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Climate change time machine

Adaptation to 30 years of warming in the Baltic Sea

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2016

ISSN 1651-6214
ISBN 978-91-554-9448-3
urn:nbn:se:uu:diva-271575

Dissertation presented at Uppsala University to be publicly examined in Lindahlsalen, Norbyvägen 18, Uppsala, Friday, 26 February 2016 at 10:15 for the degree of Doctor of Philosophy. The examination will be conducted in English. Faculty examiner: Professor Kerstin Johannesson (University of Gothenburg).

Abstract

Ermold, F. 2016. Climate change time machine. Adaptation to 30 years of warming in the Baltic Sea. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 1334. 46 pp. Uppsala: Acta Universitatis Upsaliensis. ISBN 978-91-554-9448-3.

Earth mean surface temperature has increased by 1 °C since the industrial revolution, and this has already had considerable effects on animal and plant species. Ecological responses to the warming climate – often facilitated via phenotypic plasticity – are ubiquitous. However, even though evolution can occur rapidly there are only few examples of genetic adaptation to climate change.

In my thesis, I used a near-natural system to study if and how organisms have adapted to 30 years of warming, and how this has affected competitive species interactions. I investigated Baltic Sea populations of the aquatic snails *Galba truncatula* and *Theodoxus fluviatilis,* which had been subjected to cooling water discharge from power plants, resulting in water temperatures 4 to 10 °C higher than in the surrounding sea.

G. truncatula had high upper thermal limits and large acclimation potential. This plasticity may have helped the species to survive under the new conditions, allowing evolution through natural selection to take place. I found that the populations of the two thermal origins had diverged in SNP markers associated with warmer temperature, whereas divergence in selectively neutral markers was mainly related to geographical distance. Adaptation occurred from standing genetic variation, emphasizing the importance of genetic diversity and population size in enabling the persistence of populations. Changes in thermal sensitivity of growth and survival were subtle yet significant, and complied with theoretical models of thermal adaptation in ectotherms. At the community level, pre-adaptation to warmer conditions aided the native *T. fluviatilis* when competing with the alien *Potamopyrgus antipodarum*. However, interspecific competition limited the snails most in those traits favored under warming, highlighting the challenge of adapting to different selecting forces during global change.

The persistence of species and populations under climate change depends on several factors - plasticity allowing for initial survival, evolvability in allowing the genetic changes, and species interactions affecting the new ecological niches. The results of my thesis indicate that persistence under climate change is possible when these factors align, but the relative roles of ecology and plasticity may explain why there are so few observed instances of evolution in response to climate change.

Keywords: climate change, thermal adaptation, evolution, Baltic Sea, Biotest Basin, ecological interactions, biological invasions, phenotypic plasticity

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ISSN 1651-6214
ISBN 978-91-554-9448-3
urn:nbn:se:uu:diva-271575 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-271575)

Pippi & Päron

For what are we
without hope in our hearts?
- Bruce Springsteen

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I	**Ermold, F.**, Meyer-Lucht, Y., Höglund, J. and Laurila, A. (2016) Do the (rapid) evolution: genetic differentiation after 30 years of warming. *Manuscript.*
II	**Ermold, F.**, Islam, M.T., Jokela, J. and Laurila, A. (2015) Life history evolution of *Galba truncatula* in cooling water discharge: evidence for rapid thermal adaptation? *Manuscript*.
III	**Ermold, F.**, Nannstedt, E., Johansson, M.P. and Laurila, A. (2015) Thirty years of warming has not affected preferred and critical maximum temperatures in *Galba truncatula*. *Manuscript*.
IV	**Ermold, F.** and Laurila, A. (2015) Competitive interactions in a warming world: a transplant study. *Submitted manuscript.*

The following papers were written or published during the course of my doctoral studies but are not included in this thesis.

Liess, A., Lange, K., **Schulz, F.**, Piggott, J.J., Matthaei, C.D. and Townsend, C.R. 2009. Light, nutrients and grazing interact to determine diatom species richness via changes to productivity, nutrient state and grazer activity. *Journal of Ecology*, 97(2), 326-336.

Johansson, M.P., **Ermold, F**., Kristjánsson, B.K. and Laurila, A. 2015 Population divergence in gastropod life history between contrasting thermal environments in a geothermal lake. *Submitted manuscript*.

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Abbreviations

GBS	genotyping by sequencing
CnV	countergradient variation
CoV	cogradient variation
IBD	isolation by distance
IBE	isolation by environment
IPCC	Intergovernmental Panel on Climate Change
SNP	single nucleotide polymorphism

Introduction

Since the industrial revolution and all through the past century, mean Earth surface temperature has increased by 0.06°C per decade, and this increase is projected to accelerate in the future (Collins *et al.*, 2013). Additionally, extreme weather events such as heat waves and droughts are expected to become more frequent. As temperature is a crucial abiotic factor defining ecological niches and affecting every level of organismal organization from enzymes and cells to ecological interactions and whole ecosystems (Gillooly *et al.*, 2001; Kingsolver & Huey, 2008; Angilletta, 2009), climate change will have a considerable impact on life. Already, examples of plant and animal shifting ranges towards higher altitudes and latitudes, and phenological events taking place earlier in the season are ubiquitous (Menzel *et al.*, 2006; Parmesan, 2006; Chen *et al.*, 2011).

Rapid evolution

Historically, evolution was assumed to be a slow process acting out over many generations, but recently it has been found that genetic adaptation can in fact occur rapidly and affect ecological interactions (Hendry & Kinnison, 1999; Hairston *et al.*, 2005; Carroll *et al.*, 2007; Pelletier *et al.*, 2009). Plants and animals have been shown to adapt to new biotic or abiotic environmental conditions within just a few generations (Reznick & Ghalambor, 2001). But while ecological responses to ongoing climate change have been found frequently (Parmesan, 2006), only few studies have shown genetic change in response to current climate change (Bradshaw & Holzapfel, 2008; Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014). This is partly due to the fact that until recently it has been difficult to accurately assess genetic change, and at the same time demonstrate that it is both caused by natural selection and adaptive (Merilä & Hendry, 2014).

Many of the ecological responses to climate change are facilitated by phenotypic plasticity. Phenotypic plasticity enables fast adaptation to new conditions, and may enable organisms to persist in a new environment for actual evolution to occur (Price *et al.*, 2003). However, it is itself a trait under selection and may thus evolve when the environment changes (Davis *et al.*, 2005; Donnelly *et al.*, 2012).

Genetic change in response to climate change is most often found in traits that are related to dispersal and phenology (reviewed in Reusch, 2014; Schilthuizen & Kellermann, 2014; Stoks *et al.*, 2014), and there is only one example of evolution of thermal sensitivity (in *Daphnia*, Geerts *et al.*, 2015). However, rapid evolution of thermal sensitivity has been shown in other contexts: upon introduction into new habitats or habitat changes in ectothermic vertebrates (Skelly & Freidenburg, 2000; Barrett *et al.*, 2011; Leal & Gunderson, 2012) and in selection experiments in invertebrates (Hoffmann *et al.*, 2003; Van Doorslaer *et al.*, 2007, 2010).

Evolution may occur in several ways. In situ microevolution of traits by new mutations may occur in theory, but in most species this is highly unlikely due to a combination of trait complexity, simple chance and the long generation times relative to the observed rates of environmental change. As organisms respond to the warming climate by shifting habitats towards higher latitudes and altitudes (Chen *et al.*, 2011; Sunday *et al.*, 2012), pre-adapted genotypes may “invade” and their alleles become more frequent (Davis & Shaw, 2001). The simplest and fastest solution is adaptation from standing genetic variation, when a favorable genotype is already present in the population and is then selected for by environmental change (Barrett & Schluter, 2008).

Thermal adaptation

Organisms differ in their sensitivity and responses to temperature both within and between species (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011). Given strong selection and enough genetic variation local adaption may occur (Kawecki & Ebert, 2004), which - in the context of thermal adaptation - will produce specific patterns of thermal sensitivity along thermal gradients. In ectotherms, these general patterns include shifts in performance curves with decreasing critical maximum and minimum temperatures, and decreasing thermal optima for a number of traits (reviewed in Addo-Bediako *et al.*, 2000; Angilletta, 2009; Sunday *et al.*, 2011), and wider thermal tolerance breadth at higher latitudes and altitudes (Janzen, 1967; Stevens, 1989).

Optimality models of thermal adaptation predict that an organism should reach its maximal performance at the temperatures experienced most frequently (Lynch & Gabriel, 1987; Gilchrist, 1995). However, there is little empirical evidence supporting this prediction: when the thermal optima of populations are diverging at all, they do so only to a small extent (reviewed in Angilletta, 2009). On the other hand, as thermodynamic rates increase with increasing temperature, warm-origin populations should always outperform cold-origin populations at their respective optima (the “Hotter is better” hypothesis, Kingsolver & Huey, 2008). While there is strong support for this hypothesis at the interspecific level (Angilletta *et al.*, 2010), the evidence at the intraspecific level is scanty (but see Frazier *et al.*, 2006; Knies *et al.*, 2009).

In empirical studies, the dominating pattern at the intraspecific level is countergradient variation, where the genotype and the environment counteract each other to produce highest growth rates in cold-origin populations irrespective of environment (Conover & Schultz, 1995). Countergradient variation has been found in a wide variety of ectotherm species and is especially commonly found in growth and development rates along latitudinal and altitudinal gradients (Conover *et al.*, 2009). The opposite pattern - cogradient variation - where genotype and environment act in the same direction and reinforce each other appears to be much rarer (Conover *et al.*, 2009).

