

Centre for Ecological and Evolutionary Synthesis

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LINKING ECOLOGY AND EVOLUTION

Ecological and evolutionary processes are inescapably intertwined. Environmental changes affect the ecology of species causing novel selection pressures to which the species respond evolutionarily. Ever since the industrial revolution the influence of human activity on earth has accelerated, and today anthropogenic impacts on the biota are of great concern to politicians, academics, and laypeople. In order to comprehend how such distortion of the environment may affect tomorrow's nature, we need more and better knowledge of how ecology determines the course of evolution, which again determines future ecological dynamics. **Understanding how living organisms respond and adapt to environmental changes remains a major and most urgent scientific challenge.**

Individual organisms constantly face challenges to which they respond through behavioural mechanisms, physiological plasticity and habitat selection. Populations may contract or expand their geographic ranges, change in densities, divide or merge with other populations, or adapt evolutionarily to new conditions. To achieve a better understanding of these subjects, some major biological questions have to be answered: How do ecological structures and processes, as well as intrinsic processes, act as drivers of, or constraints on, evolution? What determines the potential for adaptation to environmental change? Who will survive, who will become extinct, and who will adjust to new circumstances?

Answering these questions demands combined efforts. Research departments including both ecologists and evolutionary biologists are found all over the world. Nevertheless, ecological processes are typically studied under the assumption of homogenous populations whereas evolutionary processes are studied under the assumption of ecological stability. However, with the remarkable developments in molecular biology and computer science, huge amounts of data can now be obtained, analyzed, and most importantly, synthesized to answer imperative questions at the interface between ecology and evolutionary biology.

To meet these challenges we will gather scientists of various backgrounds such as theoretical and experimental biologists as well as statisticians interested in biology. Together we will target numerous obstacles for an ecological and evolutionary synthesis using old and new

data from the field and the lab. Through this Centre of Excellence (CoE) we will for the next 10 years counter the trend towards fragmentation of sciences by having several interacting research foci. These will be organized around three mutually dependent *Themes*:

- 1) The role of population structuring in adaptive evolution.
- 2) The potential for adaptation.
- 3) The evolution of reproductive isolation.

Within each research *Theme*, there is a demand for integration of ecological realism into evolutionary theory, and for evolutionary thinking into ecological modelling. In order to face problems of integrative work, such as conceptual and semantic confusion, and to promote communication across the limiting assumptions of the various research fields, we will assign targeted projects in the form of four three-year long multidisciplinary *Colloquia*. Here we will bring together staff and visiting scientists with experience from a wide range of biological and methodological systems. Each *Colloquium* will make an excellent setting for inviting highly qualified scientists to collaborate and thus contribute to the overall objective of the centre. The topics of the *Colloquia* will be:

- 1) Selection and evolvability: Concepts, measurements and statistical modelling.
- 2) Bridging the gap between molecular genetics and evolutionary genetics.
- 3) Ecology and evolution of mosaic genomes: The case of microbes.
- 4) Integration of ecology and evolution: A synthesis.

The CEES comprises a broad spectrum of expertise in ecology, evolutionary biology, molecular biology, bioinformatics, methodological and computational statistics. We will work on a wide range of well-established biological research systems, covering the terrestrial, limnic and marine world. By joining forces within a CoE, the participants will mutually benefit by sharing knowledge and tools across scientific boundaries. Moreover, the centre will facilitate collaboration with internationally prominent scientists. The activities of the CoE will allow us to offer a multi-disciplinary training program for MSc, PhD, and post docs, and thus attract a diverse group of students from biology as well as from statistics and mathematics. **The CoE will be an open, inclusive, and integrative international centre; a platform from which we can better understand the evolutionary play in the ever-changing ecological theatre.**

RESEARCH ACTIVITIES

The research of the CoE will be structured into *Themes* and *Colloquia* (Figure 1 and Table 1). The *Themes* comprise the core activities of the CoE and will run continuously throughout the 10-year period. The *Colloquia* constitute research arenas designed to provide conceptual clarification across disciplines.

THE THEMES

The research to be carried out within the *Themes* involves basic, but yet unresolved issues. The *Theme* members are scientists with

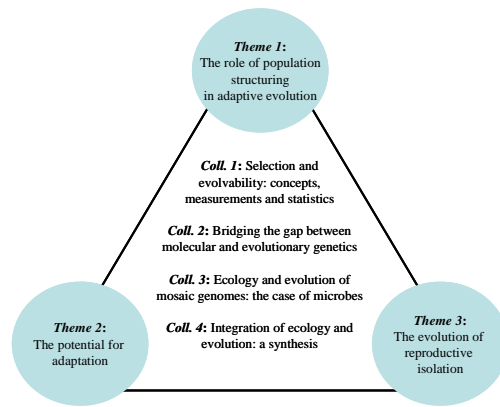


Figure 1. The long-term research activities focus on three interrelated *Themes* which are reinforced through four *Colloquia*, each lasting for 3 years, providing arenas for interdisciplinary synergetic work.

diverse backgrounds and perspectives, each familiar with the state-of-the-art methodology of her/his field. The challenge, and the most rewarding part of the project, will be to develop new tools for addressing cross-disciplinary questions. As a result new research topics are expected to emerge.

Henceforth, some examples of research topics of each of the highly interdependent *Themes* are briefly described. The empirical part of the research focuses on biological model systems for which CoE-core members have profound experience (boxes 1-6). Probabilistic modelling, statistical methodology and numerical tools will be needed for the study of the various model systems. We will encourage general statistical research to provide a basis for and strengthen more biologically-focused modelling (box 7).

Table 1. Timeline of the CEES activities. Within each section of the table, shaded areas indicate time-periods during which the activities will take place; x's indicate one-day events.

Themes	1	2	3	4	5	6	7	8	9	10
	07	08	09	10	11	12	13	14	15	16
<i>T1</i> : The role of population structuring in adaptive evolution										
<i>T2</i> : The potential for adaptation										
<i>T3</i> : The evolution of reproductive isolation										
Colloquia										
<i>C1</i> : Selection and evolvability: concepts, measurements and statistics										
<i>C2</i> : Bridging the gap between molecular and evolutionary genetics										
<i>C3</i> : Ecology and evolution of mosaic genomes: the case of microbes										
<i>C4</i> : Integration of ecology and evolution: a synthesis										
Annual lectures										
<i>Darwin Day</i> (Friday closest to February 12)	x	x	x	x	x	x	x	x	x	x
<i>Kristine Bonnevie Lectures in Evolutionary Biology</i> (September 2)	x	x	x	x	x	x	x	x	x	x
Training programs										
CoE PhD training program - a <i>Graduate School</i>										
<i>Marie Curie Early Training Site</i> (PhD level)										

Theme 1: The role of population structuring in adaptive evolution

Theme leaders: H.M. Lampe & L.A. Vøllestad; *collaborators include:* M. Achtman, E. Carniel, T.O. Haugen, K. S. Jakobsen, C. Nesbø, G. Ottersen, T. Slagsvold, N.C. Stenseth.

All species are structured into subgroups or sub-populations by more or less obvious boundaries. Physical barriers may directly prevent gene flow through habitat fragmentation, whereas temporal or behavioural differences concerning dispersal and/or reproduction may indirectly have the same effect. To better understand how gene flow prevents or facilitates local adaptations, and how local adaptations may prevent gene flow, detailed knowledge about the interaction between organisms and their environment is needed; what are the traits under selection and what are the selection pressures?

We will study the importance of gene flow in adaptive evolution in two different fish systems combining neutral genetic and functional data. In spite of the natal homing behaviour of the **European grayling (box 1)**, some gene flow among populations has been demonstrated as an isolation-by-distance pattern in neutral genetic markers (microsatellites). Preliminary experiments using a common-garden design have revealed rapid evolution of life history traits (e.g., spawning time, egg size and early development), this will be explored further. We will also undertake reciprocal transplant experiments in the wild to estimate the fitness of dispersing and non-dispersing individuals, and to assess to what extent the phenotypic variation is heritable, or due to plastic responses.

Candidate genes will be analyzed for differential expression patterns (cf. *Theme 2*).

Coastal populations of the **Atlantic cod (box 2)** receive large, but temporally variable, numbers of larvae from exogenous offshore populations. Rapidly changing environmental (ocean currents) and ecological parameters (offshore larval production) thus have a direct effect on gene flow and are expected to counteract selection for local adaptations. We will study certain ecological traits of local coastal populations (spawning behaviour, egg buoyancy, etc.) as potential evolutionary responses limiting gene introgression.

Establishment and maintenance of local adaptations can also be strongly influenced by genetic drift. For the **European grayling (box 1)**, extensive microsatellite data will be generated and used for modelling of different scenarios for colonization and bottleneck events. Combined with data on demography and adaptive differences among populations, we have an outstanding setup for exploring the role of stochasticity in adaptive evolution.

For the **Plague system (box 3)** the high degree of genetic variability observed in Central Asia (presumably the cradle of all the big plague epidemics, including the Black Death of the middle ages) might be linked to the ecology of the main rodent host (gerbils) that exhibits extensive density variation in both time and space. We will obtain specimen samples (collected as part of a time-series study) of infected gerbils and of the microbes' flea

vectors. DNA isolated directly from infected individuals, as well as from isolates, will be screened for polymorphisms. Population genetic modelling, incorporating the ecological dynamics of the host-vector-plague system and taking into account the genetics of *Yersinia pestis*, will provide important insight into the biology of this deadly bacterium.

