that the director and vice-director of CBD was awarded the Møbius-prize by the Research Council of Norway on September 18 2013.

## COMMENTS BY THE SCIENTIFIC ADVISORY BOARD

THE SCIENTIFIC ADVISORY BOARD (SAB) of the Centre for Biodiversity Dynamics (CBD) met from 14-16 October 2013 and 21-23 January 2015 in Trondheim to review the state of the centre and its accomplishments since the opening of CBD July 1 2013. During the visits SAB listened to presentations of graduate- and postdoc-students associated with CBD, received reports from the CBD Director Professor Saether, and discussed the accomplishments and directions of the centre.

SAB was deeply impressed by the quality of the presentations by the younger scientists at the centre, the range of topics, and the gender and age diversity of presenters. Many of the presenters displayed a strong potential for a successful career in science. Particular progress has been achieved in the analysis of the dynamics of biological system under stochastic dynamics, with a goal of understanding general patterns

that can be used to predict dynamics and patterns of biodiversity.

Based on these presentations and discussions with the leadership of CBD, the SAB concludes that important scientific progress is currently being made at CBD. Advances have been particularly strong on questions related to the interface between ecology and evolution. We expect some of the results to have important impacts for the future development of this entire field of research. The SAB concludes, without any doubts, that CBD is emerging as an internationally leading research centre at the interface of biology and mathematics.



**Steven A. Beissinger**  
Professor  
Chair of SAB

## 2. SCIENTIFIC ACTIVITY

### RESEARCH AREA 1: POPULATION ECOLOGY

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

#### Questions

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

#### Achievements

- Dynamics of age-structured populations not subject to density regulation can be well described following a suggestion by R.A. Fisher by the temporal variation in the total reproductive value of the population.
- Analyses of several long-term studies of the dynamics of bird and mammal populations showed that changes in population growth rates can be surprisingly well explained by basic species-specific life history characteristics.

House sparrows at the coast of Helgeland.



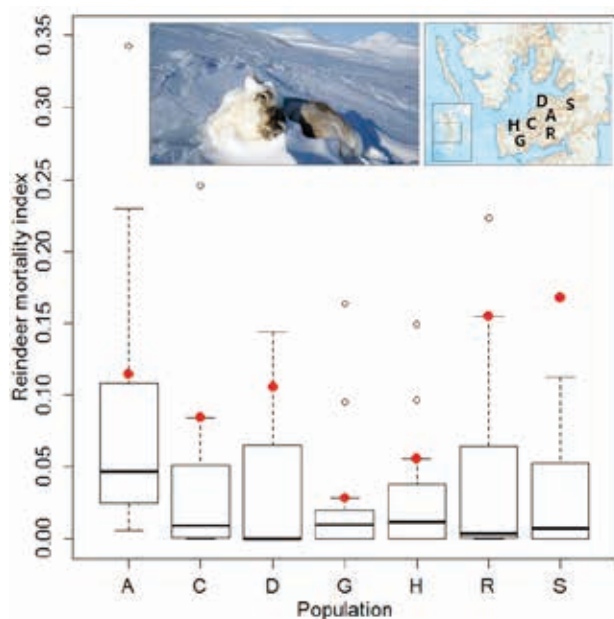
## AN EXTREME RAIN-ON-SNOW EVENT AND ITS IMPLICATIONS FOR WILDLIFE IN HIGH ARCTIC SVALBARD

Brage Bremset Hansen

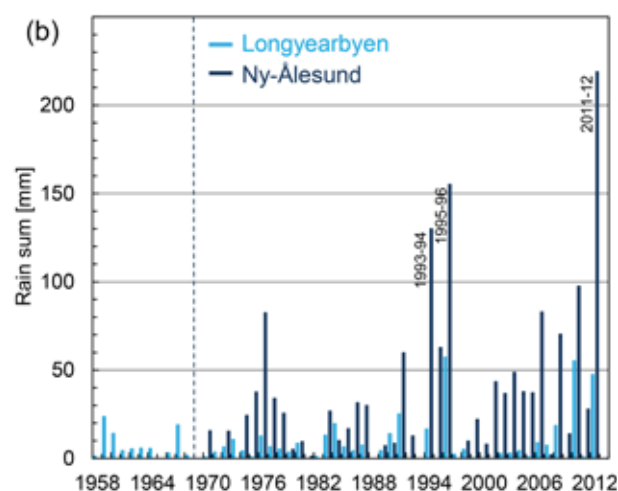
No biome on Earth is subject to more rapid or pronounced climate change than the Arctic. In particular, winter climate is warming at unprecedented rates in many regions, possibly increasing the frequency of warm spells and rain-on-snow (ROS). Studying the ecological implications of extreme weather events such as ROS is inherently challenging, given their rarity and the poor spatiotemporal resolution of most Arctic time-series data. In a recent inter-disciplinary study led by CBD and published in *Environmental Research Letters* (Hansen et al. 2014), we took the advantage of an extreme warm spell and historical ROS amounts in high Arctic Svalbard in January-February 2012 in order to document the geophysical characteristics, spatial extent and implications for wildlife and society of such rare events. We showed that this two-week warm spell, with temperatures exceeding 7 °C and frequent rainfall (up to 100 mm in one single day), seriously affected snow conditions by causing numerous slush avalanches and solid ground-ice exceeding 20 cm thickness. Previous studies from CBD have shown that the ground-ice encapsulates most of the vegetation and hence “locks” the winter pastures for herbivores. Accordingly, the (in an international context) unique research infrastructure and availability of long-term time-series enabled us to

demonstrate that this extreme climate event resulted in high die-offs in all the monitored wild reindeer populations (Fig. 1.).