Ecological responses to climate change

Ecological communities are widely affected by climate change (Walther *et al.*, 2002; Parmesan, 2006). More recently, there has been an increasing interest in how climate change affects ecological communities and species interactions, as due to the importance of temperature on living systems, climate change can be expected to have strong effects on biotic interactions and ultimately species composition of communities (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Walther, 2010). On the other hand, it is these biotic interactions that drive evolution and can thus mediate responses to climate change (Blois *et al.*, 2013; Post, 2013) – and in fact may very well be the ‘determining factor’ (Post, 2013) in how species and even whole ecosystems respond to climate change.

As responses to climate change are species-specific, species composition in natural communities will be reshuffled creating no-analogue communities in both time and space (Williams & Jackson, 2007; Urban *et al.*, 2012; Blois *et al.*, 2013). Because of their mutual dependence in complex trophic networks, the loss of a single species can cascade in multiple coextinctions or alter community structure and dynamic (Allesina & Pascual, 2009; Thierry *et al.*, 2011). Trophic interactions are especially sensitive, as top consumers tend to be more affected by changes in temperature (Voigt *et al.*, 2003), and changes in their abundance will have a disproportionate effect on the whole food web (Zarnetske *et al.*, 2012). But also competitive interactions at the same trophic level may be affected by environmental change with species that perform better at the new conditions out-competing their rivals (Davis *et al.*, 1998; Walker *et al.*, 2006; Urban *et al.*, 2012; Post, 2013). For example, zooplankton species differ in how well they track the seasonal food peak now occurring earlier, resulting in a long-term decline of the non-adapting species, while numbers of its competitor remain stable (Winder & Schindler, 2004). Studies in several systems have emphasized the role of climatic variation in determining the outcome of competition (e.g. Saetre *et al.*, 1999; Helland *et al.*, 2011; Kordas *et al.*, 2011).

The effects of climate change may be exacerbated by the appearance of novel species, either by range shifts or due to human-assisted invasions. Invasive species often have higher thermal tolerance than native species (Bates *et al.*, 2013). Climate change may thus aid alien species to survive in new habitats where they could not exist before, and allow them to become invasive, as the very traits that make species successful invaders (e.g. high plasticity, large geographic range, short generation time and effective dispersal) may help them adapt to a changing climate and environment (Dukes & Mooney, 1999; Thuiller, 2007; Hellmann *et al.*, 2008; Walther *et al.*, 2009). Consequently, alien species may be superior competitors to their native rivals by more effectively exploiting shared resources (Snyder & Evans, 2006). For example, in an experimental warming study conducted in mesocosms, invasive *Daphnia* were found to drive the native populations extinct, even in cases when the native populations were pre-adapted to warmer conditions (Van Doorslaer *et al.*, 2009).

Ecology and evolution interact, and adaptation to environmental changes by one species can have an impact on its interactions with other species with potential feedback effects across the community (Lavergne *et al.*, 2010; Norberg *et al.*, 2012).

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Aims

In a world that is changing so rapidly, it is important to understand how change affects individuals, species and ecosystems. The big question for my thesis was if, and how, organisms adapt to rapid warming and how warming affects species interactions.

I used the aquatic snail guild in the Baltic Sea as my study system. Biotest Basin, off the Baltic Sea coast in central Sweden, has been receiving most of the cooling water discharge from nearby nuclear power plants for over thirty years. As a result, water temperatures are 4 to 10 °C higher than in the surrounding sea, corresponding to more pessimistic predictions for climate warming in Scandinavia until the end of this century (Collins *et al.*, 2013).

In paper **I**, I assessed using molecular methods whether populations of the dwarf pond snail *Galba truncatula* affected by cooling water discharge have genetically diverged from unaffected control populations.

In paper **II**, I asked whether and how cold- and warm-origin populations of *G. truncatula* differed in the thermal sensitivity of traits related to life history. To answer this I conducted both a common garden experiment in the laboratory and a transplant experiment under natural conditions.

In paper **III**, I tested whether thermal performance curves, i.e. thermal optima (measured as preferred temperature) and the upper thermal limits differed between cold- and warm-origin *G. truncatula* populations, and assessed the role of acclimation.

After studying individuals and populations, I was in paper **IV** interested in how warming affects species interactions. I investigated the competitive outcome between a native species (*Theodoxus fluviatilis*) and a thermo-tolerant alien species (*Potamopyrgus antipodarum*). Additionally I wanted to know if pre-adaptation to increased temperatures gave the native species an advantage for competition.

Material & Methods

Biotest Basin

Biotest Basin (BTB) is located by the Baltic Sea coast in Forsmark in central Sweden (60°25’N, 18°11’E, see map Fig. 1). Its size is 0.9 km^2 and mean depth 2.5 m. It was built in 1980 to study the effects of warm cooling water discharge on the ecosystem of the Baltic Sea (for more information see Snoeijs & Prentice, 1989), and it receives most of the cooling water discharge from two of the three Forsmark nuclear reactors located near the basin via a tunnel under the seabed. Water temperature within the basin is 4 to 10 °C higher than in the sea outside the basin, with the largest temperature difference in winter (Fig. 2). This corresponds to the more extreme IPCC projections, which predict surface temperature increases of 8 °C until the end of this century at high northern latitudes (Collins *et al.*, 2013).

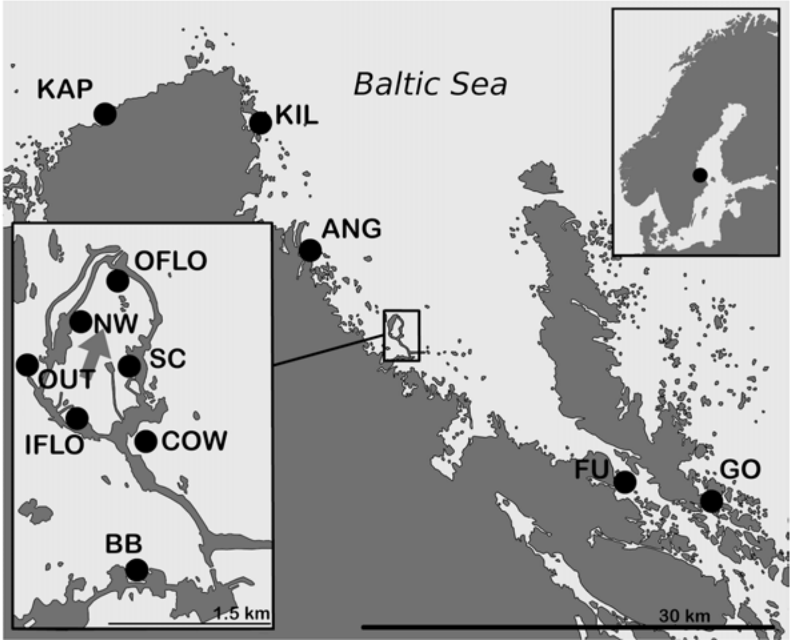

Figure 1. Map over the study area. Insert 1 Scandinavia with the approximate location of Biotest Basin, insert 2 the Biotest Basin. The four populations subjected to cooling-water discharge are Iflo, Oflo, NW and SC; all others are cold-origin control populations. The arrow denotes the direction of flow of cooling water discharge.

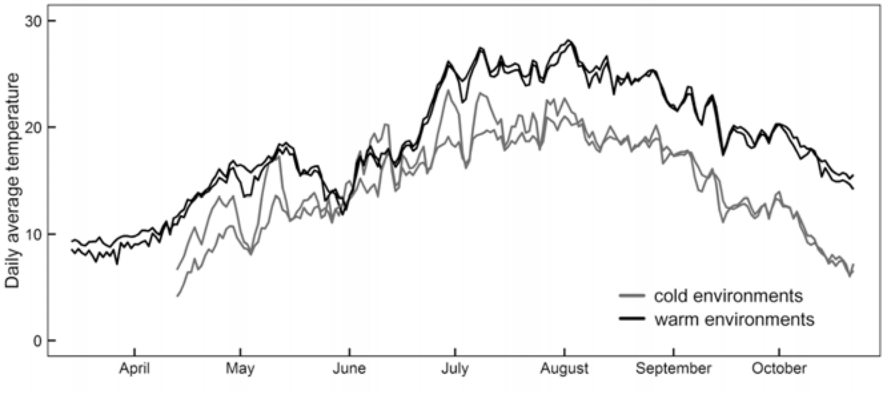

Figure 2. Daily average temperatures at two sites within Biotest Basin (black) and at two control sites close-by (grey) in 2011. During the late spring, one of the reactors was under revision and cooling water discharge limited, resulting in similar temperatures in both thermal environments.

Table 1. Overview over the location of sampling sites of *G. truncatula*. For Paper II, the first x denotes use in the common garden experiment, the second x in the transplant experiment. The sites Out and Cow (x*) were pooled.