Competitors may be a crucial part of a species' environment. Climatic variation has been shown to affect the competitive interactions between **piebald flycatcher** and **collared flycatcher (box 4)** and between **great tit** and **blue tit (box 4)** differentially. Since these birds are hole-nesters, experimental studies in the wild are feasible, and fitness as well as microevolutionary responses to varying and conflicting selection pressures induced by climate and/or competition can be estimated and compared between the pairs of competing species.

Dispersal patterns within a species often vary on a geographic scale. For instance, in **piebald flycatcher (box 4)**, there is a north-south cline with respect to sex-biased dispersal, with male-biased sex ratios in northern populations. Comparative analyses of populations along geographic transects will be undertaken in order to study potential adaptive responses (e.g., in sexual selection and in mating system evolution) to differences in dispersal and sex ratio.

Habitat-specific genes may be found in bacteria from different phylogenetic lineages strongly indicating an adaptive value in that environment. For strains of **Thermotogales and Cyanobacteria (box 3)** isolated from certain environments (e.g., oil reservoirs) habitat-specific genes will be identified through subtractive hybridization. These genes may be obtained or lost through homologous recombination (cf. *Theme 3*). In order to gain insight into how local adaptation affects gene flow in these populations, rates of recombination between regions flanking habitat-specific genes and the rest of the genome will be compared.

Theme 2: The potential for adaptation

Theme leaders: T. Slagsvold & G. Storvik; *collaborators include:* T. F. Hansen, T.O. Haugen, N. Jonzèn, H. M. Lampe, A. Mysterud, G. Ottersen, L.A. Vøllestad.

One of the great discoveries within population genetics over the last decades is that most phenotypic traits appear to have higher capacity to evolve than previously assumed. However, different types of organisms and traits differ tremendously in their evolvability, and many traits appear inexplicably conservative or maladaptive. There is a need to develop theoretical models and empirical model systems to better understand and predict why some traits evolve readily and others do not.

Although evolvability is initially determined by the amount of genetic variation that selection can act upon, it is becoming increasingly clear that only parts of this variation may be useful for adaptation. Formal analytical models have been developed to describe how genetic architecture (patterns of pleiotropy and epistasis) affect evolutionary capacity by structuring character variability. This has led to new hypotheses about the links between genetic architecture and evolvability, and identified novel genetic parameters in need of empirical estimation. Further work with theoretical models will be to investigate these hypotheses and parameters in explicit gene-regulatory networks, and develop methods for their estimation.

Parameters describing epistatic and pleiotropic constraints can be based both on classical quantitative-genetic breeding designs and on Quantitative Trait Loci (QTL) analysis. We will attempt to estimate these parameters using different empirical systems. For instance, various types of quantitative-genetic analysis will be undertaken on the **grayling system (box 1)** to understand genetic potential, and the genetic basis of phenotypic differences among recently diverged populations. Information about possible genetic constraints will be checked against the actual patterns of diversification.

Learning and plasticity have been seen both as drivers of and constraints on evolution. Either by inducing novel selection pressures by allowing organisms to explore new ways of living (the Baldwin effect), or as buffers against evolutionary change by stabilizing the niche.

Most studies of learning have focused on animals in captivity. With our model systems of **passerine birds (box 4)**, we can undertake pioneering experiments on life-time reproductive success of cross-fostered and control birds in the wild. We will study evolutionary consequences of sexual selection by female choice and species recognition in hybrid zones depending on whether traits are culturally (e.g., song) or genetically inherited (e.g., plumage colour). Using the same experimental passerine bird system we will assess to what extent climate change has led to evolutionary changes in migration timing. This will be done by estimating fitness components based on the accumulated data from our long-term studies on the pied flycatcher.

Selective harvesting is potentially a strong evolutionary force. For both **fish (box 1 & 2)** and **mammals (box 5)** we will assess how harvesting affects multiple traits (such as age and size at maturation, reproductive investment and immature growth) and then compare these results with estimates of the evolvability of such traits. For instance in **pike and Atlantic cod (box 1 & 2)** harvesting selects for reduced growth and thus smaller body size and decreased reproductive potential. This phenomenon has consequences for management and may also apply to mammals like **deer (box 5)**. Another important aspect of harvesting that we will study is the relative roles of active selection (induced by human practice) and passive selection (due to animal behaviour, harvesting method, etc.).

Theme 3: The evolution of reproductive isolation

Theme leaders: A.K. Bryting & G.-P. Sætre; collaborators include: T.O. Haugen, D.O. Hessen, H.M. Lampe, C. Nesbø, T. Slagsvold, G.O. Storvik, L.A. Vøllestad.

The development of reproductive isolation (speciation) is a key event in evolution, and hence for the origin and maintenance of the tremendous diversity of life on earth. For sexually reproducing organism there is general agreement that reproductive isolation is a necessity for divergence. Nevertheless, the mechanisms involved in the formation of reproductive barriers are poorly understood. For organisms where reproduction and recombination do not necessarily coincide,

controversies on basic properties (such as species concepts) remain unresolved.

For prokaryotes, in particular, taxonomic boundaries are obscure and it is questionable if a species concept in terms of reproductively isolated units is meaningful (cf. *Colloquium 3*). In order to understand the high levels of homologous recombination among ***Thermotoga* (box 3)** strains across large geographic and phenotypic distances, global population genetic approaches are needed. A large number of *Thermotogales* isolates will be sampled worldwide and used in multilocus-sequence-typing and-analysis (MLST; closely related strains, and MLSA; more distantly related isolates). We will investigate population structure and how species-like boundaries (if present) may form in the face of high levels of recombination. In the cases of ***Yersinia* and *Salmonella* (box 3)** we will explore the evolution of distinct taxonomic units within each genus, focusing on pathogenic strains. This work will be carried out using available DNA sequence data and a bioinformatic approach.

Some **passerine birds (box 4)** coexist in certain regions as species that are distinct, but not completely reproductively isolated (hybrid zones). Thus the evolution of species boundaries is still in action. When hybrids are unfit, females should avoid mating with males from the other species. Different signals may provide information of varying reliability regarding species identity and mate quality. We will expand on optimality models developed for a one-species setting to investigate how information content of sexual signals and relative abundance of con- and heterospecifics may affect mate search strategies of females in a hybrid zone and test specific predictions from the models using experimental studies. We will further explore the often-neglected alternative hypothesis that intersexual competition may account for unidirectional hybridization.

For **pied and collared flycatcher (box 4)**, it has been documented that unfit hybrids can reinforce prezygotic isolation, for instance through sympatric divergence in traits used in mate recognition. Prezygotic isolation includes lack of sexual attraction between members of differentiated populations and often involves sex-specific traits controlled directly or

indirectly by genes linked to the sex chromosomes. We suggest that sex chromosome evolution and the particular architecture of sex-linked genes (hemizygoty and reduced rate of recombination) play a crucial role in speciation. We will investigate speciation traits using genome-wide genotyping of various hybrid and backcrossed birds, and by correlating genotypes with phenotypic traits, such as fertility and viability (post-zygotic isolation traits), mate preferences and sexual signals (pre-zygotic isolation traits).

In the **European grayling system (box 1)** several viable demes have been established within 25 generations. The population structure may be a result of founder events (non-random colonization), selection for spawning time (variable environments leading to isolation-by-time) or selection against dispersal (isolation-in-space). We aim to identify the ecological factors that facilitate the strong selection. We will then perform *in-situ* testing for pre-zygotic isolation mechanisms (mate choice experiments, timing of maturation) and post-zygotic isolation mechanisms (early development, selection against hybrids). Reproductive isolation may follow from development of phenotypic differences. This will be studied by estimating field-based variance-covariance matrices for important traits.

Through polyploidization, reproductive isolation (i.e., new species) may arise in a single or few generations. In certain **plants and invertebrates (box 6)** the frequency of polyploids is particularly high in harsh environments such as the Arctic, where asexuality is also common. Polyploidy is thought to be important for maintenance of genetic diversity in the absence of recombination and could also enhance expression of genes. By comparative studies of a range of species, including both diploids and polyploids, we will assess whether particular ecological settings favour the establishment of polyploids and test whether polyploids are more diverse and fitter than diploids in the Arctic. Populations from a wide latitudinal range will be screened for ploidy-level, heterozygosity and for correlations between ploidy-level and important life history (e.g., growth rate, size) and related features (e.g., RNA/DNA-ratios). For Arctic plants with both diploid and

polyploid cytotypes genetic and phenotypic characterization, manipulative field studies, experiments under controlled conditions and simulation models incorporating varying ecological conditions and data on rates of clonal growth and seed set will be used.

THE COLLOQUIA

The *Colloquia* will facilitate interaction among scientists with diverse backgrounds and hence the further progress on cross-disciplinary issues. An international workshop will be held in the first year of each *Colloquium*. In the fourth and last *Colloquium* all CoE-members and partners will be involved at various stages throughout the three years. The results of each *Colloquium* will be published in high-impact journals, and in addition compiled in an edited book.

Colloquium 1: Selection and evolvability: Concepts, measurements and statistical modelling

Colloquium leaders: T.F. Hansen & T. Schweder together with two appointed Kristine Bonnevie Professors; *collaborators include:* D. Houle, H. Kishino, N.L. Hjort and G.P. Wagnier.

The overall goals of this *Colloquium* are to resolve misunderstandings, clarify the meaning of fundamental parameters and measurement procedures, and to establish models that are operational in the sense that they can be fitted to data from experiments and field work.