The study in *Environmental Research Letters* has important implications for how we should model and predict ecological climate change effects on the tundra under future global warming. In particular, using state-of-the-art downscaled climate scenarios and 100 years of weather data the study showed that the recent increase in winter temperatures and ROS in Svalbard (Fig. 2) will probably continue throughout the century. In only few decades, the average mid-winter temperatures in this high Arctic hotspot of climate change are likely to exceed 0°C in occasional years (Fig. 3), suggesting increased likelihood for ROS events and thus more frequent icy winters. Another recent study published in *Science* by several researchers at CBD (Hansen et al. 2013) provides strong indications that this may directly or indirectly affect the dynamics of the whole tundra ecosystem. Based on population monitoring data, the study demonstrated that occasional rainy and icy winters force the long-term population dynamics of all overwintering herbivore species (wild reindeer, rock ptarmigan and sibling vole) into cross-species synchrony, probably due



**Figure 1.** Mortality rates were high in all the monitored populations of wild Svalbard reindeer in the extremely rainy and icy winter 2011-12. From Hansen et al. (2014). Photo: Eva Fuglei, Norwegian Polar Institute



**Figure 2.** Changes in winter rain-on-snow (ROS) amounts in Svalbard. From Hansen et al. (2014).



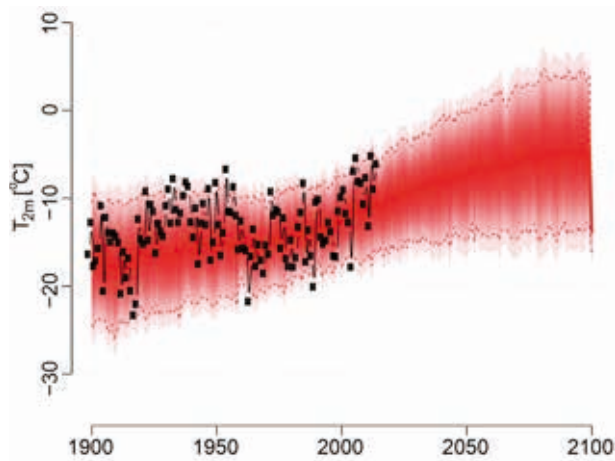
to their common reduction in winter forage accessibility with delayed effects on population growth. Because their shared predator and scavenger, the Arctic fox, largely relies on reindeer carcasses found on the tundra, its population dynamics follow the high-amplitude herbivore fluctuations with a time-lag. The Arctic fox also represents the main predator of migratory birds such as

geese, and one plausible hypothesis is that major ROS events may cascade throughout the entire food-web in this simple trophic system. Clearly, changes in the frequency of mild, rainy and icy winters, as predicted by Hansen et al. (2014), can seriously impact the ecosystem dynamics on the Arctic tundra.

#### FURTHER READING:

Hansen BB, Isaksen K, Benestad R, Kohler J, Pedersen ÅØ, Loe LE, Coulson SJ, Larsen JO and Varpe Ø (2014). Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. *Environmental Research Letters* 9: 114021.

Hansen BB, Grøtan V, Aanes R, Sæther B-E, Stien A, Fuglei E, Ims RA, Yoccoz NG and Pedersen ÅØ (2013). Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science* 339: 313-315.



**Figure 3.** Historical (black symbols) and projected average mid-winter temperatures in Longyearbyen, Svalbard. Red area shows the spread between 108 different GCM (Global Circulation Model) simulations, and the dashed lines indicate the 90% confidence interval. From Hansen et al. (2014).

Like most harvested populations, the moose population at Vega is also female biased. However, recent results show that this may have negative impacts processes such as inbreeding avoidance. The moose cow in the picture is a three year old female that have yet to breed successfully.



Photo: Endre Olstad

## RESEARCH AREA 2: EVOLUTIONARY BIOLOGY

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

### Questions

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

### Achievements

- A method is developed based on a modification of the Price-Robertson equations for evolution of quantitative characters that enables us to partition selection into age-specific components due to demographic and environmental stochasticity.
- A theory is developed for phenotypic evolution by  $r$ - and  $K$ -selection in fluctuating environments
- Estimates are provided of age-specific components of selection on morphological characters of house sparrows.

## A NEW WRAPPING OF THE CLASSICAL ROBERTSON-PRICE EQUATIONS FOR PHENOTYPIC EVOLUTION

Steinar Engen and Bernt-Erik Sæther

The concept of individual fitness  $W_i$  provided the foundation for Alan Robertson and George R. Price when they derived exact expressions for the change  $\Delta \bar{z}$  in mean phenotype  $\bar{z}$  of  $N$  individuals during a time step (e.g. a year or generation),