Site	Thermal origin	Paper I	Paper II	Paper III	Coordinates
Kap	cold	x			60°34.585'N, 17°49.272'E
Kil	cold	x		x	60°33.760'N, 18°0.692'E
Ang	cold	x	x		60°29.068'N, 18°4.231'E
BB	cold	x			60°24.548'N, 18°11.571'E
Out	cold	x	x/x*	x	60°25.544'N, 18°10.731'E
Cow	cold	x	-/x*		60°25.256'N, 18°11.635'E
NW	warm	x	x/x	x	60°25.866'N, 18°11.123'E
Iflo	warm	x			60°25.336'N, 18°11.045'E
Oflo	warm	x	-/x	x	60°26.072'N, 18°11.650'E
SC	warm	x	x/x	x	60°25.582'N, 18°11.710'E
Fu	cold	x	-/x	x	60°19.076'N, 18°28.124'E
Go	cold	x	-/x	x	60°18.117'N, 18°35.627'E

Study species

Aquatic invertebrates are the perfect organisms to study thermal adaptation with. As ectotherms they have only limited possibilities to control body temperatures themselves, and thus are especially vulnerable to temperature changes. Water as a homogenous habitat offers little respite from environmental conditions.

G. truncatula (family Lymnaeidae), the dwarf pond snail, is a small (up to ca 12 mm) freshwater pulmonate snail (Fig. 3) with an almost worldwide distribution. It is native to Europe, but has spread to North and South America, Africa and Asia (Seddon *et al.*, 2015). It is found in the shallow zones of freshwater habitats including temporary habitats such as ditches and wetlands, and it is common in many brackish water habitats including the northern Baltic Sea. *G. truncatula* is hermaphroditic and preferential selfer (Trouvé *et al.*, 2003; Meunier *et al.*, 2004), however, it does not lack adaptive potential as indicated by its capacity of locally adpating to habitat heterogeneity (Chapuis *et al.*, 2007; Chapuis & Ferdy, 2012).

The river nerite *Theodoxus fluviatilis* is a freshwater snail (Fig. 3) of up to 9-10 mm length which occurs throughout Europe and is also abundant in brackish water. It is common along the coast of the Baltic Sea including the Bothnian Bay and the Åland islands (Zettler *et al.*, 2004). Compared to other freshwater snails, it has a rather slow life cycle maturing only after several months and a total life span of up to 3.5 years. It has separate sexes and females lay relatively few eggs (ca. 60 eggs per female/yr; Kirkegaard, 2006).

The New Zealand mud snail *Potamopyrgus antipodarum* (Fig. 3) is a small aquatic snail that was first found in Europe in 1859. It has high dispersal abilities and has since then become invasive in Europe, Australia and North America (Alonso & Castro-Diez, 2008, 2012). It achieves high population growth rates due to reproducing clonally and giving birth to live young, and as it can occur at extremely high densities (up to 800 000 individuals/m^2), it has become the dominant species in many native ecosystems (Alonso & Castro-Diez, 2008, 2012). *P. antipodarum* arrived to the Baltic Sea in the late 1800s, was first detected in the central Baltic in the Åland Islands in 1926, and now occurs throughout the coast of the Baltic proper (Leppäkoski & Olenin, 2000). It is very abundant in the Biotest Basin and the dominant snail species in many microhabitats, but it is more rarely found outside the basin in areas unaffected by cooling water discharge (F. Ermold, pers. obs.).

Figure 3. Snail species of Biotest Basin: *Galba truncatula* (left), *Theodoxus fluviatilis* (upper right), and *Potamopyrgus antipodarum* (lower right).

G. truncatula, T. fluviatilis and *P. antipodarum*, together with another lymnaeid *Radix balthica* make up the main snail guild of Biotest Basin. Of these only *G. truncatula* and *T. fluviatilis* appear readily also in the cooler habitats along the shore of the Baltic. Additionally, snail fauna along the coast is dominated by a third lymnaeid (possibly *Stagnicola*), and locally the ramshorn snail *Planorbis planorbis*.

Molecular genetic differentiation after rapid warming (I)

To assess genetic differentiation between *G.truncatula* populations and especially to find out whether snails in the warm Biotest Basin have diverged in molecular markers from cold populations, I sampled snails from a total of twelve sites: four populations within Biotest Basin, from four (cold) control populations close by, two sites in Gräsö (located 20 to 27 km southeast of Biotest Basin) and two sites in Hållnäs (20 to 34 km northwest of Biotest Basin, Fig. 1). DNA was extracted from the mantle following a modified high salt extraction protocol (Miller *et al.*, 1988, Rudh *et al.*, 2007).

Three Illumina 96-plex genotyping-by-sequencing libraries of 270 individuals (15 duplicated; 20-23 individuals per population) were prepared following the Genotyping-By-Sequencing protocol (GBS; Elshire *et al.*, 2011). Library preparation, genotyping and SNP calling were conducted by the BRC Genomic Diversity Facility at Cornell University, USA. Raw genetic sequences were analyzed with the UNEAK pipeline, as implemented in Tassel v3 (Glaubitz *et al.*, 2014) without a reference genome.

Due to strong geographic structure in the data set, the data was subset into a BTB set – containing the four warm sites at Biotest Basin and four (cold) control sites nearby (Fig.1, Table 1); and the complete ALL set. Both isolation by distance (i.e. populations are genetically more different as distance increases) and isolation by environment (i.e. populations become more different as difference between the environments of their habitats increase) shape population divergence. To control for that, I analyzed neutral and outlier loci separately. To identify markers under putatively divergent selection (outliers), outlier detection was run with populations as sampling units. Additional outlier detection was run for "thermal outliers" with the eight sites from the BTB set pooled according to their thermal environment (cold or warm sites, i.e. two populations). Two methods were used for outlier detection to minimize the risk of false positives (De Mita *et al.*, 2013): the hierarchical Bayesian method as implemented in BayeScan (Foll & Gaggiotti, 2008) and the Fdist approach in Lositan (Antao *et al.*, 2008).

Pairwise F_{ST} on both neutral and outlier datasets were calculated (R package diveRsity, Keenan *et al.*, 2013), and the level of genetic variation was analyzed with AMOVAs (Arlequin v 3.5.2.2, Excoffier & Lischer, 2010). Mantel tests were used to test for isolation by distance (IBD), correlating pairwise F_{ST}s with the pairwise shortest geographic distance (R package vegan, Oksanen *et al.*, 2015). Genetic clusters were identified in STRUCTURE v 2.3.4 (Pritchard *et al.*, 2000; Falush *et al.*, 2003) for all three data sets separately. For further visualization, discriminant analyses of principal components (DAPC) were run (R package adegenet, Jombart, 2008; Jombart & Ahmed, 2011).

Divergence in life history (II)

In Paper II, I studied how cold- and warm-origin populations differed in thermal sensitivity of life history traits.

Common Garden

Founding populations of ca. 50 individual *G. truncatula* were collected in September-October 2008 at two sites within Biotest Basin and at two unaffected sites in the vicinity of the Basin (Fig.1, Table 1). The snails were kept in the laboratory at 19 °C and 18L:6D photoperiod (corresponding to summer conditions) in aerated plastic tanks (27 L) containing artificial brackish water (4 ppm, AWA standard, Instant Ocean). Snails were fed a standardized mixture of spinach, fish food flakes and *Spirulina ad libitum*. Juvenile F1 and F2 snails, produced by multiple parental individuals, were moved to generation-specific tanks after reaching a transferable size.

The common garden experiment was conducted in four temperature treatments: 12, 16, 20 and 24 °C. When juvenile F2 snails approached maturation, they were placed pairwise, separated when reproduction occurred and hatchlings (F3) were then placed individually into the experiment in 0.15 L cups at the age of 14 days. From each population I used 11- 25 families (individuals in the same family were either full- or half-sibs), and on average 3 to 4 individuals per family in each temperature treatment. Survival was checked twice a week. Growth was recorded by photographing the snail against a background of millimeter paper at eight and 16 weeks and later measuring the maximum shell length using ImageJ (version 1.47v, Schneider *et al.*, 2012).

Transplant experiment

The founding *G. truncatula* populations (ca. 50 individuals in each) for the transplant experiment were collected in September-October 2011 at three sites within Biotest Basin and at three control sites (Fig. 1, Table 1). Snails were reared as described above. The transplant experiment was conducted in summer 2012 at four sites, two within the Biotest Basin and two at control sites unaffected by cooling water discharge. Each population was replicated five times at each site (120 units in total). The experimental units (hereafter cages) were modified 0.5L plastic bottles with the bottom cut off and additional holes were drilled in the sides to allow water exchange. A tile (16.5 cm^2) was placed in the bottom to aid periphyton colonization, and a mesh bag (mesh size 650 x 180 µm) was wrapped around the bottles to prevent snails from escaping and other animals from intruding. The cages were attached upright three by three to floating Styrofoam rafts (50 x 50 x 4.7 cm). Each cage was attached to the raft so that light for periphyton was available in the cages. Cages were randomly placed in each raft, and the rafts were anchored to the bottom at a depth of ca 1 m. To allow periphyton colonization, the cages were placed in the field two weeks before the start of the experiment. At the start of the experiment, three juvenile F2 snails (length 1.68 ± 0.03 (SE) mm) were placed in each cage 2 July 2012, and the experiment was run for 37 days ending 8 August 2012.The average daily temperature was 23.4 °C in BTB and 17.1 °C at a control site during the experimental period (data provided by SLU Aqua, Adill *et al.*, 2013). Snails were photographed at the beginning and end of the experiment and measured as described above. Survival of the snails until the end of the experiment was recorded.

Thermal sensitivity (III)

Another measure of thermal adaptation is an organism's optimal temperature and thermal tolerance. To measure preferred temperature (a proxy for optimal temperature) and the upper thermal limit, snails were collected at three locations affected by cooling water discharge inside Biotest Basin (Fig. 1, Table 1) and at four control sites situated from a few meters from Biotest Basin up to 26 kilometers away (Fig. 1, Table 1). To assess the effect of acclimation, I used both F1 snails raised in the laboratory and wild-caught snails that were in the laboratory for only a short time. Parental snails for the F1 generation were collected in autumn 2012 and reared as described above. F1-snails were moved to generation-specific tanks after reaching a transferable size. Wild snails were caught from the same seven populations in June 2013, and kept under the conditions above for two weeks until the experiment started.