R. A. Fisher had a paradigmatic impact on both genetics and statistics. His additive-effects model successfully clarified the first principles of character evolution. In his definition of additive effects, Fisher insisted on these primary parameters being connected to underlying processes of interest, and not just to data description. This *Colloquium* will extend this modelling approach to provide operational definitions of gene interactions that allow for directional epistasis, pleiotropy, canalization and other features of dynamic population genetics (Hansen 2006). This will be combined with a measurement-theoretical approach to defining parameters describing fundamental evolutionary entities such as fitness, selection strength, evolvability, and genetic constraint. Representational measurement theory is a formal mathematical discipline for studies of how quantitative concepts are defined and what their mathematical properties are. The purpose being to identify parameters that preserve

theoretical context, mathematical consistency, and statistical operationality.

The joint demands of theoretical relevance and statistical feasibility raise interesting statistical challenges; the statistical models are constrained from above by the structure of the theory and from below by the structure of the data. Often the theoretically relevant variables are latent and must be inferred from observed variables of different types, and the data might be extensive and have sources of different type (e.g., measurements of genotype and phenotype of individuals; of populations in the field or in the laboratory; or of the ecological context and the environment). Statisticians and theoretical biologists will work together to develop novel models and methods to efficiently extract theoretically relevant information case by case. The resulting models will typically be hierarchical, and distributional inference based on the computationally challenging likelihood will be sought (**box 7**).

For illustration we briefly outline three pertinent lines of investigation. The first is to further develop measures of selection strength, building on Hereford *et al.* (2004), in order to include correlated and stabilizing selection. A highly relevant question is how to combine measures of spatially and temporally varying selection pressures. The second concerns measures of short-term evolvability, and how to interpret data on genetic variances and covariances (e.g., Houle 1992; Hansen *et al.* 2003a,b; Mezey & Houle 2003, 2005). The third focuses on measures of genetic architecture (i.e., pleiotropy and epistasis). We will develop statistical methods for detection of directional epistasis, which is fundamental for understanding the evolution of evolvability (Hansen & Wagner 2001; Carter *et al.* 2005) both from classical breeding designs and from QTL data. We will pay close attention to how proposed parameters can be used to predict patterns of evolutionary divergence among populations and species, and thus to test hypotheses about the importance of, for example, variational constraints on evolution. This necessitates consideration of how to measure evolutionary divergence and evolutionary rates.

Colloquium 2: Bridging the gap between molecular genetics and evolutionary genetics

Colloquium leaders: E.K. Rueness together with the appointed Kristine Bonnevie Professor; *collaborators include:* D. Chourrout, K.S. Jakobsen, C. Nesbø and M. Pigliucci.

The goal of this *Colloquium* is to unify different understandings of the genetic basis of adaptation.

The heyday of genomics has revealed that the genetics underlying most phenotypic traits is extremely complex, including numerous genes and regulatory networks. With increased understanding of individual responses to environmental variation through phenomena like genetic redundancy, epigenetic effects and phenotypic plasticity, it has become evident that when it comes to genotype-phenotype relationships the total is not necessarily equal to the sum of its parts.

Despite the great progress achieved using molecular markers and the impact genomics has had on QTL mapping, the field of evolutionary (including population genetics and quantitative genetics) and molecular genetics still remain separate fields. A fact that is reflected not least in the lack of coherence of terminology; identical terms, like epistasis, are used in both fields, but in conceptually very different senses. Generally, molecular geneticists focus on molecular mechanisms at the individual level, while evolutionary geneticists essentially describe statistical relationships at the population level. This discrepancy is a huge obstacle we need to overcome in order to establish a conceptual common base for understanding genotype-phenotype relationships (Rueness & Pigliucci 2006). Additional challenges will be to implement molecular discoveries into evolutionary genetics and ecological and evolutionary perspectives into molecular studies. In collaboration with the *Sars International Centre for Marine Molecular Biology* (<http://www.sars.no/>) we will approach integration of empirical molecular genetic research and evolutionary genetics utilizing model systems and eventually natural populations.

Colloquium 3: Ecology and evolution of mosaic genomes: The case of microbes

Colloquium leaders: C.L. Nesbø together with the appointed Kristine Bonnevie Professor; *collaborators include:* W.F. Doolittle, K.S. Jakobsen and N.C. Stenseth.

Microbes are responsible for the bulk of metabolic activity on earth and all life depends on their existence. Still most ecological and evolutionary theory concern larger eukaryotes. The goal of this *Colloquium* is to contribute to the conceptualization of the evolutionary implications of some ecological traits typical for microbes, from a genomic point of view. Asking what are their units, and how do they diversify?

There is no consensus among microbiologists as to what constitutes a prokaryotic species (e.g., Gevers *et al.* 2005). Prokaryotes do not recombine every time they reproduce – and they are also notoriously promiscuous when it comes to what partners they interact with genetically; transfer of genes from distantly related lineages (lateral gene transfer or LGT) has been shown to be one of the most important forces in prokaryotic evolution (Doolittle 1999; Boucher *et al.* 2003). In some prokaryotic populations almost every cell may show a distinct genotype with extensive allelic diversity and genome size variation (Thompson *et al.* 2005). For the many prokaryotic lineages in which LGT rates are high, separate parts of a genome might behave as belonging to different biological species since they can interact through homologous recombination with other microbial lineages (Nesbø *et al.* 2006a), suggesting that genes rather than genomes should be the units of study. We will work towards an ecologically and evolutionary relevant classification of prokaryotes and aim at understanding the selective value of mosaic genomes.

In contrast to macroorganisms, microorganisms are, due to the tiny sizes of their individual members and their enormous populations, easily dispersed and much more difficult to eradicate than are species of multicellular organisms, which are generally biogeographically restricted. Notwithstanding this fact, the current consensus appears to be that microbes may have among them a “wide variety of colonization, diversification and extinction rates” (Martiny *et al.* 2006). A major task will be to explain these differences in terms of species’ specific traits and to investigate what

unique features of microbial life have influenced the generation and maintenance of their diversity.

This *Colloquium* will address the above-described questions by bringing together environmental microbiologists, evolutionary biologists, bioinformaticists, ecologists and theoretical population biologists. We will utilize the growing numbers of publicly available genomic and metagenomic datasets, as well as MLST and biogeographical data, and will aim at establishing models incorporating the often-unique ecological and evolutionary mechanisms acting on microbial genomes.

Colloquium 4: Integration of ecology and evolution: A synthesis

Colloquium leaders: N.C. Stenseth together with the appointed Kristine Bonnevie Professor; *collaborators include:* M. Doebeli, A. Hendry together with all CoE-core members.

In this concluding *Colloquium* we will synthesize the results derived within the CoE to assess the current state of the insights gained and to develop an agenda for future research linking ecological and evolutionary concepts and models.

Ecological interactions generate the selection pressures that lead to evolutionary change in life history traits. These trait changes, in turn, affect the strength of the ecological interactions, thus altering selection regimes. Understanding this feedback between ecological and evolutionary processes lies at the heart of comprehending the dynamics of the ecosystems surrounding us. Even though it has been acknowledged that linking ecological and evolutionary time-scales and processes can often lead to new insights (cf. Stenseth & Maynard Smith 1984; Doebeli & Dieckmann 2000), the theoretical and analytical frameworks of ecology and evolutionary biology are currently largely incompatible. On one hand, ecologists typically perceive the genetic constituents of the species as constant, facing the dual problem of not taking into account that evolutionary changes of ecological importance may occur over very short time spans, and of ignoring the evolutionary history of the species. On the other hand, evolutionary biologists tend to disregard ecological interactions and typically assume extensive time periods with constant parameters (i.e., selection coefficients, effective population size). Traditional evolutionary genetics and the

statistical tools for analysing genetic data are not geared towards solving problems involving dynamically interacting species and populations but, rather, are limited to static entities, such as spatially fixed populations and constant and independent parameters. Technically speaking, we will incorporate ecological dynamics into the population genetic models (typically assumed to be in equilibrium or in stationary

growth), and genetic variance into the ecological models (typically ignoring genetic variance among the individuals constituting the population). In short, uniting the time-scales of evolutionary biology, population ecology and behavioural ecology, we will summarize, expand on, and assess the significance of concepts and tools that have emerged during the CoE period.

Box 1: Freshwater fish: The European grayling (*Thymallus thymallus*) is a salmonid that in the 1880s colonized Lake Lesjaskogsvatnet, a shallow mountain lake in Norway. While juveniles and adults reside in the lake for most of their life, spawning takes place in more than 20 tributaries (demes) differing in environmental conditions (mainly water temperature). Genetic differentiation and pronounced phenotypic differences (life history and early development) have been detected among demes. Candidate genes, presumably with major effects on life history traits such as growth regulation, have been identified. The small size of the system, the short and well-documented history and the detailed knowledge of the ecology of the species makes this a rare case where it is feasible to test whether or not the observed phenotypic differences are adaptations to environmental differences, and to study the rate of the diversification process. The grayling system also provides a unique opportunity to investigate the relative role of stochastic processes (e.g. due to founder effects) and selection.

The pike (*Esox lucius*) in Lake Winemere, UK, has been studied intensively during the past 50 years leading to unique time series data (individual capture-mark-recapture data). Climate and fishing intensity has varied strongly, making it possible to study the evolutionary effects of harvesting on a top predator after adjusting for variation in density-dependent and density-independent factors. This provides a great potential for assessing the speed and magnitude of evolutionary responses by combining long-term data and statistical modelling.

Key refs involving core members and their partners: Haugen (2000), Haugen & Vøllestad (2000, 2001), Haugen *et al.* (2006), Koskinen *et al.* (2002).

