Impact of climate change on freshwater snail species' ranges

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How poor are they that have no patience […]
Thou know’st we work by wit, and not by witchcraft
And wit depends on dilatory time
Othello, W. Shakespeare

For my mum
Time has come to thank you for telling us “mice tales” where everything was possible!

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General Introduction

What exactly determines the range boundaries of a species is a question that has kept biologists busy ever since Wallace wrote his *Geographical distribution of animals* (1876): Why is a beetle species found on this beech tree but not on the next one? Why did this snail settled in this lake and not the neighbouring ditch? In the context of global change, it is particularly relevant to better know the processes determining species ranges. Human activities are responsible for habitat fragmentation and the resulting barriers to gene flow among populations. On the contrary, global trade is enhancing the dispersal of some organisms. Finally, increasing levels of greenhouse gases are causing worldwide climatic changes.

Species ranges

The range of a species can be defined as the area where stably reproducing populations are found (Gaston, 1996). Ecological factors as well historical factors shape the range of a species. Two conditions are fulfilled in this area: (1) abiotic and biotic conditions match the fundamental ecological requirements (niche, Hutchinson, 1957), so that populations can survive and reproduce successfully and (2) the species was actually able to reach this region during its life-history (Holt, 2003). The biotic conditions encompass the intrinsic physiological and ecological characteristics of the organism itself as well as the interactions with other organisms, among others predation, competition and parasitism.

In the face of environmental change, populations can avoid declining in three ways: be plastic, move, or evolve (Jackson & Overpeck, 2000). Three processes thus govern the species range dynamics: phenotypic plasticity, adaptation and dispersal. The intrinsic phenotypic variability of a population may allow maintenance of a positive growth rate. As well, the ability of a species to adapt to conditions outside its ancestral niche would enable surviving a new parasite or an increase in temperature, for example. Dispersal, on the other hand, allows tracking the environmental niche and establishing populations in newly suitable habitats. The interplay of these processes determines the range changes and eventually the fate of a species. If unable to adapt, a poor disperser is unlikely to survive important environmental changes.

Climate change and its consequences on the environment

The evidence for a rapid and profound climate change within the next century is now largely undisputed. Temperatures are predicted to rise further at a rapid rate (Houghton *et al.*, 2001) and without proper action to limit anthropogenic greenhouse gases emissions, the intergovernmental Panel on Climate Change (IPCC) predicts increases in global average surface temperature of 1.1°C to 6.4°C for the year 2100 (IPCC, 2007), associated with changes in precipitation patterns. These alterations in abiotic conditions on large spatial scales (Gates, 1993) will have economical consequences such as increased risk of forest fires, loss of agricultural potential and water shortage in the Mediterranean region, and will cause a rise in the elevation of snow cover and alter river runoff regimes in mountainous regions (Schröter *et al.*, 2005).

Inland waters make up only 0.01% of the world's total water, yet they support an important part of the overall biodiversity (Dudgeon *et al.*, 2006). Freshwater ecosystems are essential contributors to the diversity and productivity of the biosphere (Poff *et al.*, 2002) and their biodiversity provides a broad variety of valuable goods and services for human societies. Despite their importance for the sustainability of functioning ecosystems, (Baron *et al.*, 2002; Dudgeon *et al.*, 2006 and citations therein), freshwater habitats have been rather neglected in studying the influence of climate change on biodiversity.

In freshwater habitats, predicted climate change will mainly affect runoff regimes, the seasonality of water availability and the average temperature, as an increase in air temperature translates directly into warmer water temperature (Carpenter *et al.*, 1992; Poff *et al.*, 2002). This in turn is likely to affect the life processes of many aquatic organisms such as reproduction and growth rate. Furthermore, warmer waters hold less dissolved oxygen, which could have consequences for organisms requiring high oxygen levels.

Consequences on species ranges

While some of the emerging conditions may be buffered by phenotypic plasticity and/or local adaptation, significant changes in species ranges may also be expected, as past climate changes have shown (Hewitt, 1999; Davis & Shaw, 2001). Significant effects of global climate change have already been observed on the ranges of a variety of organisms, from fungus to fishes and trees (Parmesan & Yohe, 2003; Root *et al.*, 2003). The first expected symptoms of a climate change-generated biodiversity crisis in the northern hemisphere are range contractions and extinctions at lower elevational and latitudinal limits to species distributions. Indeed, the study conducted by Araujo *et al.* (2005a) showed a northward shift of birds breeding ranges on Great Britain, while Wilson *et al.* (2005) observed an upward shift of butterflies species ranges in the last 30 years in Spain, correlated with temperature increases. For freshwater habitats, Burgmer *et al.* (2007) showed that trends in average temperature have already had profound impacts on macrozoobenthos species composition in lakes.