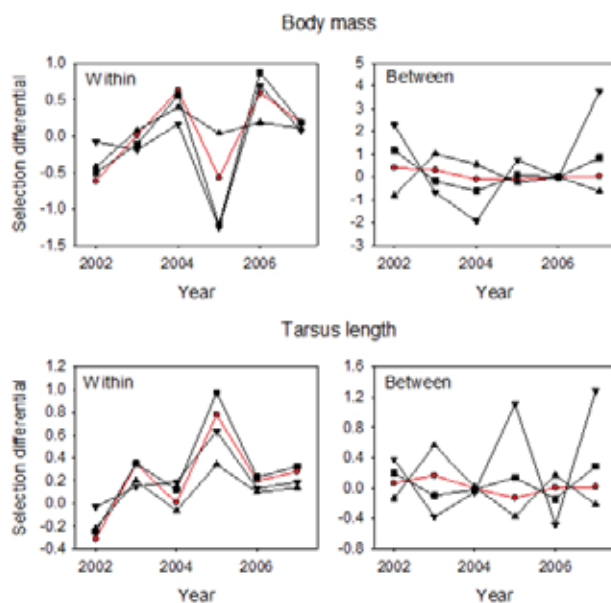
$$\Delta \bar{z} = \frac{1}{N} \sum_i (W_i - \bar{w})(z_i - \bar{z}) + \frac{1}{N} \sum_i (w_i \bar{\Delta z}_i)$$

where  $\bar{\Delta z}_i$  is the mean difference between the phenotype  $z_i$  of individual  $i$  and that of its offspring, including the individual itself if it survives and  $w_i = W_i/\bar{W}$  is the relative fitness of individual  $i$ . The first term in this equation is the selection differential  $S = \text{cov}(\mathbf{w}, \mathbf{z})$ . The second term is a transmission term generated by the difference in phenotypes between adults and their offspring. Thus, the Robertson-Price equation originally formulated using fitness across generations enables statistical analyses of how phenotypes respond to phenotypic selection and how this response is affected by changes in the environment (e.g. as a consequence of trophic interactions).

We decomposed the selection differential  $S$  into mean value and components due to demographic and environ-

mental stochasticity so that  $S = ES + \Delta S_e + \Delta S_d$ . This partitioning provides a direct link to one of the fundamental equations in quantitative genetics provided by Russell Lande, who showed that the response to selection on multivariate characters is  $\mathbf{R} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S}$ , where  $\mathbf{S}$  is a column vector denoting the selection differential,  $\mathbf{G}\mathbf{P}^{-1}$  is the heritability matrix and  $\mathbf{G}$  and  $\mathbf{P}$  is the additive genotypic and phenotypic covariance matrix, respectively. Our partitioning of the covariance formulation of the selection differential originally provided by Alan Robertson in 1966 shows that the response to fluctuating selection and random genetic drift is  $\mathbf{G}\mathbf{P}^{-1}\Delta \mathbf{S}_e$  and  $\mathbf{G}\mathbf{P}^{-1}\Delta \mathbf{S}_d$ , respectively. This provides an approach to separate the effects of selection due to random variation in individual fitness from fluctuating selection caused by environmental variation.

Another advantage of this covariance approach in studies of selection is that it enables us to account for fluctuations in age-distribution, which can cause temporal changes in the mean phenotype that can mistakenly be interpreted as selection. We show that these fluctuations in the mean phenotype will disappear if reproductive value weighting is applied. Changes in



**Figure 4.** Selection differential within- and between-age classes for two morphological characters (body mass and tarsus length) of fledglings in a house sparrow population in northern Norway. The selection differential is calculated for the reproductive weighted mean (red solid line and circles), arithmetic mean (squares), mean of newborns (downward triangles), and mean of adults (upward triangles).

any weighted mean phenotype in an age-structured population can then be decomposed into between- and within- age class components. An advantage of using reproductive value weighting is that the between-age class component becomes pure noise (Fig. 4), generated by previous genetic drift or fluctuating selection. This component, which we call transient quasi-selection, can therefore be omitted when estimating age-specific selection on fecundity or viability within age classes.

We illustrated the application of this approach analyzing selection on two morphological characters of fledglings of house sparrows: tarsus length and body mass (Fig. 4). Although this small passerine species has a relatively simple life history, failure to account for fluctuations in age-distribution will result in biased estimates of selection on these two characters.

#### FURTHER READING:

- Engen, S., and B. E. Saether. 2014. Evolution in fluctuating environments: decomposing selection into additive components of the Robertson-Price equation. *Evolution* **68**:854-865.
- Engen, S., B.-E. Sæther, and T. Kvalnes. 2014. Estimating phenotypic selection in age-structured populations by removing transient fluctuations. *Evolution* **68**:2509-2523.

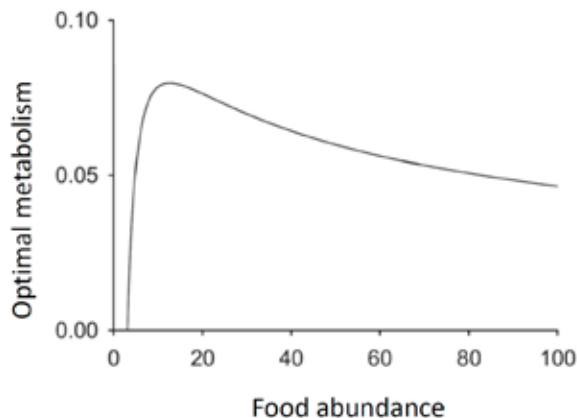
## DOES THE OPTIMAL METABOLISM DEPEND ON THE ENVIRONMENT?

Sigurd Einum

Breathing, or more specifically the consumption of oxygen due to metabolism, is a prerequisite to living for most animals. This is true even during periods of no behavioral activity, when a certain level of metabolism is required to maintain vital organs and body functions. Such resting metabolism represents an energetic cost to individuals, and from this perspective should be kept at a minimum. Yet, extensive variation is observed both within and among species after controlling for body size effects, begging the question what maintains such variation? Is the observed variation adaptive? Can the optimal level of metabolism during inactivity depend on environmental conditions? This has for a long time been a crucial remaining issue in understanding the evolution of variation in this trait. There is a poor mechanistic understanding of how the optimum metabolism varies across environments, and hence which environmental factors might cause evolutionary responses, and in which directions these might work. This also precludes a mechanistic understanding of empirical studies demonstrating context-dependent fitness effects of

metabolism, particularly in relation to food abundance.