Box 2: Atlantic cod: The Atlantic cod (*Gadus morhua*) is an economically important species both as a natural resource and increasingly for the aquaculture industry. Coastal cod of Skagerrak and Kattegat are structured into local populations on the scale of single fjords, genetically distinct (as documented by microsatellite analysis) from each other and from the North Sea stock. Environmental conditions vary considerably among fjords implying that there is potential for local adaptation, but dispersal is at times very high due to ocean currents. Interestingly, spawning sites appear to be localized so that eggs and the larvae remain within the fjords. The coastal cod allows us to investigate local adaptations in light of small scale (fjord habitat) and large scale (ocean currents) environmental factors.

Many cod stocks are intensively harvested at a level where evolutionary changes in the life-history traits, such as age and size at maturation, are to be expected. We have gathered a wealth of data (on size- and age-specific abundance, harvest, growth rates and maturation for many of the most significant stocks), that when analyzed will improve our understanding of the direction and rate of evolution, as well as the ability for stocks to recover after relaxed fishing pressure.

Key refs involving core members and their partners: Knutsen *et al.* (2004), Stenseth *et al.* (1999, 2006a), Olsen *et al.* (2004).

Box 3: Microbial organisms: The plague bacterium (*Yersinia pestis*) displays little genetic variation except in Central Asia. This pattern may be related to the ecology of the main host, gerbils. We have access to host and vector specimens collected annually over decades providing a unique opportunity to link bacterial microevolution to the ecology of the host and vector. Furthermore, we will study the origin of the 11 recognized 'species' of *Yersinia*: MLST analyses of O-antigen switching and genetic recombination within and among taxa show how boundaries may form when homologous recombination is still occurring. We will collaborate with Central Asian experts on plague ecology and will obtain additional data through agreements with the Ministry of Health in Kazakhstan and the Chinese Academy of Science

Pathogenic *Salmonella enterica* are divided into a large number of serovars (~2000) according to their surface antigens. The serovars are often associated with different symptoms, and certain haplotypes within specific serovars may be responsible for separate epidemic episodes. We will compare rates of evolution in epidemic vs. non-epidemic strains, relating genetic background to traits such as drug resistance, using high-resolution typing to survey global diversity and population-genetic structure of *S. enterica*.

Gene flux is common, even among genetically and geographically distant ecotypes and 'species' in **Thermotogales** bacteria such as the hyperthermophilic *Thermotoga* strains, which seem to adapt to new growth environments through lateral gene transfer (LGT). Hence, we will use Thermotogales to investigate how geographic populations separated by uninhabitable areas may interact genetically.

LGT also appears important in how **Cyanobacteria** adapt to ecological changes by non-ribosomally synthesized peptides/polyketides. The operons encoding the peptide synthetases (PS) may spread by LGT. Certain PS variants may correspond to specific cyanobacterial ecotypes. Comparisons between Cyanobacteria and the ecologically and evolutionarily very different *Thermotogales* will be of great value.

Key refs involving core members and their partners: Achtman *et al.* (2004), Carniel & Hinnebusch (2004), Davis *et al.* (2004), Mikalsen *et al.* (2003), Nesbø *et al.* (2002), Nesbø *et al.* (2006a,b), Stenseth *et al.* (2006b,c); see also <http://www.cees.no/content/view/378/>.

Box 4: Passerine birds: Common hole-nesting passerine birds are well suited for studies of learning, sexual selection, speciation and interspecific interactions. **Pied flycatcher** (*Ficedula hypoleuca*) and **collared flycatcher** (*F. albicollis*), have overlapping breeding ranges in parts of Europe where hybridization occurs at a moderate frequency although hybrids are strongly selected against due to low fertility. In sympatry, female choice leads to reinforcement of premating isolation by divergence of male traits. Recent evidence suggests a significant role of sex-linked genes in mediating pre- and post-zygotic isolation.

In contrast, **great tit** (*Parus major*) and **blue tit** (*P. caeruleus*) rarely hybridize in nature, probably because of past selection pressure through a long history of sympatry. Cross-fostering shows that heterospecific pairs may form when the birds are sexually imprinted on the foster species early in life.

Climate is changing at a rapid rate, and this affects local and global ecosystems. The North Atlantic Oscillation is known to affect competition between the two flycatcher species leading to competitive exclusion in parts of their ranges and a change in optimal time for long-distance migration. The two **tit** species on the other hand respond by coexisting at a new equilibrium level. This provides a splendid opportunity for studying evolutionary responses to climatic change in two different ecological systems.

Key refs involving core members and their partners: Jonzén *et al.* (2006), Lampe & Sætre (1995), Slagsvold *et al.* (2002), Stenseth *et al.* (2002), Haavie *et al.* (2004), Sætre *et al.* (1997, 2003).

Box 5: Large mammals: Selective hunting is a main cause of mortality for most populations of large herbivores and carnivores, in many cases accounting for more than 90% of the adult mortality. The life histories of large mammals are thus increasingly affected by the changing selective regime caused by humans. Having studied how harvesting affects population ecology and life history, we will proceed to look at the possible evolutionary consequences of harvesting. For **red deer** (*Cervus elaphus*), **roe deer** (*Capreolus capreolus*) and **brown bear** (*Ursus arctos*), we have large quantities of long-term data. For the deer we have data suited to assess whether allometric relations (e.g., between body size and deer antler size) have changed over time due to selective harvesting. For brown bear, we will exploit a uniquely detailed, long-term data set on life history traits (size, weight, reproductive history) and genetic makeup available to us through one of our partners.

Key refs involving core members and their partners: Manel *et al.* (2004), Mysterud *et al.* (2001, 2006).

Box 6: Arctic Polyploids: The crustacean *Daphnia* is a facultative asexual organism with increasing incidence of polyploidy in arctic regions, where it becomes obligately asexual. Extensive data on physiological properties from field and lab experiments and extensive genetic data on phylogeny and evolutionary history make it a good candidate for studying genotypic and phenotypic responses to environmental change. The role of polyploidy for maintenance of heterozygosity, clonal variation and eventually for speciation, with or without hybridization, will be approached by comparative studies on temperate and arctic *Daphnia*, as well as other selected invertebrate species (both aquatic and terrestrial). **The Arctic flora** consists of numerous recently evolved polyploids, excellent as model systems for studying the ecological and evolutionary consequences of polyploidy. In particular selected plant species or species groups consisting of both diploids and polyploids are ideal for testing which ecological conditions favour the establishment and persistence of polyploids and their possible advantage in regions with harsh climate.

Key refs involving core members and their partners: Brochmann *et al.* (2004), Brysting *et al.* (2004), Hessen *et al.* (2004), Andersen *et al.* (2004).

Box 7: Statistical methodology: Statistical modelling required in ecological and evolutionary synthesis will pose challenges to statisticians. These challenges will allow us to further develop general statistical concepts and modelling strategies, e.g. for directional interaction, multiple causation and stabilizing dynamics and other phenomena of multivariate statistical dynamics. Models that have latent structures and/or integrate diverse sources might have complex likelihood functions requiring sophisticated numerical tools (e.g. optimization by automatic differentiation; integration by Laplace approximation; stochastic simulation), which we will continue to improve and employ. We will also address questions of identifiability of parameters, potential bias as well as consistency and approximate distribution of estimators. Tools for model diagnostics/criticism and model selection will also have to be tailored for these complex models. In the analysis of evolutionary data, Bayesian methods have gained increasing interest, while in other fields the frequentist methods are preferred. By combining Fisher's fiducial distributions with Efron's bootstrap we wish to contribute towards a synthesis of the hitherto opposing Bayesian and frequentist traditions of statistics.

Key refs involving core members and their partners: Hjort *et al.* (2006), Kitikado *et al.* (2006), Kitada & Kishino (2004), Schweder (2003); Schweder & Hjort (2002), Hereford *et al.* (2004), Skaug (2002), Storvik (2002).

THE ORGANIZATION OF THE COE

The CoE team (Table 2) includes members from several departments at the University of Oslo (UoO). The team members have extensive experience in interdisciplinary collaborations and some of the CoE core members have since 2001 been involved in the *Centre for Ecological and Evolutionary Synthesis* (CEES), an interdisciplinary platform for biologists and statisticians within the Dept. of Biology. This research unit was established for a 5-year period with strategic funding provided by the UoO, and

awarded the status as a Nordic Centre of Excellence. All funding ends in 2007. While the CEES has mainly focused on ecological research, we have recognized the great challenges and opportunities for an ecological and evolutionary synthesis. The CoE will therefore be a restructured unit with (i) new members, (ii) a scientific focus redirected towards the interface between ecology and evolution, and (iii) a novel research structure with *Themes and Colloquia*.

Table 2. Core members and their distribution on *Themes* and *Colloquia* in the CoE (58% being members of the current CEES, indicated by *); x indicates membership, and L indicates leading responsibility. *T1* = The role of population structuring in adaptive evolution; *T2* = The potential for adaptation; *T3* = The evolution of reproductive isolation; *C1* = Selection and evolvability: concepts, measurements and statistical modelling; *C2* = Bridging the gap between molecular genetics and evolutionary genetics; *C3* = Ecology and evolution of mosaic genomes: the case of microbes; and *C4* = Integration of ecology and evolution: a synthesis. Collaborative partners' involvements is listed in Table A2-7 in Appendix 2.

