

Review of the mid-term report of activities (2007-2009) of the program 'Center for Theoretical Biology: an interdisciplinary research platform at the University of Gothenburg'

Two years ago, the proposal to build up a Centre for Theoretical Biology at Göteborg University appeared highly relevant and was very convincingly justified. The outstanding quality of the participants and the very promising research plan suggested that the build up of such a centre should be most successful and thus should be supported. Letters of supports came from the most prominent international scientists in the field (Prs M. Begon, J.M. McNamara, U. Dieckman, R.D. Holt) and they were very clearly supportive. Two years after, it is clear that these high expectations have been met and that the current activities of the centre are very promising. The report of activities nicely highlights how the centre was successful at developing productive activities in theoretical biology, at the interplay among disciplinary fields, including mathematical epidemiology, speciation, comparative phylogeny and extinction risk analysis. The plans for further developments of the platform in the next years are sound and logical.

Being myself more an empirical researcher than a theoretician, I especially value the development of such a centre of excellence that *both* promote general theory development and our understanding of specific biological systems and questions. The two main research programme axes developed, dealing with ecological epidemiology and the modelling of evolutionary processes, show nicely how the skills of prominent researchers from different fields can be combined to address questions at the interplay between hard core theory and empirical questioning. The involvement of students and postdoctoral researchers seem to have been very successful, as can be witnessed by the list of recent published/in press papers and the many manuscripts mentioned as submitted or in preparation (which clearly involve the 5 postdocs employed by the CTBio platform). The organization of workshops (n = 6) and regular seminars has also been very active and has certainly contributed to the development of new ideas and productive collaborations. All members of the centre have been involved in several types of international scientific activities, which highlights the relevance of the research developed and its impact in an international setting.

The interdisciplinary research program is very strong both in the identification of key research questions in which the participants have clearly the skills to contribute to great advances for theoretical biology, and in the efficient development of collaborations of top researchers with theoretical and biological backgrounds. It also highlights well how the development of the research programmes directly benefits from the top training of graduate students in the Centre and the associated international network of renowned collaborators. Such a centre appears to contribute directly to the training of future skilled scientists in a field that is expanding and very demanding in terms of qualifications. Theoretical biology is needed to improve our understanding of factors affecting the dynamics of biodiversity, from the genetic levels to the level of interacting species in ecosystems, and the centre nicely develops science in this field.

I would like to recall that one particularity of the centre is that its contributors are internationally renowned scientists, with a rare balance of "classical" most prominent contributors in their fields (e.g., Peter Jagers for Branching process theory and Pr Malte Andersson for Sexual selection) and younger excellent scientists (e.g., Karin Harding in Spatial epidemiology of wildlife diseases and Bernahrd Mehlig in Statistical genetics). The successful implication of several other productive scientists and young researchers (doctorate students, postdocs) in the last two years shows that the centre is contributing efficiently to the development of a network of excellence in these fields.

Minor comments on the report:

I appreciated the factual tone of this mid-term report, with both conceptual and practical information about how science is developed at the centre. Given the broad field of the centre ('theoretical biology') and the relatively focused topic of some of the research developed, a few more lines of justifications would have been welcome for some of the research topics. This is notably the case regarding the paragraphs about 'models of speciation in Littorinoids snails'; for instance, why is it important to develop a background for interpreting patterns of partly isolated ecotypes of *Littorina saxatilis*? The research developed is clearly of high quality, but the answer to this question may not be obvious to some readers. Overall, the report nevertheless clearly outlines the productive developments of this young centre of excellence, since it was set up, two years ago.

Overall, the activities of the Centre for Theoretical Biology platform are of an outstanding level by international standards and the further expected developments of that platform are highly promising. I thus **most strongly support the award of continued funding** for the Centre of Theoretical Biology at Göteborg University.

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Re: Evaluation of the Centre for Theoretical Biology 2007-2009

September 19, 2009

Dear Dean Turner,

I am writing to provide an evaluation of the activities of the Centre for Theoretical Biology between 2007 and 2009. Without a doubt, the Centre has been successful in its key aim of establishing new and exciting research at the interface of mathematics and biology. The main questions addressed, about the mathematics of evolution and the epidemiology of emerging diseases, are of broad importance to society and are key areas where a mathematical-biological integration is required to advance knowledge. Overall, the platform has established an outstanding international cross-disciplinary mathematical program in epidemiology and evolution. The Centre is a credit to the university and I highly recommend that it is elected to continue to support the platform. It is clear from the information presented that the project personnel have benefitted enormously from the funds available, and that there have been knock-on benefits for education, and international recognition of the University.