I approached this question using optimality modeling. The starting point for the model is the accumulating evidence for a link between resting metabolism and activity metabolism. In other words, it is not possible for an organism to have a low resting metabolism while at the same time being able to maintain intense sustained activity. As a result, observed variation in resting metabolism may simply be an evolutionary side-effect of differences in the optimal levels of activity among species and populations. The model then goes on to describe how the rate of energy acquisition can be expressed as a decelerating function of activity metabolism based on the Holling disc equation. Results with respect to optimality could be found both analytically and with numerical calculations, and showed that optimal metabolism is highest at intermediate food abundances (Fig. 5). Intuitively the results from the present model can be understood by considering that as food abundance becomes sufficiently high, a lower activity (and hence



**Figure 5.** Illustration of the predicted relationship between food abundance and optimal metabolism based on a numerical example

metabolism) is required to approach maximum energy acquisition. This contrasts with previous verbal arguments that individuals with a high resting metabolism are at an advantage when environmental conditions are favorable. The results from this work will set the stage for future work on ecological correlation of variation in metabolic rates, an area of ecology and physiology that is receiving increasing empirical interest but which suffers from a lack of theory regarding optimality.

To study these problems, we have chosen a model organism that is extremely suitable for these kinds of projects, the water flea *Daphnia magna*, which CBD has now built up a lab for. Important characteristics of these organisms are that they reproduce clonally and have short generation times. In addition, logistically they are relatively easy to rear and to run experiments with high numbers of replicates.

This experimental set-up allows us to address the fundamental question in evolutionary ecology how fast organisms can respond to changing environmental conditions. Such effects are often divided into, and studied separately as (1) direct effects on phenotypes, with corresponding effects on demographic rates (e.g. births, deaths) and population dynamics, and (2) changes in the relative fitness of different phenotypes/genotypes that are used to predict evolutionary changes. Here we will study these effects simultaneously using an easily manipulated environmental factor, temperature.

#### FURTHER READING:

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

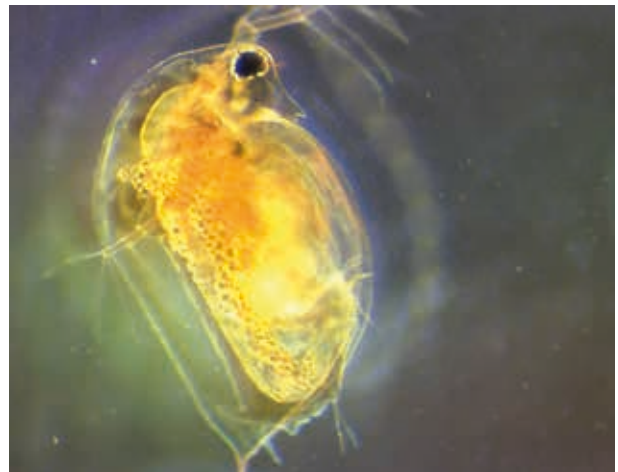


Photo: Varvara Yashchenko

*Daphnia* will be used as a model organism in our lab to study eco-evolutionary responses to environmental change, with particular focus on temperature.

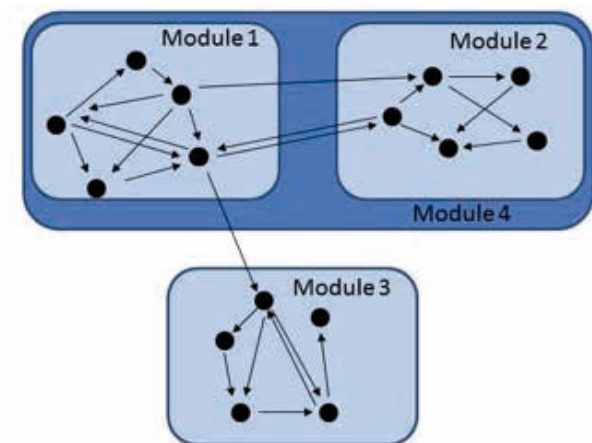
## PHENOTYPIC INTEGRATION AND MODULARITY IN PLANTS AND ANIMALS

Christophe Pelabon

Organisms are not random collections of traits and organs. They are highly organized and integrated in a hierarchical manner, simple organs consisting of numerous subunits that must grow and vary in a coordinated manner to remain functional. The pervasiveness and evolutionary importance of correlated variation in phenotypic traits have been recognized since Darwin himself raised the issue in *The Origin of Species*, and the evolutionary consistency of these patterns of organization have fascinated evolutionary biologists such

as Thompson and Huxley since the beginning of the previous century. In a seminal book published in 1958 "Morphological integration", Olson and Miller provided the first mathematical framework to quantify these patterns of organization. These authors defined *morphological* (i.e. *phenotypic*) integration as the patterns and magnitude of covariation among phenotypic traits. Phenotypic integration is tightly linked to the concept of modularity, that is, the organization of organisms into quasi-independent units that can evolve, at least to some extent,





**Figure 6.** Modularity and integration. Modules are defined by a set of traits (black circles) with more interactions (arrows) among them than with traits in other modules. Integration refers to the patterns of relationship between traits within module. Modules are organized in a hierarchical manner (e.g. module 4 consists of two subunits; modules 1 and 2). Depending on the nature of the traits considered (genes, traits, organs) modularity can be defined at different levels (redrawn from Klingenberg 2008).

without disrupting the rest of the organism. Integration therefore refers to the tightness or density of relationships among traits within modules, while modularity tends to characterize the autonomy among modules, that is, the density of relationship among modules (Fig. 6).