THE CoE MEMBERS	T1	T2	T3	C1	C2	C3	C4
Centre leader							
Nils Christian Stenseth*	x	x	x	x	x	x	L
Core members at the University of Oslo							
Anne K Brysting			L		x		x
Thomas F Hansen*		x		L			x
Dag O Hessen*			x	x			x
Nils L Hjort		x		x			x
Kjetill S Jakobsen*	x		x		x	x	x
Helene M Lampe	L	x	x				x
Ole Chr. Lingjærde*		x		x			x
Atle Mysterud*		x					x
Camilla L Nesbø	x		x			L	x
Geir Ottersen*	x	x					x
Eli K Rueness	x	x	x		L		x
Tore Schweder*	x	x	x	L			x
Tore Slagsvold	x	L	x				x
Geir Storvik*	x	L		x	x	x	x
Glenn-Peter Sætre*	x	x	L	x	x		x
Hildegunn Viljugrein	x					x	x
Asbjørn Vøllestad*	L	x	x	x	x		x

The CoE is chaired by Nils Chr. Stenseth, a professor of ecology and evolution. Through his scientific career Stenseth has developed a research strategy combining biologists, statisticians, economists and computer scientists in teams addressing a broad spectrum of ecological and evolutionary questions. Eli K. Rueness, who has been instrumental for the development of CEES, will serve as deputy chair.

Teams consisting of CoE-core members and external collaborators will join forces within the *Themes* and *Colloquia*. Each *Theme* is headed by two CoE-core members (Table 2), and 2 post doc and 3 PhS positions will be allocated to the *Themes*. We also expect additional funds. The *Colloquium* will be headed by CoE-core members. Each *Colloquium* will be allocated 1 post doc position from CoE funding. In addition, at any given time there will be 1 post doc position allocated to statistical work linked to topics within the *Themes* or the *Colloquia*. Tore Schweder and Geir O. Storvik will be in charge of the overall incorporation of statistical modelling to the biological research.

Visiting scientists, to be named *Kristine Bonnevie Professors*, will be invited to each of the *Colloquia*. The first *Colloquium* ought to be broader than the others, in order to develop, and integrate, biological theory and statistical modelling capacity for continued use in the CoE. The first *Colloquium* will thus be allocated two *Kristine Bonnevie Professors*, one biologist and one statistician.

The CoE leader will in day-to-day management collaborate closely with the *Theme* and *Colloquium* leaders, assisted by an executive administrator. All core members will meet monthly to discuss issues important for the management of the centre. **A Board** will meet twice a year to focus on strategic and control functions as well as handling budgets, accounts and annual reports.

A Scientific Advisory Board will evaluate the centre's scientific performance. This board will meet with the CoE-core members once a year in order to assess recent progress and future strategies.

THE RESEARCH TEAM

The team of scientists in the CoE has a broad spectrum of competence within ecology, evolution and methodology. A high publication rate in top international journals confirms the contribution of the members in defining the cutting edge of their fields (see CVs in Appendix 1 to the electronic application form). Since 2001, 387 papers have been published by the CoE core members. Two of the core members, Nils Chr. Stenseth and Tore Slagsvold are listed as *Highly Cited Researcher* by Thomson-ISI. Nils Lid Hjort is recognized by ISI as author of a fast breaking paper in mathematics. Moreover, Stenseth is the most cited Norwegian biologist and the second-most cited Norwegian scientist over the last 10 years. Atle Mysterud has been awarded the status as an *Outstanding Young Investigator* (2004) and Stenseth has been awarded the *Prize for Excellence in Research* of both the UoO (1996) and the Norwegian Research Council (RCN) (2000). Slagsvold received in 2006 the *Nansen Award*; Stenseth was awarded this prize in 1985. Glenn-Peter Sætre was awarded the *Nansen Endowment Prize for Young Excellent Scientist* in 2000; in 2005 Atle Mysterud was awarded the same prize. Eli K. Rueness

received, in 2004, *His Majesty the King's gold medal* for brilliant young researchers.

The core members have ample experience in supervision of students at all levels. Their students have a high publication rate in good journals and have established successful careers relevant to their education.

The core team has an extensive international network, which will strengthen the CoE through the *Themes*, and particularly through the *Colloquia*, where highly qualified international scientists will be invited to participate for a year or more as core researchers (*Kristine Bonnevie Professors*). In addition there will be five annual part time visiting scientists (II-positions in the Norwegian terminology), allocated most appropriately to the *Themes* and the *Colloquia*.

THE EDUCATIONAL PROGRAM

The graduate training program of the CoE will be organized within a *Graduate school* (a status which CEES has been awarded by the UoO). The newly established *Marie Curie Early Training Site on Ecological and Evolutionary Responses to Climate Change (CEES-MCO)* will be an integral part of the *Graduate school*. This program will supply the centre with top international PhD students.

The broad spectrum of experience and skill at the CoE allows us to offer a unique interdisciplinary PhD training program where the students will benefit from a stimulating international environment. Students will work in research teams, supervised by two core members, and follow an Individual Personal Career Development Plan.

Courses and seminars will be taught in English. Internationalization of training will further be ensured through the European Credit Transfer and Accumulation System (ECTS) and Diploma supplements.

The CoE status will allow us to employ a significant number of PhD students during the 10-year period. Additional funding, for the employment of more students will be sought through ordinary research funding.

GENDER PROFILE OF THE COE

We suggest several mechanisms to even out the gender balance in science (for further details see Appendix 2 of the electronic application form,

or the last two pages of this project description). In particular we take action to counteract the loss of women from Master levels, to the PhD and post doc levels, to high rank academic positions. Following guidelines of UoO and RCN, a mentor project will be offered to female students. The CoE will provide a unique opportunity to employ the female candidates, Eli K. Rueness and Camilla L. Nesbø, as full-time researchers throughout the period, and Hildegunn Viljugrein as well as other female collaborators on a 20%-basis. Altogether we will aim at 50% of the Professor II (employed at a 20% basis) appointments at the centre being offered to outstanding female scientists. If funded as a CoE, one technician will be allocated by UoO exclusively to support female scientists.

The *Kristine Bonnevie Professorship* will contribute to the promotion of women in science, as will the fact that female scientists will chair both the Board and the Scientific Advisory Board.

COE ACTIVITIES

All core members, collaborators as well as other scientists will be invited to a **CoE opening conference with workshops** towards the end of the first half-year. One or two keynote speakers will be invited to chair the conference around topics covered by each of the *Themes* and *Colloquia*. Keynote papers will be published as a special issue of *Phil. Trans. Roy. Soc. Lond.* Immediately following the conference, *Theme-specific* workshops will be held for the development of detailed work-plans. Likewise, workshops for each of the *Colloquia* will be held in the beginning of each three-year period.

At the end of the CoE-period we will host a **concluding conference on ecology and evolution** for members and collaborators as well as external participants. In such a meeting we will discuss where the field ought to move in the next decade. The *Kristine Bonnevie Professors* will play key roles in this meeting.

Specially invited guests will speak at the **CoE weekly seminars**. The annual **Kristine Bonnevie Lecture in Evolutionary Biology** (supported by the Faculty of Mathematics and Natural Sciences of the UoO) will enable us to invite a distinguished guest to give a high profiled lecture for a broad audience (on

September 2, the official opening of the academic year).

Each year master and PhD students will present their projects and progress at an **internal CoE symposium**.

A **journal club** will be held weekly where students, in particular, will be encouraged to critically read and discuss scientific papers.

CoE web pages and newsletters will be developed to ensure information flow and communicate science to researchers, sponsors and prospective students.

PUBLIC RELATIONS

The CoE will work for an increased awareness of science in the general population. Communication of scientific findings, our own (reported in the primary literature) or by others, to a broad public audience will be prioritized. Annually we will celebrate **Darwin Day** on February 12 (<http://www.darwinday.org/>).

Several core members commonly appear in radio and TV, Dag O. Hessen is the most prominent one in this respect, in 1998 he received RCN's prize for excellence in communication of science. Hessen will be given responsibility for coordinating the Public Relation of the CoE.

RESOURCES AND INFRASTRUCTURE

The CoE will have a state-of-the-art **molecular biology laboratory** fully equipped for DNA-sequencing and genotyping with two new ABI GA3730 (48 capillary) sequencing machines. The CoE has access to an Internet-based service for **computational biology** (e.g., phylogeny, population genetics and high throughput sequence analysis) at UoO (the BioPortal; see <http://www.biportal.uio.no/>). Furthermore members of the CoE have access to several **field stations** for large-scale terrestrial or marine experiments such as: *the Alpine Research Centre of Finse*, *the Landscape Ecology Field Station of Evenstad* and the marine field stations at Drøbak, Solbergstrand and Flødevigen.

QUALITY ASSURANCE MECHANISMS

The Ministry of Research and Education has in a letter to the RCN (30.06.00) specified three criteria for the scientific quality of the CoEs: originality, solidity and scientific relevance. We

will follow these guidelines and employ a number of measurable mechanisms including:

- CoE-core members will meet monthly to assess progress.
- The Board will meet in order to assess the activities of the centre.
- The Scientific Advisory Board the CoE activities will be evaluated.
- Originality and scientific relevance will be measured by the number of publications in high-impact journals.
- The training programme will be reviewed on an annual basis, both the programme as such and each individual student.
- The number of students completing the training programme and their success in pursuing further relevant careers will ultimately assess the vitality of the CoE.

INSTITUTIONAL SUPPORT

The following support will be provided by different levels at the UoO:

- Allocation of scientific staff to the CoE.
- Four technicians (1 for field- & 3 for lab work).
- Necessary infrastructure and administrative support.
- Remaining relocation expenses. Two million NOK per year for 10 years.
- Funding for at least 2 recruiting positions (post docs and PhDs) throughout the CoE-period.