Preferred temperature trials

The experimental temperature gradient consisted of three blocks of five channels (500 × 22 × 20 mm) cut into a single aluminium block. The channels were separated from each other by 2 mm. To construct a temperature gradient, one end of the channels was placed on a cooling plate and the other end on a heating plate, and the channels were insulated with sheets of Styrofoam. Experimental snails were fed and placed individually in cups (200 mL) one day prior to the preferred temperature trials. For each trial, one snail was put into each channel at the position corresponding to the ambient temperature (19 °C). Snail position in the channel was tracked with a camera (Canon 400D, with 18-55 mm standard zoom lens) placed above the temperature gradient and programmed to take pictures at 15 minute intervals for nine hours. The position of each snail was then tracked with ImageJ (1.47v, Schneider *et al.,* 2012), and the corresponding temperature estimated from the linear relationship between position in channel and temperature. The first four hours of each trial were disregarded as these are often influenced by acclimation temperature (Reynolds & Casterlin, 1979). Each snail was only used once in the experiment.

Critical temperature trials

After the preferred temperature trials, surviving snails were tested for their critical maximum temperature. Snails were individually placed in 50 mL Falcon tubes containing brackish water and placed in a water bath. Trials started at room temperature (19 °C), after that temperature was increased by 1 °C every 15 minutes. Critical temperature was defined as the temperature at which a snail lost attachment to the surface. The vial was then taken out of the water bath and left at room temperature to cool. I registered critical temperature, time to recovery (when the snail would regain movement) and survival.

Competition experiment (IV)

After studying how individuals and populations react to warming (Paper I-III) I was interested in how species interactions are affected, especially when a thermo-tolerant alien species is involved.

Warm-origin *Theodoxus fluviatilis* and *Potamopyrgus antipodarum* snails were collected inside the Biotest Basin in late May 2011. The cold-origin *T. fluviatilis* were collected at two sites on the Hållnäs peninsula, 18 and 32 km north of Biotest Basin (Fig. 1, Table 1). Snails were acclimatized at 19 ºC in the lab for at least three weeks prior to the start of the experiment. During acclimation, snails were maintained as described above for *G. truncatula.*

The transplant experiment included three factors: *T. fluviatilis* origin (cold- or warm-origin), thermal environment (cold and warm sites) and competition (two intraspecific or four interspecific densities). The experimental sites were inside Biotest Basin (two warm sites) and in the Baltic Sea on the other side of the Basin's embankment (two cold sites). Intraspecific competition treatments consisted of low (5 individuals) and high (10 individuals) *T. fluviatilis* density. For interspecific competition we had four treatments with five individual *T. fluviatilis* and increasing densities of *P. antipodarum* (5T: 0P (low intraspecific density), 5T:15P, 5T:30P, 5T:60P). These densities correspond to those observed in the field (F. Ermold, unpubl. data). Each treatment combination was replicated four times at each site, i.e. there were eight replicates for each thermal environment.

The same experimental units were used as in the transplant described earlier. The snails were added in the cages 18 June 2011, two weeks after the cages had been placed into the water, and the experiment was run for 37 days ending 25 July 2011. Daily average water temperatures were 24.2 °C in BTB and 19.0 °C during the experimental period.

T. fluviatilis growth per cage was measured in the same way as that of *G. truncatula* in the transplant experiment. Number of *T. fluviatilis* egg capsules was counted at the end of the experiment. *P. antipodarum* number at the end of the experiment was assessed by counting the snails in each cage from a photograph in ImageJ (version 1.47v, Schneider *et al.*, 2012) and population growth rate (λ) was determined.

Results and Discussion

Molecular genetic differentiation after rapid warming (I)

Genetic analyses show that warm-origin Biotest populations of *G. truncatula* have adapted to the new thermal conditions. Within Biotest Basin there was strong divergence in markers associated with warmer environment between warm- and cold-origin populations, to the extent that the vast majority of individuals now carry the warm instead of the original cold alleles. At the same time, these populations were very similar in neutral markers, suggesting that adaptation has occurred from standing genetic variation and not from pre-adapted migrants. Single individuals with warm genotypes were present in all cold-origin populations (Fig. 5B), i.e. genetic variation is present in all populations and if selection pressure become intense enough, natural selection is likely to make these alleles increase in frequency. Warm-origin populations were more similar to two inner archipelago populations (Gräsö; Fu and Go), which – sheltered from the cold sea water in the shallow archipelago – experience warmer temperatures, although not as warm as in the Biotest Basin.

Our results show evidence of local adaptation at a small geographic scale, even in an open system such as the sea shore (Sanford & Kelly, 2011). Most importantly, local adaptation to increased temperatures occurred rapidly by

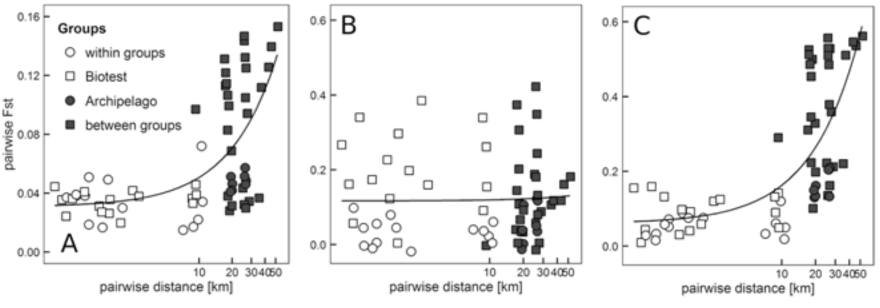

Figure 4. Genetic distance vs geographic distance for A) 1488 neutral loci, B) 5 thermal outliers, C) 9 non-thermal outliers. Within-group comparisons – empty circle; between BTB-W and BTB-C – empty square; between inner archipelago populations (BTB-W and GRAS) – filled circle; other between group comparisons – filled square.

adaptation from standing genetic variation. Evidence for genetic change in response to a warming climate is still rare (Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014), but rapid thermal adaptation has been shown in other settings – both upon the introduction into new habitats, rapid environmental change or in the laboratory (e.g. Skelly & Freidenburg, 2000; Van Doorslaer *et al.*, 2007; Barrett *et al.*, 2011).

Adaptation from standing genetic variation is the most straightforward way to adapt to changing conditions as the "new" alleles are already present in the populations (in higher frequencies as compared to novel mutations or even single dispersal events of pre-adapted genotypes) and thus less prone to disappear due to genetic drift. Moreover, they have already been "pre-tested" and shown to function (Barrett & Schluter, 2008).

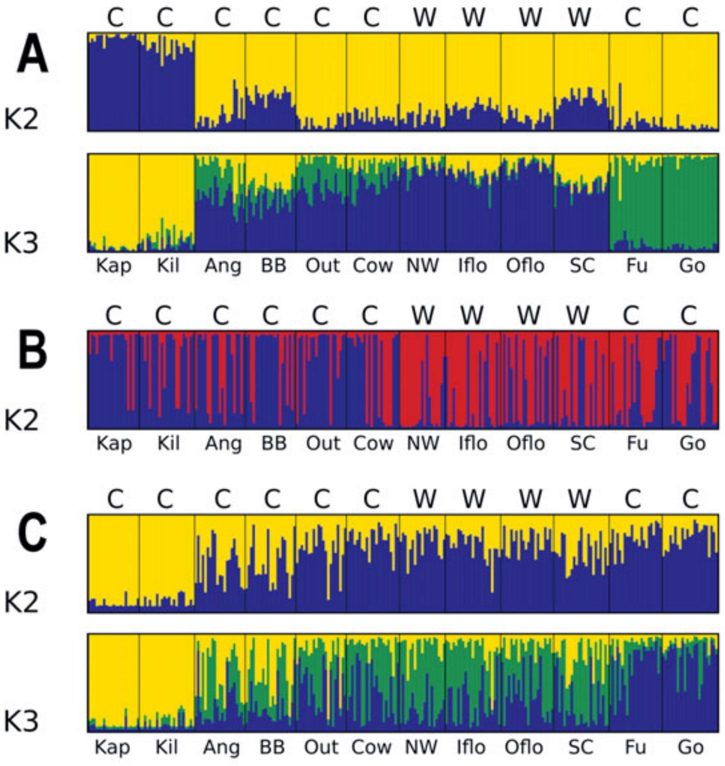

Figure 5. Cluster analysis plots from STRUCTURE runs. A) 1488 neutral loci (K=2-3), B) 5 thermal outlier loci (K=2), and C) 9 non-thermal outlier loci (K=2-3). Sites are arranged from west to east, but separated for thermal origin within the Biotest Basin.

In both neutral and non-thermal outlier markers, I found strong population divergence with isolation by distance at geographic scales of only 10 to 50 km (Fig. 4A, C). The three groups (Hållnäs, Biotest and Gräsö) clustered separately from each other (Fig. 5A, C), but within each group populations were similar suggesting gene flow occurs on that scale. Other studies found population structure of *G. truncatula* already at a much smaller scale (hundreds of meters, Trouve *et al.*, 2005), but there the habitat was more structured as well, while the Baltic is essentially open.