Recent insights into the consequences of climate change on biodiversity have also been gained through climatic envelop models, based on the niche concept (Hutchinson, 1957). The niche of a species is the set of environmental conditions that allow a positive growth rate for a given organism (Emerson & Gillespie, 2008 for a review). Ecological Niche Modelling (ENM) infers the niche of a species from its known geographic distribution (for an extensive review see Guisan & Zimmermann, 2005). This niche is then projected on a map, showing the extent of the suitable area given the variables included in the model. This modelling approach was extensively used to quantitatively predict the impact of climate change on the potential future distribution of e.g. trees (Thuiller *et al.*, 2006), forest herbs (Skov & Svenning, 2004) and other higher plants (Bakkenes *et al.*, 2002). All found a substantial northward shift of species ranges (in the northern hemisphere) and many taxa at extinction risk (Thomas *et al.*, 2004).

Such changes in the species ranges, meaning for example the disappearance of key species or the invasion of non-indigenous species, are likely to affect in turn the ecosystem as a whole. It is therefore a major challenge for ecology to estimate and predict the consequences of global warming on biodiversity.

The Pulmonate group

In this thesis, I will focus on the effect of climate change on freshwater pulmonates, which represent a substantial part of freshwater biodiversity. They inhabit a large variety of freshwater ecosystems, from creeks and rivers to ponds, lakes, ditches and sewages (Dillon, 2000). Most freshwater pulmonates carry an air bubble in their richly vascularised mantle cavity (the ‘lung’), which they replenish at the surface, and which they also use to regulate their vertical movements. This allows many species to inhabit warm, eutrophic waters where dissolved oxygen may be quite low. However, some smaller and cold-water species (e.g. limpets) do not seem to breathe at the surface, and their mantle cavities are found to be filled with water rather than air (Dillon, 2000). Pulmonates mainly feed on periphyton and detritus resulting from the decomposition of other freshwater organisms (plants and animals), and are a food source for fishes and other macrozoobenthos (Økland, 1990; Brönmark & Hansson, 1998). Thus, they occupy a prominent place in the foodweb of aquatic ecosystems (Vadeboncoeur *et al.*, 2002; Woodward & Hildrew, 2002; Liu *et al.*, 2006), shaping the community structure of both their food resources and theirs predators (Brönmark & Hansson, 1998; Dillon, 2000). Any change in gastropod community structure is therefore likely to have profound effects on entire freshwater ecosystems (Dillon, 2000). Furthermore, freshwater pulmonates are well known intermediate hosts in the transmission of parasite larvae (e.g. Lymnaeid/fasciolid parasites, Remigio, 2002), and changes in their ranges are likely accompanied by simultaneous changes in the parasites ranges.

There are reasons to presume that the ranges of these freshwater snails will be significantly affected by a changing climate. Range changes as a result of past climate changes have already been shown for numerous other gastropod taxa (Hugall *et al.*, 2002; Pfenninger & Posada, 2002; Wilke & Pfenninger, 2002; Pfenninger *et al.*, 2003a; Pinceel *et al.*, 2005; Dépraz *et al.*, 2008). The predicted climatic shifts may affect freshwater pulmonates as follow:

1) The presence of more or less permanent water bodies is a mandatory requirement for the entire taxon. Increasing evaporation due to global warming and changes in precipitation will cause periods of drought, particularly at lower latitudes, leading to partial habitat loss.

2) Survival, fertility and generation lengths depend on ambient water temperature (van der Schalie & Berry, 1973; Costil & Daguzan, 1995a, b). Therefore, shifts of water temperature will likely induce a shift of the regions where reproduction is possible (change of latitudinal limits).

3) The pulmonates species that lost the air reservoir function of their mantle cavity ensure their oxygen intake through dissolved oxygen. These species, such as *Ancylus fluviatilis*, may be affected by the reduction of oxygen concentration in water due to the rising temperatures.