ETHICAL ISSUES

Our research will be conducted in accordance with the *Norwegian 'Animal Welfare Act' (#73)* of 20.12.74, the *Norwegian 'Regulation on Animal Experimentation'* of 15.01.96, as amended, established pursuant to §22 of the *Animal Welfare Act* and the *European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes* (18.03.86). Work on *Yersinia pestis* will, together with one of our collaborators (Elisabeth Carniel), be carried out at *Institut Pasteur* in Paris, as well as at the laboratories of our collaborators in Kazakhstan and China, in accordance with EU standards. All CoE-funded personnel involved in physical handling of animals are required to attend a compulsory course *Procedures for ethical treatment of animals in experimental work*. The convention, acts and regulations referred to above are required subject matter at this course.

RELEVANCE TO SOCIETY

The new insight achieved through the research and training will be essential for addressing many applied issues requiring a solid understanding of how environmental changes affect evolutionary processes. Specifically the research and training within the CoE will provide improved understanding of:

- How the living world responds and adapts to environmental changes.
- How evolution and speciation depend on ecosystem properties.
- How bacterial pathogenicity evolves.
- How populations and species might be affected as a result of external forcing such as climate change.
- How anthropogenic stressors like harvesting affect ecological and evolutionary processes.

The *Rio Convention* of 1992 called for "research which contributes to the conservation and sustainable use of biological diversity" (Article 12). By providing basic knowledge about ecological systems, the CoE will contribute to this goal. In addition the CoE will train a new generation of inter- and multidisciplinary scientists at all levels from Master and PhD students to post doctoral candidates, and as part of this contribute to a more even gender balance within the scientific community.

ADDED VALUE

The research groups funded via the CoE-program are expected to become internationally influential within their fields. We will put together a team of highly qualified faculty members, who have not worked extensively together in the past, but who are eager to focus

on common goals. Through the CoE structure we can:

- use our strong foundation in ecology and statistical methodology to extend our research into the interface between ecology and evolutionary biology.
- Use the broad spectre of biological systems available to the group as a basis for developing and testing general hypotheses at the interface between ecology and evolution.
- Implement a new research structure based on *Themes* and *Colloquia*.
- Extend our collaborative network with current and new partners.
- Provide a basis for new interdisciplinary work at the UoO.
- Contribute to a more equalized gender balance in high rank academic positions at the UoO.
- Provide international, interdisciplinary training for a new generation of students and post docs.

The CoE team is at a stage where we can develop a strongly needed synthesis of ecology and evolution – becoming a leading institution in this field. The CoE will in 10 years vitalize biology at the UoO, and thereby considerably strengthen interdisciplinary science in Norway. Altogether the CoE team aims at becoming an important player in the international scientific arena, not least within the European science funding system. Within the international scientific arena the CoE will advance our **knowledge of intrinsic biological processes of evolution and ecology and their interplay, and thus contribute to an improved understanding of how the living world responds and adapts to environmental changes.**

REFERENCES

- Achtman, M., Morelli, G., Zhu, P.X., Wirth, T., Diehl, I., Kusecek, B., Vogler, A.J., Wagner, D.M., Allender, C.J., Easterday, W.R., Chenal-Francisque, V., Worsham, P., Thomson, N.R., Parkhill, J., Lindler, L.E., Carniel, E., Keim, P. 2004. *PNAS* 101, 17837-17842.
- Andersen, T., Elser, J.J. & Hessen, D.O. 2004. *Ecol. Let.* 7, 884-900.
- Boucher, Y., Douady, C., Papke, R., Walsh, D., Boudreau, M., Nesbø, C.L., Case, R.J., Doolittle, W.F. 2003. *Annu Rev Genet* 37, 283-328.
- Brochmann, C., Bryusting, A.K., Alsos, I., Borgen, L., Grundt, H.H., Scheen, A.-C. & Elven, R. 2004. *Biol. J. Linn. Soc.* 82, 521-536.
- Bryusting, A.K., Fay, M., Leitch, I. & Aiken, S. 2004. *Taxon* 53, 365-382.
- Carniel, E., Hinnebusch, B.J. 2004. *Yersinia: Molecular and Cellular Biology*. Horizon Bioscience, UK.
- Carter, A.J.R., Hermisson, J. & Hansen, T.F. 2005. *Theor. Pop Biol.* 68, 179-196.
- Davis, S.A., Begon, M., de Bruyn, L., Ageyev, V.S., Klassovskiy, N., Pole, S.B., Viljugrein, H., Stenseth, N.C. & Leirs, H. 2004. *Science* 304, 736-738.
- Doebeli, M., Dieckmann, U. 2000. *Am Nat* 156, S77-S101.
- Doolittle, W.F. 1999. *Science* 284, 2124-2129.
- Gevers, D., Cohan, F.M., Lawrence, J.G., Spratt, B.G., Coenye, T., Feil, E.J., Stackebrandt, E., Van de Peer, Y., Vandamme, P., Thompson, F.L. & Swings, J. 2005. *J. Bacteriol.* 187, 8312-8321.
- Haavie, J., Borge, T., Bures, S., Garamszegi, L.Z., Lampe, H.M., Moreno, J., Qvarnström, A., Török, J. & Sætre, G.-P. 2004. *J. Evol. Biol.* 17, 227-237.
- Hansen, T.F. 2006. *Ann. Rev. Ecol. Evol. Syst.* 37, 123-157.
- Hansen, T.F. & Wagner, G.P. 2001. *Theor. Pop. Biol.* 59, 61-86.
- Hansen, T.F., Armbruster, W.S., Carlson, M.L. & Pélabon, C. 2003a. *J. Exper. Zool.* 296B, 23-39.
- Hansen, T.F., Pélabon, C., Armbruster, W.S. & Carlson, M.L. 2003b. *J. Evol. Biol.* 16, 754-765.
- Haugen, T.O. 2000. *Oikos* 90, 107-118.
- Haugen, T.O. & Vøllestad, L.A. 2000. *J. Evol. Biol.* 13, 897-905.
- Haugen, T.O. & Vøllestad, L.A. 2001. *Genetica* 112/113, 475-491.
- Haugen, T.O., Winfield, I., Vøllestad, L.A., Fletcher, J.M., James, J.B. & Stenseth, N.C. 2006. *PRSB* (in press; available on-line).
- Hereford, J., Hansen, T.F. & Houle, D. 2004. *Evolution* 58, 2133-2143.
- Hessen, D.O., Ågren, G., Anderson, T., Elser, J.J. & de Reuter, P. 2004. *Ecology* 85, 1179-1192.
- Hjort, N.L., Dahl, F.A. & Steinbakk, G.H. 2006. Post-processing posterior predictive p-values *J. Amer. Stat. Assn.* (in press).
- Houle, D. 1992. *Genetics* 130, 195-204.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. & Stenseth, N.C. 2006. *Science* 312, 1959-1961.
- Kitada, S. & Kishino, H. 2004. *Genetics* 167, 2003-2013.
- Kitakado, T., Kitada, S., Kishino, H., & Skaug, H.J. 2006. An integrated likelihood method for estimating genetic differentiation between populations. *Genetics* (in press).
- Knutsen, H., André, C., Jorde, P.E., Skogen, M.D., Thuróczy, E. & Stenseth, N. C., 2004. *PRSB* 271, 1337-1344
- Koskinen, M., Haugen, T. & Primmer, C.R. 2002. *Nature* 419, 826-830.
- Lampe, H.M. & Sætre, G.-P. 1995. *PRSB* 262, 163-167.
- Manel, S., Bellemain, E., Swenson, J.E. & François, O. 2004. *Mol. Ecol.* 13, 1327-1331.
- Martiny, J.B.H., Bohannan, B., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreas, L., Reysenbach, A.L., Smith, V.H., Staley, J.T. 2006. *Nat Rev Microbiol* 4, 102-112.
- Mezey, J.G. & Houle, D. 2003. *Genetics* 165, 411-425.
- Mezey, J.G. & Houle, D. 2005. *Evolution* 59, 1027-1038.
- Mikalsen, B., Boison, G., Skulberg, O.M., Fastner, J., Davies, W., Rudi, K. & Jakobsen, K.S. 2003. *J. Bacteriol.* 185, 2774-2785.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. 2001. *PRSB* 268, 911-919.
- Mysterud, A., Tryjanowski, P. & Panek, M. 2006. Selectivity of harvesting differs between local and foreign roe deer hunters. *Biol. Let.* (in press).
- Nesbø, C.L., Nelson, K.E., & Doolittle, W.F. 2002. *J. Bacteriol.* 184, 4475-4488.
- Nesbø, C.L., Dlutek, M., & Doolittle, W.F. 2006a. *Genetics* 172, 759-769.
- Nesbø, C.L., Dlutek, M., Zhaxybayeva, O. & Doolittle, W.F. 2006b. *Appl Environ Microbiol* 72, 5061-5068.
- Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J., Bratney, J., Ernande, B. & Dieckmann, U. 2004. *Nature* 428, 932-935
- Ruense, E.K., Pigliucci, M. 2006. Deconstructing Genetic Architecture. *Ms in progress.*
- Sætre, G.-P., Moum, T., Bures, S., Král, M., Adamjan, M. & Moreno, J. 1997. *Nature* 387, 589-592.
- Sætre, G.-P., Borge, T., Lindroos, K., Haavie, J., Sheldon, B.C., Primmer, C.R. & Syvänen, A.C. 2003. *PRSB* 270, 53-59.
- Schweder, T. 2003. *Scientia Marina* 67 (Suppl. 1), 89-97.
- Schweder, T. & Hjort, N.L. 2002. *Scand. J. Stat.* 29, 309-332.
- Skaug, H.J. 2002. *J. Comp. & Graph. Stat.* 11, 458-470.
- Slagsvold, T., Hansen, B.T., Johannessen, L.E. & Lifjeld, J.T. 2002. *PRSB* 269, 1449-1455.
- Stenseth, N.C. & Maynard Smith, J. 1984. *Evolution* 38, 870-880
- Stenseth, N.C., Bjørnstad, O.N., Falck, W., Fromentin, J.-M., Gjørsater, J. & Gray, J. 1999. *PRSB* 266, 1645-1654.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. 2002. *Science* 297, 1292-1296.
- Stenseth, N.C., Jorde, P.E., Chan, K.-S., Hansen, E., Knutsen, H., André, C., Skogen, M.D. & Lekve, K. 2006a. *PRSB* 273, 1085-1092.
- Stenseth, N.C., Samia, N., Viljugrein, H., Kausrud, K., Begon, M., Davis, S., Leirs, H., Dubyanskiy, V., Esper, J., Klassovskiy, N., Pole, S. & Chan, K.-S. 2006b. *PNAS* 103, 13110-13115.
- Stenseth, N.C., Atshabar, B.B., Begon, M., Belmain, S.R., Bertherat, E., Carniel, E., Gage, K.L., Leirs, H. & Rahalison, L. 2006c. Plague, Past, Present and Future. *PLoS Medicine* (in press).
- Storvik, G. 2002. *IEEE Trans Signal Processing* 50, 281-289.
- Thompson, J.R., Pacocha, S., Pharino, C., Klepac-Ceraj, V., Hunt, D.E., Benoit, J., Sarma-Rupavtarm, R., Distel, D.L. & Polz, M.F. 2005. *Science* 307, 1311-1313.