While patterns of phenotypic integration were in the beginning considered in terms of evolved properties in response to selection for functionality, others tended to consider these patterns in terms of constraints imposed by genetic/developmental processes. Constraints may themselves result from selection, and phenotypic integration, and modularity, most likely evolve. Evolutionary causes and consequences of phenotypic integration therefore represent a very fertile ground for debating some of the core questions in evolutionary biology about multivariate evolution. In October 2012, Scott Armbruster invited leading scientists from seven nations in order to assemble a diverse group of evolutionary biologists to address these issues. This meeting gathered people using very different approaches, from theoretical to molecular-genetic, developmental, ecological, and paleobiological, and studying different system both in animals and plants. Although this group contained people of often diverging viewpoints, there was a shared interest in attaining a deep understanding of multivariate evolution. The contributions to the workshop included the following topics 1) Historical aspects, 2) Theory and measurement of phenotypic integration, 3) Molecular and developmental factors affecting integration, and 4) Functional, ecological, and evolutionary consequences of phenotypic integration. These contributions reflect the diversity of views exposed during the workshop and the

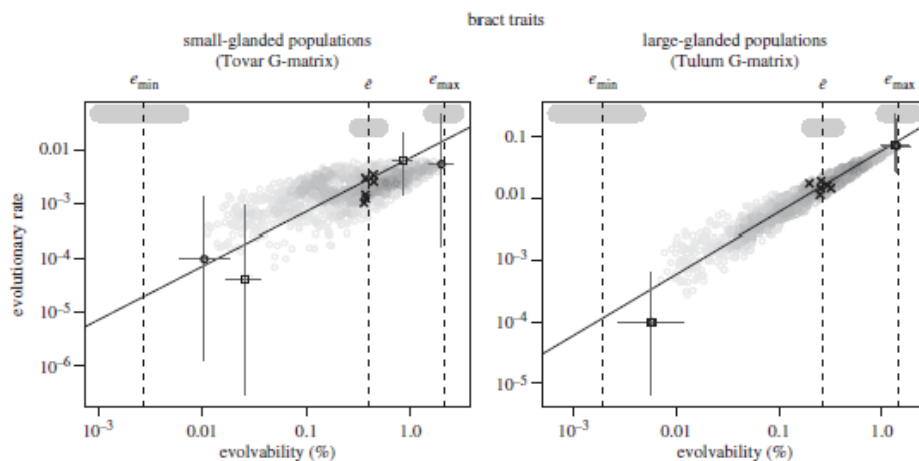
dynamism of this field of research in evolutionary biology. A subset of these contributions has been published in an issue of the Philosophical Transactions of the Royal Society in August 2014: Phenotypic integration and Modularity in Plants and Animals: <http://rstb.royalsocietypublishing.org/content/369/1649>. Contributions by the members of the CBD focused around two main themes 1) the measurement of integration and 2) whether pattern of integration constrain phenotypic evolution.

The popularity of phenotypic integration and modularity as a research area in evolutionary biology has produced a large number of methods to quantify these patterns. Unfortunately, most of the indices aiming at summarizing and comparing patterns of variance and covariance among multiple traits have been developed independently of any theoretical context. For example, a large number of integration indexes have been developed and estimated from patterns of correlation or from correlation matrix eigenvalues. Contrary to what was often advocated, these indexes, mostly based on the mathematical properties of correlations, largely ignore the developmental or functional processes that create patterns of covariance among traits. In the opening contribution, Armbruster et al. (2014), after reviewing the various concepts of phenotypic integration and modularity, reemphasized the importance of developing measurement methods based on solid theoretical ground. In the case of phenotypic integration, they advocate that integration index should account for either the genetic/developmental or functional mechanisms that generate patterns of covariance among traits.

This approach is the one followed by Bolstad et al. (2014), who used the concept of conditional evolvability



Phenotypic selection experiment on *Dalechampia scandens* in Costa Rica (autumn 2014)

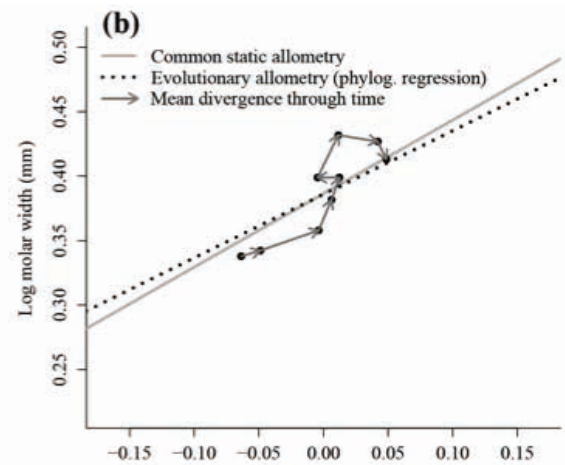


**Figure 7.** Scaling relationship between evolutionary rates and evolvability for the bract traits (From Bolstad et al. 2014).