The level of staffing seems appropriate for the activities conducted, with an emphasis on organization of seminars, conducting meetings to promote new collaborations and projects, and employing postdocs to work on these projects. The joint supervision of the postdocs by physicists, mathematicians and biologists is to be commended as a means of creating valuable cross training. The center has promoted a good level of activity, with about 10 international visitors, 10 seminar days, and three workshops per year. The level of productivity of the centre in terms of publications is above the average (of about 2.0) for ecologists, with the Centre producing 2.59 papers per research member per year (assuming 29 months of center activity). A good proportion of these products are also directly as a result of the collaborative projects promoted by the Centre. The list of journals spanned by the authors is impressive, both in its diversity (e.g., ecology, evolution, mathematical biology, molecular biology, physics, chemistry, and general science) and in including highly-ranked journals in physics (*Physical Review Letters* and *A* and *E*), ecology/evolution (*Evolution*, *American Naturalist*), and general science (*Proc. Natl Acad. Sci. USA*, *Plos One*, *Phil Trans. R. Soc. Lond.*).

The evaluation criteria chosen by the platform are useful and reflect current trends in evaluating science and mathematics. The platform's personnel are all active and internationally respected.

Each of them has a strong number of citations for their published work, indicating that other scientists and mathematicians are referring to their work. I am familiar with looking up H-index values for job applicants and overall the list of personnel have respectable numbers of papers that have been cited a good number of times. International recognition of the personnel is also apparent based on their invited seminars and involvement as examiners for PhD defenses (and so on).

International visitors to the Centre included several leaders in theoretical ecology. Overall while this is respectable, I would encourage the center to further develop sabbatical visits and other forms of involvement that extend a bit more deeply than workshops. One model that works well for this in the USA is the development of “working groups” which meet several times over the course of a year or two and international scientists collaborate on projects that benefit from a broad range of expertise. One model for such groups is provided by the National Center for Ecological Analysis and Synthesis in Santa Barbara, California, USA, where proposals are submitted to form such groups and funds are provided to support travel expenses but not salaries; clearly this is beyond the scope of the funding currently available for the platform, but could be worth pursuing if opportunity arises.

The personnel involved in the proposal have been expanded relative to the proposal by including more physicists. This is a valuable addition since the links between statistical physics, evolution and epidemiology are strong and growing; the techniques developed in physics to deal with stochastic behaviour (e.g., of particles) have been especially valuable for understanding the properties of genes and individual organisms. It is also clear that the physicists at the Centre have been extremely productive.

Contributions come from four major subject areas. (1) In mathematical epidemiology Hardin, Wennberg and Kleinhans (and collaborators) have made progress in understanding the emergence of new diseases by analyzing the effects of spatial subdivision of habitat, evolution of pathogen virulence, and affects of species jumps on stability. (2) By using snails as a model system for studying speciation, Johannesson, André, Mehlig, Eriksson and Panova (and other collaborators) have studied interesting links between mating system (sexual selection), phylogeny and ecological specialization. (3) Andersson, Mostad and Spaulding have also used comparative phylogenetic methods to understand patterns of evolution, sexual selection and ornamentation in weaverbirds (as a model group); this project is notable for the diversity of approaches used and the ability of such techniques to test important hypotheses in evolution. (4) Finally, Jagers, Harding, Åberg, and Nordvall-Lagerås are developing models for analysis of extinction risk based on branching processes that link evolution and demography. In a part of this project analysis of real populations of a migratory sandpiper add biological realism to the modeling work and address questions about the causes of population declines. All of these projects represent important contemporary problems in ecology and evolution, and all include creative uses of mathematical models to add insight to the biology. Reading through the report there is a sense that the last three of these projects are just coming to maturity, with the hardest and most productive parts of the mathematical-biological integration occurring now or being in the form of manuscripts that are being written. I don't see this as a weakness, rather it is a sign of the difficulty of the integration that is sought, and that continued support is essential to this platform.

The Centre personnel have been central in teaching valuable and innovative courses both locally and internationally. The courses developed would rival any top research university for their choice of modern subjects that train graduate students in contemporary research techniques. A solid and diverse set of undergraduate courses that are relevant to the Centre's mission were also taught by the platform personnel. The workshops organized are valuable at a number of levels, such as forming important new interdisciplinary collaborations, bringing in external expertise and offering valuable training opportunities for graduate students. The topics of workshops were also entirely appropriate for the kind of cross-disciplinary integration of expertise and topics that have been targeted by the platform.