Divergence in life history (II)

G. truncatula populations had diverged in regard to the thermal sensitivity of growth and survival probability. In the common garden experiment, warm-origin snails survived better than cold-origin snails (Fig. 6B) at high intermediate temperature (20 °C). In the transplant experiment, cold-origin snails always grew faster than warm-origin conspecifics, indicating countergradient variation (Fig. 7A).

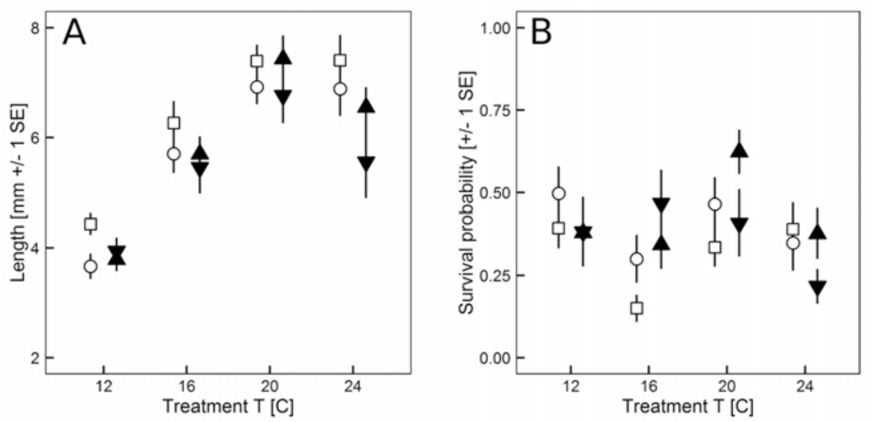

Figure 6. Common garden experiment: Size after eight weeks (A) and survival probability to 16 weeks (B). Open symbol – cold origin, filled symbol – warm origin; ANG: circle, OUT: square, SC: upward triangle, NW: downward triangle.

Survival probability in the common garden experiment follows what is expected from theoretical models, that organisms should maximize performance in those conditions they experience most frequently (Lynch & Gabriel, 1987; Gilchrist, 1995). Intriguingly, there was no divergence in growth between populations of thermal origin (Fig. 6A), even though there was considerable variation within populations and while there was counter-gradient variation in the transplant experiment. The most likely explanation is that it reflects the differences in the experimental venues, the more artificial common garden environment effectively concealing the genetic differences.

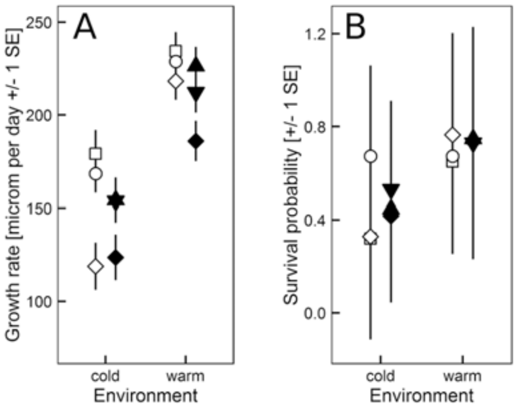

Figure 7. Transplant experiment on *G. truncatula*: Growth rate (A) and survival probability (B). Open symbol – cold origin, filled symbol – warm origin; GO: circle, FU: diamond, CO: square; SC: upward triangle, OFLO: diamond, NW: downward triangle.

Countergradient variation is commonly observed in ectotherms (Conover *et al.*, 2009), among others in marine snails (Trussell, 2000; Pardo & Johnson, 2005). It evolves especially when time constraints in cold habitats select for fast growth rates allowing fast maturation and/or higher overwinter survival (reviewed in Conover *et al.*, 2009). However, high growth rate is expected to trade-off with other fitness components such as vulnerability to natural enemies, starvation risk and various physiological costs (e.g., Dmitriew, 2011). It is likely that cold-origin populations are time-limited, while this time constraint is relaxed in Biotest Basin and selection there may have favored slower growth in these populations, possibly to avoid fitness costs associated with rapid growth.

Hence, while *G. truncatula* has large tolerance and acclimation potential enabling its persistence in a changing environment (**III**), warming has had subtle yet significant effects on thermal sensitivity of the populations.

Thermal sensitivity (III)

There was little evidence for divergence between *G. truncatula* originating from areas exposed to cooling water discharge for 30 years and those originating from the unaffected areas. Specifically, there was no divergence between the thermal origins in thermal tolerance or in preferred temperature, but cold-origin snails had larger thermal ranges and tended to visit higher upper temperatures (Fig. 8B, C). However, acclimation influenced thermal sensitivity as laboratory reared F1 snails had significantly higher upper tolerance limits than the wild-caught snails, and also tended to prefer slightly higher temperatures and reached higher upper ranges (Fig. 8).

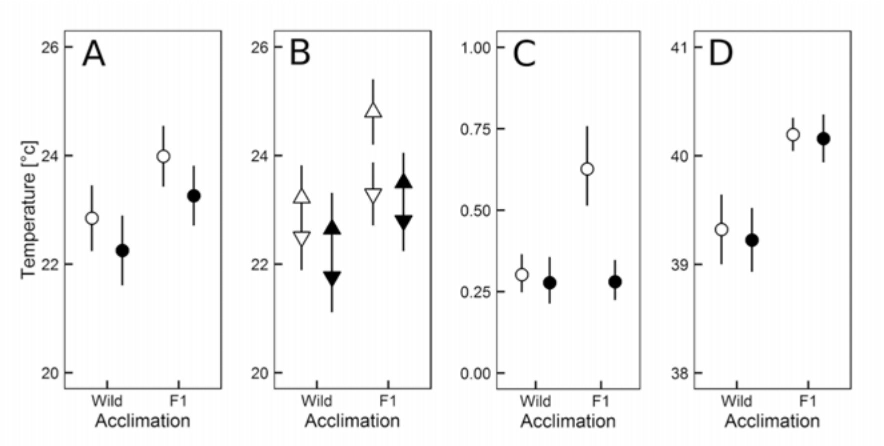

Figure 8. Mean preferred temperatures (A), maximum and minimum temperatures visited (B), thermal ranges (C) and CT_{50} (D) (± 1 SE) in the two acclimation treatments and thermal origins. Populations were pooled by thermal origin, cold-origin populations: empty symbol, warm-origin populations: filled symbol.

While populations often differ in thermal optima and tolerance (Sunday *et al.*, 2011), rapid adaptation of thermal sensitivity has been found only in a few cases in natural systems. In Biotest Basin, summer water temperatures are increased by 4-5 °C, with maximum temperatures just below 30 °C. These temperatures are well below the CT_{50}s at 39-40 °C measured in this study, and are likely to pose only a very weak selection pressure. The preferred temperature was near, but slightly higher, than the optimal temperature measured for growth and survival (20 °C in Paper II), which may be a temporary choice to maximize growth. As cold populations experience a more variable climate in nature, they should have wider thermal tolerance breadth (Janzen, 1967; Stevens, 1989), and this is reflected to the larger range of visited temperatures in this experiment.

Instead of local adaptation, I found a strong effect of acclimation, with laboratory - reared F1 *G. truncatula* having higher critical and preferred temperatures. Acclimation enables organisms to increase performance under changed environmental conditions, although perfect acclimation with similar performances at old and new conditions is rare. A positive effect of acclimation on thermal limits has been found in many systems (reviewed in Angilletta, 2009), while its effect on preferred temperatures (and optima) is, as in our study, less comprehensive.

These results suggest that the acclimation ability of *G. truncatula* is large and helps buffer against effects of climate change, emphasizing the role of phenotypic plasticity in adaptation to climate change (Merilä & Hendry, 2014).

Competition in a warming world (IV)

While temperature generally had a positive effect on individual growth rates, cold-origin *T. fluviatilis* grew faster than warm-origin snails in all thermal environments, whereas warm-origin snails matured at smaller size and laid more eggs. These results suggest countergradient variation in growth and, at the same time, smaller size at maturation and higher reproductive effort in warm-origin snails. Competition by the alien *P. antipodarum* decreased individual growth rate and reproduction of native *T. fluviatilis* (Fig. 9A, B), however, this effect was largely independent of temperature.

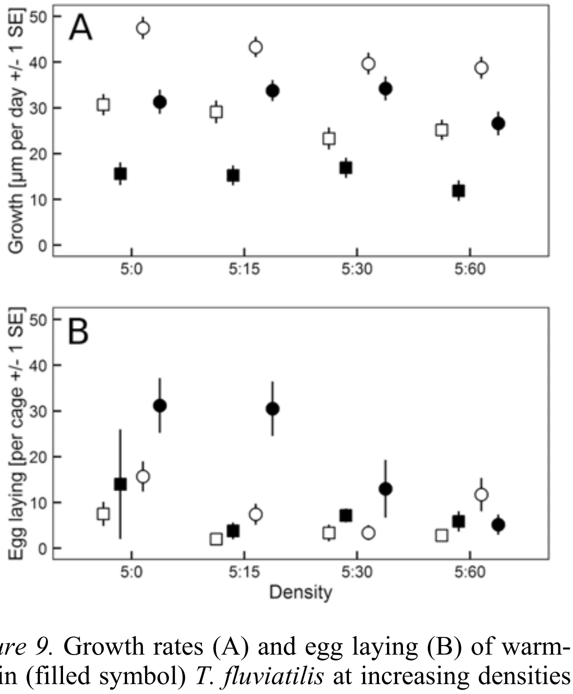

Figure 9. Growth rates (A) and egg laying (B) of warm- (empty symbol) and cold-origin (filled symbol) *T. fluviatilis* at increasing densities of *P. antipodarum*, and in two thermal environments (cold – square; warm – circle). For egg laying, cages without mature snails were disregarded.