to investigate whether or not integration, defined by the genetic architecture of multivariate traits constrains phenotypic evolution. This question introduced by Russell Lande in the 1980s in relation to the evolution of allometry was further developed by Dolph Schluter with the introduction of his concept of evolutionary lines of least resistance, continues to garner great interest. Indeed, answering this question could help solving the long standing issue of linking macro-evolutionary patterns to micro-evolutionary processes. The paper by Bolstad et al. (2014) is the first to develop a series of predictions solidly anchored in the quantitative-genetic theory about the different relationships we expect between evolvability (and conditional evolvability) and the patterns of phenotypic divergence among populations, depending on the evolutionary forces generating the divergence. In this paper, a data set of high quality comprising G-matrices of floral traits from two cryptic species of *Dalechampia scandens* and morphological divergence among 24 populations belonging to these two species to test these predictions. Doing so, Bolstad et al. were able to demonstrate that directions of preferential evolution (i.e. directions in the multivariate phenotypic space showing the highest variation among population) were congruent with the directions of highest evolvability, that is, the directions with the highest level of multivariate genetic variance (Fig. 7).

Interestingly, the contribution by Firmat et al. (2014) confirmed the hypothesis of integration-as-a-constraint using a very different approach. In collaboration with Spanish palaeontologists, Firmat and colleagues reanalysed paleontological data of extremely high quality describing the morphological evolution of the first lower molar of the rodent species *Miomys savini*. This data set, combining measurements from nine populations spread over 600,000 years, allowed them to test the congruence between the pattern of morphological integration and the patterns of population divergence. As expected from the integration-as-a-constraint hypothesis, these two patterns were highly congruent (Fig. 8), suggesting that

**Figure 8.** Bivariate divergence and allometric slopes for the first lower molar (M1) within the *Miomys savini* lineage in the Iberian Peninsula. Arrows represent the transitions through time between population means (dark circles).



morphological integration effectively canalizes phenotypic evolution along preferential routes.

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## RESEARCH AREA 3: COMMUNITY DYNAMICS

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

### Questions

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

### Achievements

- A review of the theoretical foundation and potential application of the lognormal species abundance distribution in analyses of community dynamics was published in *Journal of Animal Ecology*.
- A paper on the seasonal variation in the community structure of a tropical butterfly community in Costa Rica was published.



Photo: Thor Harald Ringsby

Central parts of Prof. Phil DeVries in Costa Rica, Central America 2009, including his hand holding a Blue Morpho (*Morpho menelaus*).

## SEASONALITY IN THE COMPOSITION OF A TROPICAL BUTTERFLY COMMUNITY

Vidar Grøtan

A fundamental climatic feature of all terrestrial habitats is the occurrence of seasonal cycles in temperature and precipitation that affect the resident biological communities. Although seasonality in tropical rainforests may be considerably less obvious than in temperate forests, seasonal precipitation has effects on tropical species abundance and diversity [Grøtan et al. 2012]. The high species diversity in tropical communities makes them important not only for biological conservation, but also for testing basic theories of species diversity. Despite the importance of understanding the effects of tropical seasonality on ecological diversity, few studies have investigated the influence of environmental factors on seasonal community composition, and even fewer use standardized sampling and robust analytical methods that are directly comparable. A longterm study of 106 fruit-feeding butterfly species in a lowland tropical forest in Costa Rica demonstrated biannual cycles in species diversity, whereas community similarity showed an annual cycle that peaked in the driest months [Grøtan et al. 2014]. We found that community diversity and similarity did not decline with increasing time lag, which we attribute to lack of long-term changes in species abundances. The apparent presence of a biannual cycle of species diversity represents a striking difference between this study and a similar study based on data from Amazonian Ecuador [Grøtan et al. 2012]. A comparison of periodograms of community diversity, precipitation and temperature for the two localities shows a distinct biannual cycle (period length of 6 months) in community diversity and precipitation at the study site in Costa Rica while cycles are annual for Ecuador. At both localities the variation in temperature showed an annual cycle. In concert the

present study and Grøtan et al. [2012] suggest that wet season-dry season cycles are major factors influencing neotropical rainforest butterfly species diversity and community similarity. Moreover, a significant number of fruit-feeding nymphalid genera and species occur at both sites. This implies that Central and South American butterfly communities have evolved different responses to local seasonal weather patterns.

By illuminating potential differences in seasonal community diversity patterns in Central and South America this study not only reveals how little we understand of seasonal cycles of neotropical diversity, but it provides a model system and the analytical methods for seeking comparative patterns in other tropical forests. Given the certainty of tropical forest destruction and climate change, we feel that conducting many similar studies of community dynamics in changing environments can enhance our ecological understanding of tropical communities and inform conservation strategies. Moreover, such studies can also help test and refine predictions on the ecological impacts of future climate change.

### Further reading:

- Grøtan, V., R. Lande, S. Engen, B.-E. Sæther, and P. J. DeVries. 2012. Seasonal cycles of species diversity and similarity in a tropical butterfly community. *Journal of Animal Ecology* **81**:714-723.
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### 3. INTERNATIONAL COLLABORATION

Collaboration with international researchers forms an integrated part of the research activity in all the three Research Areas at CBD. An important part of the international strategy is to actively involve leading scientists in the research at CBD by use of shared positions. Prof. Russell Lande, Imperial College, UK and prof. Otso Ovaskainen, University of Helsinki, Finland are persons who have such part-time positions at CBD. Both have made valuable contributions to all the three research areas at CBD.