Plans for years 4 and 5 of the platform are key to the success of the platform, not least because many of the collaborations that are important to the integration of mathematics, statistical physics, epidemiology and evolution are now at a point where they have data and working relationships among collaborators to address exciting questions. It would be a great loss and waste of resources expended in years 1-3 if the platform funding was to end now. While another strength of the project is the extent of funding that project personnel have attracted, it is clear that the activities that form the core of the platform require continued funding if such success is to continue in the future.

For future reports I recommend that the Centre personnel are encouraged to provide information about any press releases, media (newspaper, television, world wide web blog, etc.) coverage that the Centre and its personnel receives. Such information is useful to evaluate the public education role of a research group.

Review of the Centre for Theoretical Biology, Göteborg.

The original proposal covered a number of activities, including research focused around two broad programmes, funding of PhD students, one lecturer and one postdoc, and the organization of meetings and workshops. The overall aim was to encourage interaction between biology and mathematics. Evaluating the success of the centre is difficult because: a) the centre has changed from the one proposed in many details, but no explanation of changes has been provided; b) no actual metrics were provided originally, only the kinds of things that should be looked at, and no instructions provided to guide the review; c) in the research sections especially it is quite hard to distinguish the substantial benefits of funding for the centre from those of ongoing activity in the university departments (although page 32 is useful in this regard).

That said, the centre has been successful in promoting new interactions, generating research outputs, and providing a forum for talks and meetings. The output of papers resulting directly from Centre activities is good, and several synergistic activities have occurred. A very obvious direct benefit of the Centre is in the talks and workshops. Overall, I feel that extension is justified, but I provide the following comments in the hope that they are helpful for the review panel and the centre organizers.

1) The research programmes have changed, without obvious strategic direction and in a way that weakens the emphasis on theoretical biology. One of the programmes in the original proposal, mathematical epidemiology, remains and has achieved very strong outputs. There has been genuine interaction between disciplines and excellent publication. The other programme, models of evolutionary processes, has disappeared, to be replaced with three new fields of study, two of which are very specific and relate closely to the work of single teams within the departments. Modeling speciation in marine snails is an interesting project, and fits within the context of the original programme proposed, but it seems very specific to be one of four programmes of the Centre. Moreover, a lot of the activity is largely empirical – sure, there are some mathematical challenges with analyzing the data, and the development of new coalescent models is a good outcome - but this is not a major theoretical research programme. Similarly, phylogenetic and comparative analyses potentially could involve lots of theoretical work, but the actual work seems very focused on studies of one system – weaverbirds – and is no more mathematical than any work in this area. This project seems to be more about applying existing techniques rather than confronting new theoretical problems. I appreciate that things evolve depending on personnel and so on, but it feels like the Centre could provide a stronger, more general structuring influence for theoretical biology, rather than an umbrella for more-or-less existing activities in the departments.

2) The original application proposed appointing a lecturer, one post-doc and PhD students. For some unexplained reason, this has changed to appointing 5 post-docs and no students. In my experience, students are an excellent channel for establishing collaborations, and also the best level at which to train researchers for the interface between mathematics and biology. I'd be interested to know the

rationale for this change. By their own initial criteria for evaluation, they have failed on training centre-financed students.

3) A description of the work of each post-doc, their achievements and plans, and how that has met the centre aims would have been useful. Post-docs 1 to 3 evidently have a mathematical background, and continue to publish on non-biological subjects – is this ongoing work or are these leftovers from their previous positions? Post-doc 3 has no biological papers in press. Post-doc 4 has only one first author publication, and none in preparation. This raises concerns about the mentoring and support being given to the post-docs. Post-doc 5 is working firmly on one empirical system. Two of the post-docs are working on the same project (the snails). Overall, there is little obvious strategic direction in post-doc appointment. Productivity across the team, however, has been very good.

4) The plans for further development can be boiled down to “more of the same”, except that a call will be made for new collaborative projects. I think this is OK given the duration of the projects, but some more detail on topics for workshops over the remaining years would have been nice – some are mentioned obliquely in other sections.

5) The workshops look to have been really interesting and spot on in terms of the overall goals of the Centre. I think this is the biggest achievement and on its own merits further funding.

To conclude, the Centre has produced excellent scientific output and hosted very useful workshops and talks. It has clearly increased dialogue between biologists and mathematicians in the university, which is an important goal, and brought in excellent visitors from outside. The main weakness is the apparent lack of a strong strategic drive, especially with the post-doc recruitment and the topics of their research. There may be good reasons for how this has developed, but none were provided in the report.