Reproduction was, nevertheless, especially negatively affected in the warm origin snails in the warm environment where *T. fluviatilis* reproduction was highest. The alien *P. antipodarum*, while being negatively affected by its own density, had high population growth rates in all treatment combinations, and especially so in the warm environment.

These results agree with previous studies demonstrating negative effects of *P. antipodarum* on native snail communities, and suggest that these effects are likely to become stronger with increasing temperatures. As the climate warms, *P. antipodarum* as a pre-adapted species gains an advantage over the native species (Alexander *et al.*, 2015), and may become invasive – due to its high population growth rates – throughout the Baltic Sea.

The growth rates of cold-origin *T. fluviatilis* tended to decrease more than growth rates of warm-origin *T. fluviatilis* at intermediate densities of *P. antipodarum.* Also, while *P. antipodarum* decreased fecundity of the warm origin snails disproportionally, it still remained higher than that of cold-origin snails at these densities. This suggests that warm-origin *T. fluviatilis* may tolerate *P. antipodarum* competition better than cold-origin conspecifics, at least at low and intermediate densities. Similar results come from *Daphnia*, where (experimentally) warm-adapted populations were more successful than non-adapted populations when competing with a southern genotype (Van Doorslaer *et al.*, 2009).

It has been suggested that biodiversity and competition may hinder adaptation to changing conditions, as in communities with several species the presence of preadapted species restricts the potential for adaptive evolution in the other species (de Mazancourt *et al.*, 2008). When competing with *P. antipodarum*, values in the adaptive traits of *T. fluviatilis* (growth in cold-origin snails, reproduction in warm-origin snails) decreased disproportionately, most likely complicating its adaptation to the thermal environment. This highlights the problem of adapting to several – potentially opposing – selection pressures at the same time, resulting in trade-offs and mal-adapted phenotypes. Nevertheless, as we found evidence for divergence between warm- and cold origin *T. fluviatilis*, and as the species co-occur within the basin, it seems that there is enough niche separation between them to allow for phenotypic divergence and coexistence.

Conclusions

30 years of experimental warming have affected my study species at many levels: At the molecular level, where populations affected by warm water discharge have diverged in markers associated with thermal environment; at the individual and population levels, where populations have diverged in the thermal sensitivity of life history traits; and at a community level where an alien species has become invasive but where adaptation may have aided a native species to persist.

When quantifying the role of plasticity and evolution for climate change adaptation, plastic responses appear more common (Reale *et al.*, 2003; Merilä & Hendry, 2014). In the Biotest Basin, *G. truncatula* had high upper thermal limits and a large acclimation potential (**III**). This plasticity may have helped it to survive under the new conditions, so that evolution through natural selection could take place (Price *et al.*, 2003). This occurred over the course of 30 years, as could be shown at the molecular level (**I**) and by finding population divergence in the thermal sensitivity of life history traits (**II, IV**). The changes in thermal sensitivity of growth and survival were subtle yet significant, and complied with theoretical models of population differentiation in ectotherms. This suggests that the genetic change is adaptive. Snail populations evolved through adaptation from standing genetic variation (**I**), showing how important genetic diversity and population size are to enable populations to persist under environmental change.

Ecology and evolution interact and may feed back on each other (Lavergne *et al.*, 2010; Norberg *et al.*, 2012): evolution affects populations and individual trait values, and thus the interaction between species, while species interactions themselves affect the evolution and evolutionary potential of populations in many ways. I found that pre-adaptation to warmer conditions aids the native *T. fluviatilis* when competing with the alien *P. antipodarum* (**IV**). But competition limited the snails most in those traits that were favored under warming, highlighting the challenge of having to adapt to different selecting forces during global change. *P. antipodarum* had extremely high population growth rates under warm conditions, possibly allowing it to become invasive throughout the Baltic Sea as warming increases further. Both models (de Mazancourt *et al.*, 2008) and the historical record (Jackson & Blois, 2015) suggest that species sorting may be the main response to environmental change. In Biotest

Basin, the snail community differs markedly between warm and cold sites, with only *G. truncatula* and *T. fluviatilis* being abundant in both thermal environments.

The responses of species and populations to climate change depend on many factors - on their plasticity in initial survival, on their evolvability in obtaining the required genetic changes, and – both first and last - on species interactions who determine the new ecological niches and who feedback on species' evolutionary potential. I have shown in this thesis that persistence is possible when these factors align. Yet the relative roles of species sorting and plasticity, also in this system, may explain why there are so few examples of evolution in response to climate change.

How the future will look like especially in the Baltic Sea, with its isolation, low biodiversity and genetic diversity (Johannesson *et al.*, 2011) – and worldwide, considering that climate change is only one aspect of the global change, remains to be seen.

Svensk sammanfattning

Jordens genomsnittstemperatur har stigit med nästan 1 grad sedan den industriella revolutionen, och alla modeller är eniga om att denna temperaturökning kommer att fortsätta och accelera. Eftersom temperatur är en viktig abiotisk faktor som påverkar biologiska system på alla nivåer – från celler till hela ekosystem, kan man förvänta sig omfattande konsekvenser. Redan nu flyttar många djur och växter mot högre breddgrader och altituder och fenologiska händelser såsom äggläggning och bladsprickning sker tidigare på året.

Historiskt sett har evolutionen antagits vara en långsam process där förändring sker över många generationer, men nyligen har det visat sig att genetisk anpassning i själva verket kan ske snabbt och påverka ekologiska interaktioner. Växter och djur kan anpassa sig till nya biotiska eller abiotiska miljöförhållanden inom bara några generationer. Men medan många studier har visat på ekologiska förändringar som svar på de pågående klimatförändringarna har endast ett fåtal studier kunnat påvisa genetisk förändring som konsekvens. Istället möts många av de ekologiska förändringarna genom fenotypisk plasticitet. Fenotypisk plasticitet möjliggör snabb anpassning till nya förhållanden och kan göra det möjligt för organismer att klara en förändrad miljö så att faktisk evolution kan ske. Fenotypisk plasticitet är dock i sig ett drag under selektion och kan således evolvera när miljön förändras.

Organismers känslighet för och svar på temperatur skiljer sig både inom och mellan arter. Till exempel har populationer från en varmare miljö, enligt teorin, ett högre optimal levnadstemperatur och värmetålighet än populationer av samma art från en kallare miljö. Då svar på klimatförändringarna är artspecifika, kan det förväntas att uppvärmningen har starka effekter på biotiska interaktioner och i förlängningen även artsammansättningen i samhällen. Till exempel, om en art dör ut (lokalt), kan det leda till att fler arter dör ut på grund av det ömsesidiga beroendet i näringsväven. Dessutom samverkar evolution och ekologi, då en arts anpassningar kan påverka dess interaktioner med andra arter, men även då interaktionerna påverkar en enskild arts möjlighet att evolvera.

I den här avhandlingen ville jag undersöka om och hur arter kan anpassa sig vid snabb uppvärmning, specifikt huruvida det leder till förändringar på en genetisk nivå (**I**), på deras temperaturkänslighet (**II** & **III**), och slutligen hur konkurrens mellan två arter påverkas (**IV**).

Som försöksområde valde jag ett 1 km^2 invallat område längs Östersjökusten i Uppland kallat Biotestsjön. Biotestsjön är recipient för kylvattenutsläpp från de närliggande kärnkraftreaktorerna i Forsmark. Kylvattenutsläppet har höjt vattentemperaturen med 4 till 10 grader i över trettio år. Som försöksdjur valde jag akvatiska snäckor – den amfibiska dammsnäckan *Galba truncatula* (**I-III**) och båtsnäckan *Theodoxus fluviatilis* (**IV**). Precis som alla ektoterma djur har de bara en begränsad möjlighet att kontrollera sin kroppstemperatur, vilken därför följer omgivningstemperaturen.

Jag fann att Biotestsjöns varmvattenpopulationer av *G. truncatula* har förändringar i genetiska markörer som troligen är relaterade till temperatur och att de i dessa markörer har blivit mer lika snäckpopulationer från varmare habitat inom skärgården (**I**). Analysen av neutrala markörer visade dock att anpassningen måste ha skett inom Biotestsjön själv, dvs utifrån befintlig genetisk variation, och inte genom immigration från varmare områden.

I ett laboratorieexperiment födde jag upp snäckor från populationer från varma och kalla områden vid olika temperaturer (**II**). Det fanns små skillnader i överlevnad – dvs att snäckor från varma populationer överlevde bättre under varma temperaturer än de från kalla områden. I det här experimentet fanns det ingen skillnad i tillväxthastighet mellan snäckor från kalla och varma områden, däremot hittades skillnader vid ett transplantexperiment under naturliga förhållanden. Där växte snäckor med kallt ursprung snabbare än ”varma” snäckor, och det i både kalla och varma områden. Det är ett klassisk mönster hos ektotermer, så kallad countergradient variation, som troligen beror på att djur från kalla områden med kort tillväxtsäsong behöver evolvera för snabb tillväxt.

I ett annat experiment (**III**) testade jag temperaturtolerans och föredragen temperatur (som en proxy för optimaltemperatur), med hänsyn till acklimatisering. Det fanns ingen skillnad mellan populationerna, men det visade sig att dessa snäckor har en generell hög temperaturtolerans och stor acklimatiseringspotential, då det fanns en signifikant effekt av acklimatiserungstemperatur: varm-acklimatiserade snäckor hade både högre temperaturtolerans och föredragen temperatur.