In Research Area 1 an initiative co-ordinated by CBD and professor T. Coulson, Department of Zoology, University of Oxford, UK has produced a unique data base of individual-based demographic data of birds and mammals, involving a large number of researchers from many parts of the world. For instance, one paper published in the *American Naturalist* contained 16 international co-authors. Another truly international venture in this research area is the research on Svalbard reindeer headed at CBD by dr. Brage B. Hansen. The international members of this research group are located in United Kingdom (3) and USA (2) and have been essential for the data collection and development of biostatistical modelling tools. Three project meetings involving these international collaborators were organized during 2013 and 2014 in Trondheim, and prof. Jeffrey Welker (Univ. Alaska Anchorage, US Arctic Fulbright Chair) held an invited talk at CBD in 2013.

Research Area 2 also involves extensive international collaborations. Three of the most

important collaborators in this field of research have been prof. Marcel E. Visser, Netherlands Institute of Ecology, Wageningen, The Netherlands, ass. professor Niels Dingemans, Max Planck Institute for Ornithology, Seewisen, Germany and dr. Luis-Miguel Chevin, CEFE, CNRS, Montpellier, France. The major focus for this collaboration has been development of models and statistical methods for analysing phenotypic selection and evolution in the wild.

The extent of international collaboration in Research Area 3 has been less extensive, focusing mainly on analyses of bird communities in United Kingdom together with prof. Robert F. Freckleton, University of Sheffield, United Kingdom.

Members of CBD have during the period 1.7.2013-31.12.2014 made 29 appearances at congresses, conferences or workshops abroad. In addition, CBD organized a PhD –workshop in Trondheim (see below) and the opening conference of CBD with several international lecturers.

### CBD WORKSHOP ON 'EVOLUTION IN STOCHASTIC ENVIRONMENTS' JANUARY 13-15<sup>TH</sup> 2014

This workshop was aimed at understanding the effects of unpredictable spatial and temporal environmental variation on evolution (i.e. in the context of variable population dynamics), and more specifically the nature of adaptive responses to such environmental stochasticity. The workshop was organised by Prof Jonathan Wright (CBD), with lectures and discussion sessions also provided by Prof Philip Crowley (Kentucky, USA), Dr Aviv Brokman (Kentucky, USA), Prof Steinar Engen (CBD), Prof Dustin Rubenstein (Columbia, USA), Dr Irja Ratikainen (CBD), Dr Sean Ehlman (UCDavis, USA) and Prof David Westneat (Kentucky, USA). The workshop generated lots of interesting and illuminating discussions, mostly concerning theoretical issues around bet-hedging and reconciling the various recent models being developed by the participants and others. The workshop lectures were attended by most CBD members, whilst the discussion sessions included a more specialised audience of PhDs, post-docs and staff working in this area.

*Prof. Jon Wright*

## 4. POPULAR SCIENCE

Several research projects and members at CBD have drawn attention through mass media and other public outreach. Both the moose project at the island of Vega in northern Norway and the house sparrow study at the coast of Helgeland have been subject for interest by local and regional media.

The reindeer project at Svalbard has been the research at CBD that so far has received the greatest focus by the media both nationally and internationally. For instance, Science News published a news story in November 2014 focusing on novel findings from a cross-disciplinary project on climate change effects on Svalbard reindeer population dynamics, headed at CBD

by Dr. Brage B. Hansen. In the March 2014 issue of the Smithsonian Magazine, a science writer reported "live" from the reindeer capture-mark-recapture field work. Also, a recent publication demonstrating how an extreme climate event in the high Arctic had dramatic effects on both wildlife and society was widely covered in national (Dagsavisen, Adresseavisen) and international media (The Independent, Scientific American, Science Daily).

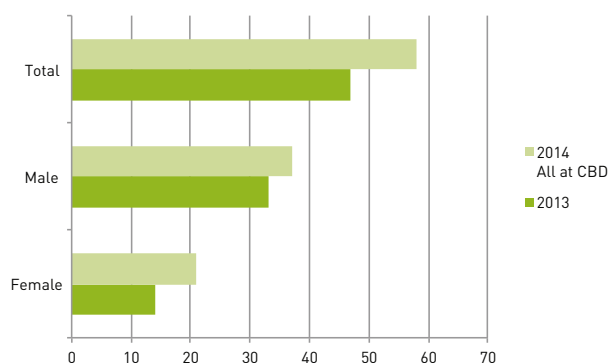
The Director presented several aspects of the research at CBD in a lecture for a broad audience on the climate conference organized by the Research Council of Norway in Oslo October 31 2013.

## 5. GENDER EQUALITY

1 female professor (G. Rosenqvist) and 1 associate female professor (I. Steinsland) were actively involved in the CBD. This means that there is a strong male-bias in the sex-composition among the

core members of the CBD. At the end of 2014 48 % of the Ph.D students and postdocs were female.

### GENDER DISTRIBUTION



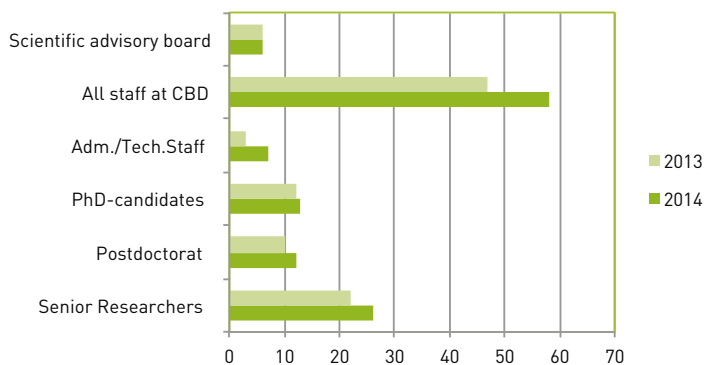
It is a central focus for the leadership of CBD to increase the recruitment of females to positions at all levels because we strongly believe that a balanced sex-ratio generates an environment that will facilitate excellence in research. One of the challenges that can affect the motivation for a continued scientific career after finishing a postdoc-period is a reluctance to accept necessary international relocations, often because of family commitments. CBD will facilitate such foreign visits by maintaining long-term collaboration with those research groups where visitors can soon obtain the logistics necessary e.g. for housing, childcare and schooling. We hope this will facilitate future recruitment also of females to senior positions at CBD.