EQUAL OPPORTUNITY

Evening out the gender balance in high-rank academic positions is a priority of both the Research Council of Norway and the University of Oslo. CEES will implement several guidelines to counter “the leaky pipeline” of women through the academic hierarchy from Master level, via the PhD and post-doc level, to tenured scientific staff .

The number of females in the CoE team is relatively higher than at the Dept. of Biology as such (29% compared to 18% female scientists; see Table A2-1).

We will use a dual approach to attract and keep female scientists, partly optimizing the conditions for our female students and staff and partly emphasizing female role models. Our overall goal is to approximate gender equality at all levels.

We specifically propose the following mechanisms:

- Two of the three *Themes* are co-chaired by female scientists, and two of the four *Colloquia* are chaired by female scientists.
- Dr. Eli K. Rueness, currently a post doc at CEES, will be offered a research position within the CoE, and – as a core member – be in charge of *Colloquium 2*. She will also be given particular duties relative to recruitment of young scientists, and serve as a deputy centre leader.
- Dr. Camilla L. Nesbø will return to the UoO, funded as an *Outstanding Young Investigator* (RCN), to join the CoE (Dr. Nesbø received here doctoral degree at the Dept. of Biology in 1999, since then she has worked with Professor W.F. Doolittle’s group in Dalhousie, Canada). She will – as a core member – be in charge of *Colloquium 3*.
- UoO-funding has been secured for appointing a lab-technician assigned female scientist;
- A mentor program will be offered all female students.
- Establishment of the *Kristine Bonnevie Professorship in Evolutionary Biology*.
- We will aim at a gender balance among the speakers in the annual *Kristine Bonnevie Lecture in Evolutionary Biology*.
- Seeking internal and external funding for hiring Professor II positions, among which the first two employed by the Department of Biology are Dr. Hildegunn Viljugrein (National Veterinary Institute, Norway) and Professor Ellen van Donk (Netherlands Institute of Ecology).
- The Board will be chaired by a woman, Prof. Reidun Sirevåg of the University of Oslo.
- The Scientific Advisory Board will be chaired by a woman, Prof. Rita R. Colwell of the University of Maryland. Fifty percentages of the members of the Scientific Advisory Board will be female scientists.

Table A2-1. Current gender balance (as per August 2006) among the CoE core-members and collaborators as well for the CoE board and scientific advisory board, Master students, PhD students and post-doc/young researchers working in collaboration with the CoE core-members (over the past 5 years).

Type of position in the CoE	Percent women	Total number
CoE core-members	29%	19
CoE collaborators	18%	33
CoE board & Scient Adv Board	40%	10
Type of position	Percent women having successfully finished their studies/working period from 2001-2006 (number in total)	Percent women currently working with CoE-members (number in total)
Master students	46% (57)	43% (44)
PhD students	27% (30)	56% (52)
Post-docs (young researchers)	30% (10)	29% (38)

Furthermore, in order to attract female scientists, when advertising for positions at the CoE, we will emphasize the general rights of women given in Norway, such as paid maternity/paternity leaves

(100% salary for 10 months or 80% for 12 months). Also, when female and male applicants otherwise are equally qualified, the women will be preferred.

MANAGEMENT AND ADMINISTRATION

The Department of Biology shall host the CoE. The CoE and the CoE director will report to the Head of the Department of Biology. The CoE director will report directly to the CoE Board and to the Board of the Department of Biology regarding scientific issues. The CoE director will report directly to the Head of Department regarding all other issues.

The CoE will be headed by the current leader of CEES, Nils Chr. Stenseth, Professor of ecology and evolution. The CoE director will in day-to-day management collaborate closely with the *Theme* and *Colloquium* leaders, assisted by an executive administrator.

Professor Stenseth will be appointed in a full time position as CoE director for a term of 5 years, with a possible extension of a further 5 years. The director's salary will be covered by CoE funding.

To ensure satisfactory information regarding CoE activities, the centre will be given its own financial code at the Dept. of Biology. The NRC and UiO grants will be allocated to this code. Project funding that is entirely included in the CoE's own funding, and new project funding belonging to the CoE will also be allocated to this code.

All CoE-core members will meet monthly to discuss issues important for the management of the centre. Several core members commonly appear in radio and TV, Dag O. Hessen is the most prominent one in this respect, in 1998 he received RCN's prize for excellence in communication of science. Hessen will be given responsibility for coordinating the Public Relation of the CoE.

The CoE Board will meet twice a year to decide on strategic issues and perform control functions, as well as making proposals for decisions on budgets, accounts and annual reports.

The Dept. of Biology will make final decisions on CoE budgets, annual plans and RCN/EU-reports.

A Scientific Advisory Board will evaluate and advice on the centre's scientific performance. This board will meet with the CoE-core members once a year in order to assess recent progress and future strategies.

PERSONNEL

The Department of Biology has personnel responsibility for all scientific staff in permanent positions. The CoE leader will be delegated responsibility for all temporary personnel (PhD student, post docs and researchers). Work contracts shall be signed for all employees specifying the share of their working hours dedicated to the CoE.

RESOURCES AND INFRASTRUCTURE

The CoE members are (as far as possible) collocated in the Kristine Bonnevie building, UoO. The Dept. of Biology makes final decisions on CoE use of floorage, CoE start-up rebuilding/renovation and all later changes in floorage. The CoE will have a state-of-the-art **molecular biology laboratory** fully equipped for DNA-sequencing and genotyping with two new ABI GA3730 (48 capillary) sequencing machines. The CoE has access to an Internet-based service for

computational biology (e.g., phylogeny, population genetics and high throughput sequence analysis) at UoO (the BioPortal; see <http://www.biportal.uio.no/>). Furthermore members of the CoE have access to several **field stations** for large-scale terrestrial or marine experiments such as: *the Alpine Research Centre of Finse, the Landscape Ecology Field Station of Evenstad* and the marine field stations at Drøbak, Solbergstrand and Flødevigen.

The following tables (Tables A2-2 to A2-6) provide a full overview of all members of the CoE. Some positions will be filled after open announcements. This information provides the foundations for the accounting and budgeting summarized in the contract. The University of Oslo (UoO) department listed in parentheses identifies where the senior scientists currently are employed. These departments will continue to provide the salary for their employees (percentage participation is given under CoE share). Acronyms: **Bio**: Dept. of Biology; **Econ**: Dept. of Economics; **Inf**: Dept. of Informatics; **Math**: Dept. of Mathematics; **IMR**: Institute of Marine Research (Bergen). **UoO** in the funding column identifies that the funding derives from the Faculty of Mathematics and Natural Sciences.

Table A2-2. CoE- Core members and associated staff on Professor/Assoc. Prof. level.

Senior scientists (Permanent staff)				
Name	Position	Period	CoE share	Funding
A. K. Brysting	Assoc. Prof.	2007-2016	75%	Host (Biol)
T. F. Hansen	Professor	2007-2016	75%	Host (Biol)
D. O. Hessen	Professor	2007-2016	75%	Host (Biol)
N. L. Hjort	Professor	2007-2016	25%	Host (Math)
K. S. Jakobsen	Professor	2007-2016	75%	Host (Biol)
H. M. Lampe	Professor	2007-2016	75%	Host (Biol)
O. C. Lingjærde	Assoc. Prof.	2007-2016	25%	Host (Inf)
A. Mysterud	Professor	2007-2016	75%	RCN/Host (Biol)
C. L. Nesbø	Research Assoc.	2009-2016	75%	External fund through UoO
G. Ottersen	Senior Research Scientist	2007-2016	50%	IMR
E. K. Rueness	Research Assoc.	2007-2016	100%	CoE
T. Schweder	Professor	2007-2016	65%	Host (Econ/UoO)
T. Slagsvold	Professor	2007-2016	75%	Host (Biol)
N.C. Stenseth	CoE-leader	2007-2016	100%	CoE
G. Storvik	Professor	2007-2016	38%	Host (Math)
G.-P. Sætre	Professor	2007-2016	75%	Host (Biol)
H.-G. Viljugrein	Assoc. Prof II	2007-2016	20%	Host (Biol)
L. A. Vøllestad	Professor	2007-2016	75%	Host (Biol)
Kristine Bonnevie professors and visiting-partner positions				
	KB-Prof for Coll 1	2008	100%	CoE
	KB-Prof for Coll 1	2009-2010	20%	CoE
	KB-Prof for Coll 1	2008	100%	Host
	KB-Prof for Coll 1	2009-2010	20%	Host
	KB-Prof for Coll 2	2010	100%	CoE
	KB-Prof for Coll 2	2011-2012	20%	CoE
	KB-Prof for Coll 3	2012	100%	CoE
	KB-Prof for Coll 3	2013-2014	20%	CoE
	KB-Prof for Coll 4	2014	100%	CoE
	KB-Prof for Coll 4	2015-2016	20%	CoE
	Other associated collaborators	2007-2016	Ca 5 people at 20% at any given time	CoE

Table A2-3. CoE-funded PhD students and post docs.