Jag undersökte om temperatur och anpassning mot varmare temperatur påverkar konkurrens mellan två snäckarter (**IV**) – en inhemsk art, båtsnäckan, och en ny främmande art (alien species) med stor potential att bli invasiv, den nyzeeländska tusensnäckan *Potamopyrgus antipodarum*. Båda snäckarterna växte bra under varma förhållanden, men speciellt *P. antipodarum* hade otroligt högt populationstillväxt vilket antyder att arten kan bli invasiv i hela Östersjön när klimatet blir varmare. Förekomsten av *P. antipodarum* begränsade den inhemska arten, och gjorde det speciellt i de egenskaper som gynnas under varma förhållanden. Intressant var att snäckor från ”varma” populationer var mindre påverkade av *P. antipodarum* än de från ”kalla” popuationer.

I den här avhandingen visas belägg för snabba genetiska förändringar som svar på stigande temperaturer i ett naturligt system. I andra studier har man visat på att plasticitet är det övervägande sättet att anpassa sig till klimatförändringen. *G. truncatula* har stor tolerans och plasticitet, dvs hög acklimatiseringsförmågan, detta kan ha hjälpt arten att överleva den första tiden efter att kylvattenutsläppet började, och gjorde det möjligt för egentlig evolution att inträffa. Den genetiska förändringen utgick från befintlig genetisk variation (standing genetic variation), vilket understryker hur viktig genetiskt diversitet är. En tillräcklig stor och genetiskt divers population möjliggör att arter och populationer överlever när omvärlden förändras. Även om anpassningar kan ske så kompliceras det när man blandar in artinteraktioner, som framtvingar en anpassning mot olika selektionstryck, vilket är förväntat under Global Change. Både modeller och historiska data tyder på att förändringar i artsammansättning är en trolig effekt av ett förändrat klimat. Snäcksamhället skiljer sig mycket mellan Biotestsjön och de närliggande, kalla områden, och *G. truncatula* och *T. fluviatilis* är de enda arter som förkommer i tillräckligt stor omfattning i båda miljöerna, som tyder på att just det har hänt här.

Huruvida populationer kan överleva klimatförändringar beror på många faktorer – deras fysiska gränser och plasticitet för att överleva (om så bara till en början), deras evolutionsförmåga och på interaktionerna mellan arter som resulterar i nya nischer och återkoppling till artens evolutionsförmåga. Att det är möjligt att överleva visar *G. truncatula* i Biotestsjön. Men hur framtiden ser ut både i Östersjön och i världen återstår att se, speciellt då man betänker att klimatförändringen bara är en aspekt av global change.

Edited and additional translation by Joel Berglund and Eva Olsson.

Deutsche Zusammenfassung

Seit der industriellen Revolution ist die Durchschnittstemperatur der Erde um etwa 1 Grad Celsius gestiegen, und dieser Anstieg wird sich noch weiter beschleunigen. Da Temperatur ein wichtiger abiotischer Faktor ist, der biologische Systeme auf allen Ebenen beeinflusst – von den Vorgängen in einzelnen Zellen bis hin zu ganzen Ökosystemen – kann man sich vorstellen, dass ein Temperaturanstieg große Auswirkungen haben wird. Schon jetzt verlagern viele Tiere und Pflanzen ihre Lebensräume polwärts, und an Jahreszeiten gebundene Ereignissen, wie das Eierlegen von Vögeln oder das erste Blühen im Frühjahr, geschehen immer zeitiger im Jahr.

Historisch hat man angenommen, dass Evolution nur sehr langsam vor sich geht, über Zeiträume von vielen Hunderten von Generationen. Inzwischen weiss man jedoch, dass sich Populationen sehr schnell an neue Bedingungen anpassen können, etwa bei Umweltveränderungen. Aber während ökologische Veränderungen als Antwort auf den Klimawandel häufig gefunden wurden, konnten nur selten genetische Änderungen (d.h. Evolution) nachgewiesen werden. Statt dessen sind viele der beobachteten Veränderungen auf phänotypische Plastizität zurückzuführen. Plastizität erlaubt es, sich schnell an eine neue Umwelt anzupassen, und kann es Tieren und Pflanzen ermöglichen, zu überleben, bis evolutionärer Wandel stattfindet. Allerdings ist die Plastizität selbst nur eine Eigenschaft, die der Evolution unterliegt, und wird sich auch anpassen müssen, wenn sich die Umwelt verändert.

Tiere und Pflanzen unterscheiden sich hinsichtlich ihrer Temperatursensibilität sowohl auf einem individuellen Niveau, als auch zwischen Populationen und Spezies. So variieren zum Beispiel die Temperaturoptima und -grenzen mit der Umwelttemperatur, d.h. Individuen aus den gemäßigten Zonen ertragen weniger hohe Temperaturen als Individuen aus wärmeren Zonen. Da Temperatursensibilität und die mögliche Anpassungen an den Klimawandel für jede Art individuell sind, wird dies auch die Interaktionen zwischen den Arten beeinflussen, und schließlich auch die Artzusammensetzung. Wenn zum Beispiel eine Art lokal ausstirbt, kann dies weiteres Artensterben auslösen. Außerdem beeinflussen sich Evolution und Ökologie gegenseitig, wodurch die Anpassung einer Art deren Interaktionen mit anderen Arten verändern kann, aber ebenso auch die Interaktionen zwischen Arten die Möglichkeiten beeinflussen, inwiefern Arten sich anpassen können.

In meiner Dissertation wollte ich herausfinden, ob sich Arten an schnelle Erwärmung anpassen können. Mich interessierte dabei speziell, ob dies sich auf die genetische Zusammensetzung von Arten auswirkt (**I**), ob sich die Temperatursensibilität verändert (**II** und **III**) und inwiefern dies die Interaktion zwischen zwei konkurrierenden Arten beeinflusst (**IV**).

Ich nutzte dafür ein System, das seit 30 Jahren durch Warmwassereinleitung beeinflusst ist, wodurch sich die Wassertemperatur um 4 bis 10 Grad Celsius erhöht hat. Dies entspricht etwa den pessimistischeren Klimawandelprognosen für Skandinavien bis zum Ende dieses Jahrhunderts. Der Biotestsee ist ein etwa 1km^2 großer See an der Ostseeküste in Mittelschweden in den das aufgewärmte Kühlwasser der nahegelegenen Kernkraftwerke von Forsmark geleitet wird. Er ist durch Inseln und aufgeschüttete Dämme von der restlichen Ostsee getrennt, und wurde 1980 dafür gebaut, um den Effekt von Kühlwassereinleitung zu erforschen. Als Versuchstiere nutzte ich verschiedene Arten von aquatischen Schnecken, hauptsächlich die kleine Sumpfschnecke (*Galba truncatula*, **I-III**) und die Kahnschnecke (*Theodoxus fluviatilis*, **IV**). Diese sind besonders gut geeignet, um den Einfluss von Temperaturveränderungen zu untersuchen, da sie wie alle ektothermen Organismen ihre Körpertemperatur kaum selbst kontrollieren können, sondern diese von der Umwelt bestimmt wird.

In einer genetischen Studie mit SNP-Markern (**I**) habe ich herausgefunden, dass Schnecken aus dem warmen Biotestsee inzwischen in divergenten Markern, die mit Temperatur in Zusammenhang stehen, Allele aufweisen, die bei Schnecken aus wärmeren Gebieten typisch sind. Analysen der neutralen Marker zeigten, dass diese Anpassung im Biotestsee selbst stattgefunden haben muss, d.h. durch standing gentic variation, und nicht durch Immigration von schon angepassten Individuen.

Im Labor habe ich Nachkommen von warmen Populationen aus dem Biotestsee und von kalten Kontrollpopulationen aus dem natürlichen Umfeld bei verschiedenen Temperaturen (12 bis 24 Grad) gehalten (**II**) und herausgefunden, dass Schnecken der warmen Populationen eine höhere Überlebensrate unter wärmeren Bedingungen haben als die der kalten Populationen. Während in diesem Experiment die Wachstumsraten zwischen den Populationen unverändert blieben, zeigten die selben Schnecken in einem zusätzlichen Transplantationsexperiment unter natürlichen Bedingungen, ein klassisches Muster, was von vielen ektothermen Tieren bekannt ist: Nachkommen der kalten Populationen wuchsen schneller als die der warmen unter beiden Temperaturbedingungen. Diese sogenannte countergradient variation kommt wahrscheinlich daher, dass Tiere in kalten Regionen nur kurze alljährliche Wachstumsperioden haben und dadurch schnelleres Wachstum selektiert wird.

In einem weiteren Experiment testete ich die Hitzetoleranz und die bevorzugte Temperatur (als Proxy für die Optimaltemperatur) von Schnecken aus kalten und warmen Populationen unter besonderer Berücksichtigung der Akklimatisierung (**III**). Es zeigte sich, dass es keine Unterschiede zwischen den thermischen Ursprüngen gab, aber dass die Akklimatisierungstemperatur eine große Rolle spielte. So tolerierten und präferierten die im Labor gezogenen Schnecken höhere Temperaturen als die Schnecken, die erst kurz zuvor direkt aus dem kühleren See geholt wurden.