Thesis outline

My general aim was to infer the impact of past and future climate change on the ranges of freshwater pulmonates. Specifically, I addressed the following questions:

1) What impact has the impending climate change on freshwater snail ranges?

2) What are the relationships between species niche characteristics and range size and -shifts?

3) Which climatic factors influence the biodiversity in north-western Europe and to what extent does climate change affect biodiversity?

4) Where were the refuges during the last glacial maximum and how did the species re-colonise its present range?

5) Did the climatic niche evolve during expansions and can we plausibly forecast the species' ranges in a climate change scenario?

To answer these questions, I relied on two different approaches. First, a macroecological analysis on North European species was conducted, of which the results are presented in CHAPTER 1. This approach comparatively analysed patterns of present day species ranges, and included information on abiotic factors (hydrological and climatic) in a phylogenetic framework (Felsenstein, 1985). This gave insight into the relative importance of climatic factors limiting the distribution of the taxon as a whole. Additionally, the assessment of phylogenetic signals in the data allowed estimating the evolutionary inertia of clades concerning e.g. climate tolerance related characters. This method thus offered an insight into the evolutionary potential of clades to adapt to changing conditions (Blomberg *et al.*, 2003). Subsequently, the information gathered on the occupied niche was used to assess the impact of future climate change on the species ranges, with ecological niche modelling.

The drawbacks of the approach outlined above are the rather global information relating to the entire taxon and of no or negligible intraspecific differences. The latter is a generally unrealistic assumption because of population history, genetic drift, isolation by distance and local adaptation.

A second approach, focused on model-species, was therefore used to address the subject of intraspecific variability, as substantial variation in relevant traits (reproduction and survival) in the European freshwater pulmonate *Radix* has been shown for example by Lam & Calow (1989) and was suggested by the results of Pfenninger *et al.* (2003b) for the genus *Ancylus*.

This approach relied on the analysis of interpopulation variation throughout ranges of model species in a phylogeographic framework. In particular, the inference of the population history allowed drawing conclusions on the impact of past climate changes on the species ranges (Hewitt, 1999). Furthermore, insights into the past colonisation patterns and their speed allowed making assumptions about contemporary reactions to the current global warming. The two model species chosen for this purpose have different ecological preferences, the freshwater limpet *Ancylus fluviatilis* being preferentially found in running waters, while *Radix balthica* inhabits all sorts of still waters, from ditches to lakes (Økland, 1990)(Glöer, 2002).

In CHAPTER 2, I present the results of a phylogeographic analysis of *A. fluviatilis s.s.* The aim was to understand the historical processes that have shaped the present day distribution of the freshwater limpet *A. fluviatilis.* I also inferred the shifts in niche requirements by measuring the variance in climatic preferences at the species level among populations. Subsequently, I assessed the possible consequences of the impending global climate change for the species' range.

In CHAPTER 3, I used a recently developed analytical framework, drawing both on phylogeography and Ecological Niche Modelling (Dépraz *et al.*, 2008) (ENM) to analyse the past range dynamics of *Radix balthica* and make reliable predictions about the influence of global warming on its range. The possible Last Glacial Maximum (LGM) refugia of *R. balthica* was first inferred through projection of the present niche requirements of the species onto climatic surface data for the LGM. The resulting and alternative hypotheses were then tested with statistical phylogeography methods. This allowed the evaluation of niche conservatism in *R. balthica*, a prerequisite to predict the future range of the species through ENM.

1ST CHAPTER

Assessing the effects of climate change on the distribution of pulmonate freshwater snail biodiversity

Abstract

Global warming is expected to be associated with diverse changes in freshwater habitats in north-western Europe. Increasing evaporation, lower oxygen concentration due to increased water temperature and changes in precipitation pattern are likely to affect the survival ratio and reproduction rate of freshwater gastropods. In this study, we showed that for a great proportion of genera the ranges were projected to contract by 2080, even if unlimited dispersal was assumed. The forecasted warming in the cooler northern ranges predicted the emergence of new suitable areas, but also reduced drastically the available habitat in the southern part of the studied region. Phylogenetic signal was inferred for some dimensions of the climatic niche. Independent contrast analyses, taking into account the phylogenetic relationships between the taxa, showed a positive correlation between niche width and the size of future suitable area. Finally, we showed that expected temperature changes by 2080 surprisingly had a greater influence on the biodiversity than changes in precipitation. In summary, the results predict a profound faunal shift for Central Europe, either permitting the establishment of species currently living south of the studied region or the proliferation of organisms relying on the same food resources, if dispersal abilities do not match the rate of climate change.