Position	Relation to CoE	Period	Number of positions	Funding
Post doc	Themes 1-3	Oct07-Sept16	8	CoE
Post doc	Colloquium 1	2008-2010	1	CoE
Post doc	Colloquium 2	2010-2012	1	CoE
Post doc	Colloquium 3	2012-2014	1	CoE
Post doc	Colloquium 4	2014-2016	1	CoE
Post doc in statistical modelling	Themes1-3, Coll 1-4	2007-2016	4	CoE
PhD	Themes 1-3	Oct07-Sept17	9	Host
PhD	Colloquia 1-4	Oct07-Sept16	2	CoE
Associated positions, PhD	CoE-projects	2007-2016	21*	Host/RCN/other
Associated positions, post doc/res	CoE-projects	2007-2016	30*	Host/RCN/other

*the number derives from people employed in these positions as of August 2006

Table A2-4. Administrative and technical personnel

Name	Position	Period	CoE share	Funding
K. E. Grønli	Head of Administration	2007-2016	100%	CoE
E. R. Nerli	Technician (lab)	2007-2016	50%	Host (Biol)
N. W. Steen	Technician (lab)	2007-2016	100%	Host (Biol)
(to be filled)	Technician (lab)	2007-2016	100%	Host (UoO/Biol)
(to be filled)	Technician (field)	2007-2016	100%	Host (Biol)
(to be filled)	Administrator of Colloquia	2007-2016	100%	Host (Biol)
(to be filled)	Administrator of research	2007-2016	100%	Host (Biol)

Table A2-5. Board, Scientific Advisory Board and Collaborators.

Board	
Chair: Reidun Sirevåg	Dept. of Molecular Biosciences, University of Oslo, Norway
Sven-Axel Bengtson	Museum of Zoology, Lund University, Sweden
Rolf A. Ims	Inst. of Biology, Dept. of Ecology, University of Tromsø, Norway
Bernt Øksendal	Centre of Mathematics for Applications, University of Oslo, Norway
Scientific Advisory Board	
Chair; Rita R. Colwell	Bloomberg School of Public Health, Univ. of Maryland, US
David R. Brillinger	Statistics Department, Univ. of California, Berkley, US
Edward J. Feil	Dept of Biology and Biochemistry, Univ. of Bath, UK
Barbara Mable	Div. of Environmental and Evolutionary Biology, Univ. of Glasgow, UK
Anne Magurran	Gatty Marine Laboratory, Univ. of St. Andrews, UK
Gordon H. Orians	Dept. of Biology, Univ. of Washington, US
Collaborators	
Mark Achtman	Max-Planck-Institute for Infectious Biology, Berlin, Germany
Emmanuelle Cam	Centre Nat. de la Recherche Scient., Univ. of Toulouse 3 Paul Sabatier, France
Elisabeth Carniel	The <i>Yersinia</i> Research Unit, Institut Pasteur, Paris, France
Kung-Sik Chan	Dept. of Statistics and Actuarial Science, Univ. of Iowa, US
Daniel Chourrout	Sars International Centre for Marine Molecular Biology, Bergen, Norway
Torben Dabelsteen	Animal Behaviour Group, Biological Inst., University of Copenhagen, Denmark
Ulf Dieckmann	Evolution and Ecology Program, Int. Inst. for Applied Systems Analysis, Austria
Michael Doebeli	Dept. of Zoology and Mathematics, Univ. of British Columbia, Canada
W. Ford Doolittle	Dept. of Biochem. and Mol. Biology, Dalhousie Univ., Canada
James J. Elser	Fac. of Ecology, Evol. and Environm. Sciences, Arizona State University, US
Michael F. Fay	Jodrell Laboratory, Royal Botanic Gardens, Kew, UK
Trond O. Haugen	Norwegian Institute for Water Research, Norway
Andrew Hendry	Redpath Museum, McGill University, Canada
David Houle	Dept. of Biological Science, Florida State University, US
Niclas Jonzén	Dept. of Theoretical Ecology, Lund University, Sweden
Hirohisa Kishino	Graduate School of Agricultural and Life Sciences, University of Tokyo, Japan
Toshihide Kitakado	Dept. of Marine Bioscience, Tokyo Univ. of Mar. Sciences and Techn., Japan
Ole Næsbye Larsen	Inst. of Biology, University of Southern Denmark, Denmark
Ilia J. Leitch	Jodrell Laboratory, Royal Botanic Gardens, Kew, UK
James D. Nichols	Patuxent Wildlife Res. Center, United States Dept. Of Interior, Maryland, US
Massimo Pigliucci	Dept. of Ecology and Evolution, Stony Brook State University of NY, US
Craig Primmer	Div. of Genetics and Animal Physiology, University of Turku, Finland
Anna Qvarnström	Dept. of Animal Ecology, Evol. Biol. Centre, Uppsala University, Sweden
David Reznick	Dept. of Biology, University of California, Riverside, US
Maria R. Servedio	Dept. of Biology., University of North Carolina, US
Hans J. Skaug	Dept. of Mathematics, University of Bergen, Norway
Jon Swenson	Dept. of Ecol. and Nat. Res. Management, Norw. Univ. of Life Sciences, Norway
Ellen van Donk	Centre for Limnology, Netherlands Institute of Ecology, The Netherlands
Günter P. Wagner	Dept. of Ecology and Evolutionary Biology, Yale University, US
Lawrence J. Weider	Dept. of Zoology, University of Oklahoma, US
Ian J. Winfield	Centre for Ecol. and Hydrology, Natural Environm. Res. Council, UK
Ruifu Yang	Inst. of Microb. and Epidem., Adademy of Military Med Sciences, Beijing, China
Zhibin Zhang	Inst. of Zoology, Chinese Academy of Sciences, Beijing, China

Table A2-6. Participation of core-members and collaborators in *Themes* and *Colloquia*. *T1* = The role of population structuring in adaptive evolution; *T2* = The potential for adaptation; *T3* = The evolution of reproductive isolation; *C1* = Selection and evolvability: concepts, measurements and statistical modelling; *C2* = Bridging the gap between molecular genetics and evolutionary genetics; *C3* = Ecology and evolution of mosaic genomes: The case of microbes; and *C4* = Integration of ecology and evolution: A synthesis.

THE CoE MEMBERS							
Centre leader	<i>T1</i>	<i>T2</i>	<i>T3</i>	<i>C1</i>	<i>C2</i>	<i>C3</i>	<i>C4</i>
Nils Christian Stenseth	x	x	x	x	x	x	L
Core members at the University of Oslo							
Anne K. Brysting			L		x		x
Thomas F. Hansen		x		L			x
Dag O. Hessen			x	x			x
Nils L. Hjort		x		x			x
Kjetill S. Jakobsen	x		x		x	x	x
Helene M. Lampe	L	x	x				x
Ole Christian Lingjærde		x		x			x
Atle Mysterud		x					x
Camilla L. Nesbø	x		x		x	L	x
Geir Ottersen	x	x					x
Eli K. Rueness	x	x	x		L		x
Tore Schweder	x	x	x	L			x
Tore Slagsvold	x	L	x				x
Geir Storvik	x	L		x	x	x	x
Glenn-Peter Sætre	x	x	L	x	x		x
Hildegunn Viljugrein	x					x	x
L. Asbjørn Vøllestad	L	x	x	x	x		x
Collaborators							
Mark Achtman	x					x	
Emmanuelle Cam		x					
Elisabeth Carniel	x					x	
Kung-Sik Chan	x						x
Daniel Chourrout					x		
Torben Dabelsteen	x	x					
Ulf Dieckmann		x					x
Michael Doebeli		x					x
W. Ford Doolittle						x	
James J. Elser			x	x			
Michael F. Fay			x		x		x
Thron O. Haugen	x	x	x				x
Andrew Hendry	x	x	x	x			x
David Houle		x		x			
Niclas Jonzén		x					
Hirohisa Kishino	x	x	x	x			x
Toshihide Kitakado	x		x	x	x		
Ilia J. Leitch			x		x		x
James D. Nichols		x					
Ole N. Larsen	x	x					
Massimo Pigliucci					x		
Craig Primmer	x	x	x		x		
Anna Qvarnström			x				
David Reznick	x	x					x
Maria R. Servedio			x				
Hans J. Skaug	x		x	x			x
Jon Swenson		x					
Ellen van Donk			x	x			
Günter P. Wagner		x		x			
Lawrence J. Weider			x	x			x
Ian J. Winfield	x						
Ruifu Yang	x					x	
Zhibin Zhang	x					x	