Schließlich untersuchte ich, inwiefern Temperatur den Wettbewerb zwischen einer heimischen (*T. fluviatilis*) und einer eingeschleppten, potentiellen invasiven Art (*Potamopyrgus antipodarum*) beeinflusst. Auf beide Schnecken hatte das warme Klima einen positiven Einfluss, doch speziell *P. antipodarum* hatte ein extrem hohes Populationswachstum, was nahelegt dass diese Art in der Ostsee invasiv werden könnte, wenn die Temperaturen weiter steigen. *P. antipodarum* hatte einen negativen Einfluss auf die heimische Art, besonders auf jene Eigenschaften, die im Warmen begünstigt werden. Interessanterweise waren Schnecken mit einem warmen Ursprung weniger beeinträchtigt durch *P. antipodarum* als Schnecken von kalten Populationen.

In dieser Dissertation habe ich Hinweise auf schnelle genetische Anpassung an einen Temperaturanstieg in einem naturnahen System gefunden. Anderen Studien haben gezeigt, dass Plastizität die vorherrschende Methode zur Anpassung ist. *G. truncatula* hat sowohl eine hohe Temperaturtoleranz als auch eine große Plastizität, d.h. großes Akklimatisierungsvermögen, und dies kann der Art anfänglich geholfen haben, die Temperaturveränderung zu überstehen, bevor Evolution stattfinden konnte. Die genetische Veränderung geschah durch Anpassung von standing genetic variation, was verdeutlicht wie wichtig genetische Diversität und eine ausreichende Populationsgröße ist, damit Arten angesichts von Umweltveränderungen fortbestehen können. Doch auch wenn Arten sich prinzipiell anpassen können, wird dies verkompliziert, wenn andere Faktoren wie z. B. Konkurrenz mit anderen Arten auftreten. Dies verdeutlicht, welche Herausforderung es ist, sich Selektionsdruck in verschiedene Richtungen anzupassen.

Sowohl Modelle als auch Daten von historischen Klimawechseln zeigen, dass Umweltveränderungen sehr oft zu Änderungen der Artzusammensetzung führen. Die Schneckengemeinschaften sind sehr unterschiedlich zwischen Biotestsee und den kalten, ursprünglichen Gebieten, *G. truncatula*, und *T. fluviatilis* sind die einzigen beiden Arten die in ernstzunehmenden Umfang in beiden Gebieten vorkommen.

Ob Populationen trotz Klimawandel weiter bestehen können, hängt von vielen Faktoren ab – von ihren physischen Grenzen und ihrer Plastizität, von ihrem evolutionären Anpassungsvermögen (evolvability) und natürlich von den Interaktionen zwischen Arten, die die neuen ökologischen Nischen festlegen und zum Anpassungsvermögen rückkoppeln. Dass dies insgesamt möglich ist, zeigt diese Studie an *G. truncatula* am Biotestsee. Aber wie die Zukunft in der Ostsee und weltweit aussieht, besonders wenn man bedenkt dass Klimawandel nur ein Teil des Global Change ist, bleibt abzuwarten.

Edited by Anne Schulz and Matthias Schulz.

Acknowledgements

When I look at my calendar – or that big pile of study plans on my desk – I realize I have spent more than seven years here at EBC while working on my thesis. This is mainly for two reasons (see last paragraph), but anyway, that's a long time. And I think it was a good time, I got to do science stuff (yey!), meet many wonderful people, learn a lot and grow a lot, and anyway… There are many people that have helped me along the way and made those years special.

At first I want to thank my supervisor Anssi, for taking me on as a PhD student and giving me the opportunity to overcome my phobia of snails, and especially – of course – for the opportunity to (learn to) do research. Thanks for giving me freedom and letting me make mistakes, for all your help and support. Thanks for all the discussions (science and not so science-y), for always having an open door, for telling me about all your travels when I was stuck in Sweden, and for helping collect snails in Forsmark (twice! – or was it just an excuse to go birdwatching?).

Thanks also to my second supervisor Jukka at EAWAG, who being the 100% opposite of Anssi (while still being Finnish) made for an interesting comparison. Being a snail guru, he was crucial in getting me started and my project off the ground when starting a snail project from scratch turned out to be not as easy as anticipated. But it looks like it actually worked out in the end!

And finally Jacob, who helped me quite a bit during the last couple of weeks with the genetics paper and whose positive optimistic outlook was much appreciated.

Big thanks also to Magnus, who being the sole other member of The Snail Group made life and science with snails bearable (water changes…) and sometimes actually fun (field trips!). Thanks for taking me on that crazy trip to Iceland, getting me (somewhat) interested in birds, and teaching me a thing or twenty about the work-life-balance. And you still owe me a puffin!

Thanks to Teija and Magnus at SLU Aqua and to Vattenfall in Forsmark for access to the megawatt thermal lab, a.k.a. Biotest Basin.

Thanks to all the people, past and present at EBC, who made life (Marianne!), lab work (and not just lab work!, Gunilla and Reija), and field experiments (Erik and Stefan) possible.

A number of people helped me with my experiments – Elin, Elaine, Rado and especially Tarik who suffered with me through weeks (months?) of common garden experiment. Thanks!

The frog group adopted me even though I had the "wrong" study species and then let me annex the basement lab: Björn (who always had time for stats questions), Emma, German and Alex (reading my manuscripts and having so many creative ideas…), Sandra and Katja – used to be the first signs of spring, and nowadays Sara, Maria and Patrik (who also helped with genetics…).

Thanks to all the people that made life in Uppsala so special. Ana, with whom I shared an office when I first started, Jonathan (living my childhood dream) who was always up for crazy philosophical/political/science discussions, Kasia for the time on Öland and for being so optimistic and inspiring, Jenny, Biao and Caro – I really should have come to Costa Rica with you guys! My roommates who regularly provided much needed distraction from work - Jenny, Emma, Joana, Niclas, Sara, Jono, and Tuuli, David and especially the fishies. Yvonne, with whom I shared many between-door-discussion, mostly on babies though; who was my guiding light doing the genetics, and for whom literally no question was stupid enough (or at least she didn't show it!). The veterans of old PopBio – Tanja, Thomas, Peter, Maria and Örjan (who helped with the temperature data). My climbing buddy Axel, Warren (one day we'll fix that play date for Z & A), Katja, Rado, Lara, Leanne, Mirjam, Karo, Murielle, Tom, the coffee club, Kevin, David O, David B, David Å, Masahito, Will, Mattias, Karl, Elisabeth, Brian, Eryn, Johanna, Gowri, Ivain, Paula and everybody that I (surely) have forgotten.

Thanks to Sophie, Bill, Frank, Fredrik and Martin for letting me teach and to my fellow teaching assistants Camille (Erken is just not the same without you), Warren, Andres, Ioana, Kerri, Stina, Anders and of course Peter.

It may be hard to imagine, but actually there is life outside EBC. Thanks to the Blodstensvägen people, past and present, and especially to Joel and Eva (for being generally awesome, and additionally for fixing my Swedish sammanfattning). Incidentally most of these people are biologists as well, what does this say about us?

My other family – a.k.a. the bestest parents in law ever! Danke Conni und Thilo für all eure Unterstützung in den letzten Jahren und euer Vertrauen (letzte Hoffnung?) darin dass das mit der Uni schon noch irgendwie mal was wird... Ohne euch hätte ich die (vor)letzte heisse Phase nicht gepackt – Danke für die beständige Versorgung mit Kaffee, Schoki und vor allem die fantastische Kinderbetreuung in DD (und Uppsala)!

My family – Ben, Anne, Matthias and especially Omi… Ihr habt ganz am Anfang mein Interesse fuer „Draussen“ geweckt, in den langen Sommern und Wintern in Altenberg, und an den Warumfragen. Danke dass ihr meinen Kinderwunsch „Naturerforscher“ zu werden unterstützt habt, auch wenn ihr manchmal nur schwer nachvollziehen konntet warum meine jahrelange Beschäftigung mit allerhand Wassergetier jetzt relevant sein soll. Danke Mom für’s professionelle Schneckenfangen und euch für die deutsche Uebersetzung.

Matti, seriously, what can I say? Ich bin so froh dich gefunden zu haben (oder du mich?), du bist wirklich the one, nicht nur weil du so furchtbar praktisch bist beim Schneckenfangen, sondern weil du immer an mich geglaubt hast wenn ich eigentlich hinschmeissen und besagten Waldkindergarten aufmachen wollte... – und das nicht nur beim thesis writing. Danke fuer all die Unterstützung – eben beim Schneckenfangen aber vor allem auch in den letzten Wochen wo du hier Zuhause alles gemanagt hast so dass ich nur noch schreiben brauchte. Du bist für mich damals an’s Ende der Welt geflogen und ein paar Wochen später standen wir mit zwei Fahrrädern und zwei Rucksäcken am Bahnhof in Uppsala. Seitdem ist ganz schön viel passiert, und ich freu mich schon auf die nächsten Jahrzehnte mit dir!

Marit and Aron, my two thesis babies, mina älskade, meine Schnuffis… Ihr seid meine Liebsten und das absolut wichtigste auf der Welt fuer mich. Danke dass ihr die Dinge immer wieder in Perspektive rückt, manchmal vergesse ich was wirklich zählt. Danke dass ihr so verdammt toll und lustig und verrückt und liebevoll seid, und so viel Geduld mit mir habt. Seit Monaten fragt ihr wann ich endlich mal mit dieser nervigen Doktorarbeit fertig bin, und immer wieder musste ich euch vertrösten. Aber jetzt! „Mamma Doktor fertig?!?“ – Fast. Und ab heute habe ich endlich wieder Zeit zum Spielen!

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