## 6. KEY FIGURES

### STAFF OVERVIEW

Key numbers in CBD 2014	2014	2013
<b>Staff</b>		
Senior Researchers	26	22
Postdoctorat	12	10
PhD-candidates	13	12
Adm./Tech Staff	7	3
All staff at CBD	58	47
Scientific advisory Board	6	6
<b>Results</b>		
Journals		12
anthologies	25	14
Reports	14	25
Media attentions	50	
Books/chapters	1	
<b>Costs and funding</b>		
Operational Costs	17 989	8 689
<b>Funding</b>		
NFR	6 899	558
NTNU	11 090	8 131

### OVERVIEW ALL PERSONELL AT CBD IN 2013 AND 2014



At the end of 2014 the overall female involvement in the centre were 36%. Of our young researchers -Postdocs and Ph.Ds 48% are female. Recruiting females researchers to scientific careers after termination of the Post-doc period, is a challenge.

## APPENDIX 1 – CBD MEMBERS



**Bernt-Erik Sæther**  
Director



**Steinar Engen**  
Deputy Director



**Solveig Johnsen**  
Centre Coordinator



### CBD BOARD



**Anne Borg**  
Decan NT-Faculty  
Chair Board



**Geir Øien**  
Professor  
Decan IME-faculty



**Reidar Andersen**  
Director  
NTNU University  
Museum



**Jorunn Myklebust**  
Director  
NINA



**Yngve Svarte**  
Managing Director  
Norwegian Environ-  
ment Agency

### SAB SCIENTIFIC ADVISORY BOARD



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



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



**John Fryxell**  
Department of  
Integrative Biology  
University of Guelph,  
Canada



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



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



**Robert O'Hara**  
Professor  
Biodiversity and  
Climate Research  
Centre  
Frankfurt am Main,  
Germany  
SAB member  
Since Oct 2014



**Otso Ovaskainen**  
Professor  
SAB member  
Until Oct. 2014.  
University of Helsinki,  
Finland

### PHD STUDENTS



**Ane Marlene  
Myhre**  
PhD IBI



**Elena Albertsen**  
PhD CBD



**Erik Solbu**  
PhD  
ERC CBD



**Erlend Fossen**  
PhD IBI



**Mathilde Le Moullec**  
PhD IBI



**Peter Skjølte Ranke**  
PhD CBD



**Endre-Grüner  
Ofstad**  
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**Stine Svalheim  
Markussen**  
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**Thomas Kvalnes**  
PhD IBI



**Øystein Nordeide  
Kielland**  
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**Øystein Hjorthol  
Opedal**  
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## PostDocs



**Arild Husby**  
PostDoc  
IBI



**Bernt Rønning**  
PostDoc  
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**Eirin Bjørkvoll**  
PostDoc  
IBI



**Maja Tarka**  
PostDoc  
CBD



**Marlene Gamelon**  
PostDoc  
IBI



**Nerea Abrego**  
PostDoc  
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**Olivia Langhammer**  
PostDoc  
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## RESEARCHERS



**Anna Billing**  
Researcher  
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**Anna Marie Holand**  
Researcher  
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**Brage Bremseth Hansen**  
Researcher  
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**Hanno Sandvik**  
Researcher  
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**Henrik Pärn**  
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CBD



**Håkon Holand**  
Researcher  
CBD



**Ingerid Julie Hagen**  
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## RESEARCHERS AT NINA



**Irja Ratikainen**  
Researcher  
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**Ivar Herfindal**  
Researcher  
CBD



**Ola Diserud**  
Sr. Researcher  
NINA



**Erling Solberg**  
Sr. Researcher  
NINA



**Bram VonMoorter**  
Researcher  
NINA



**Manuela Panzacchi**  
Researcher  
NINA

## PROFESSORS / ASSOCIATE PROFESSORS



**Christophe Pélabon**  
Professor  
IBI



**Gunilla Rosenqvist**  
Professor  
IBI



**Otso Ovaskainen**  
Professor (50%)  
IME



**Sigurd Einum**  
Professor  
IBI



**Jonathan Wright**  
Professor  
IBI



**Ingelin Steinsland**  
Professor  
IME



**Vidar Grøtan**  
Ass. Professor  
IBI



**Thor Harald Rinsby**  
Ass Professor  
IBI

## TECH STAFF



**Jarle Tufto**  
Professor  
IME



**Henrik Jensen**  
Ass. Professor  
IBI



**Hans Stenøien**  
Professor  
NTNU University  
Museum



**Russel Lande**  
IBI  
(20 %)



**Varvara Iaschcenko**  
Engineer  
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**Linn-Karina Selvik**  
Engineer  
IBI



**Kenneth Nygård**  
Engineer  
IBI



**Anna Båtnes Solvang**  
Engineer  
IBI

## APPENDIX 2: SCIENTIFIC PRODUCTION CBD 2013-2014

### 2014

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