Global Change Biology, submitted, together with A. Pfenninger, B. Streit and M. Pfenninger

1.1 Introduction

The evidence for a rapid and profound climate change within the next century is now largely undisputed. Temperatures are predicted to rise by up to 4 °C by 2100 in certain areas, associated with changes in precipitation patterns. This profound change in environmental conditions will probably strongly influence the diversity and distribution of species world wide (Gates, 1993). Numerous studies assessed the impact of climate change on diverse taxa, such as butterflies (Parmesan *et al.*, 1999), amphibians and reptiles (Araujo *et al.*, 2006), forest herbs (Skov & Svenning, 2004), most of them relying on Ecological Niche Modelling to predict future suitable areas for the analysed taxa. This method predicts potential distributions for species by deriving an environmental envelope from known distribution points and projecting this envelope onto a spatially interpolated climate surface of an area. Ecological modelling has been used to accurately model the present distribution of many species (e.g. Peterson, 2001; Anderson *et al.*, 2002; Hijmans & Graham, 2006). However, such approaches necessarily make inferences based on the realised niche rather than on the fundamental niche, and are therefore biased. The fundamental niche is a theoretical construct and represents the total range which could be occupied by a species if there were no competition, predation and historical factors that limit its observed range (Hutchinson, 1957), but see (Emerson & Gillespie, 2008, for a glossary). The realised niche is inferred from this observed range; hence it does not represent the species' complete potential. Furthermore, to use the ecological modelling approach to predict past or future ranges, one assumes that a species' climatic niche (the set of abiotic conditions under which surviving and reproduction are possible) is constant over time, a concept referred to as niche conservatism, or phylogenetic inertia (Blomberg & Garland, 2002).

A species showing niche conservatism can be affected by a change in its environment in many ways, depending on its dispersal abilities. If unable to disperse, the species would eventually go extinct. At the other extreme, when able to disperse without limits, the species may track its climatic niche almost in real time and therefore occupy all newly emerging suitable area. However, the frequency of niche conservatism is not known for many animal and plant taxa. Evidence for niche conservatism has been shown for several taxa (Peterson *et al.*, 1999; Prinzing *et al.*, 2001; Peterson & Holt, 2003; Martinez-Meyer *et al.*, 2004; Dépraz *et al.*, 2008; Cordellier & Pfenninger, 2009), but it may not be a general pattern. Niche shifts have been shown in snail species (Pfenninger *et al.*, 2007), in the Swainson's thrush (Ruegg *et al.*,

2006) and in jays (Rice *et al.*, 2003), and predictions of the future range through Ecological Niche Modelling may be invalid.

Our study aims at evaluating the effects of climate change on freshwater gastropods species' ranges and the inference of niche conservatism in these taxa. Freshwater pulmonate snails such as the ear pond snail, the freshwater limpet, the ramshorn (respectively the genera *Radix*, *Ancylus*, *Anisus*) occupy a variety of habitats, ranging from running waters to muddy ponds. Pulmonates represent a substantial part of freshwater biodiversity. They occupy a prominent place in the food web of aquatic ecosystems (Woodward & Hildrew, 2002), shaping the community structure of both their food resources and their numerous predators (Dillon, 2000). Any change in gastropod community structure is therefore likely to have profound effects on the entire freshwater ecosystem (Dillon, 2000).

There are reasons to presume that the ranges of these freshwater snails will be seriously affected by a warming climate. Climate change has already affected other freshwater ecosystems, such as stream fish assemblages (Buisson *et al.*, 2008). A recent study showed a correlation between the invertebrate community composition and temperature change in lakes (Burgmer *et al.*, 2007). Furthermore, there is a correlation between the northward range shift of freshwater pulmonates and the increase in water temperature in Swedish lakes (unpublished data, M. Pfenninger).

The changes associated with the global warming would have diverse consequences on pulmonates' survival. The presence of more or less permanent water bodies is *per se* a mandatory requirement for the entire taxon. Increasing evaporation will cause prolonged periods of drought, preferentially at lower latitudes, leading to partial habitat loss there. Survival, fertility and generation lengths depend on ambient water temperature, with substantial differences in minimum, maximum and range of tolerable temperatures among species (van der Schalie & Berry, 1973). Last but not least, the temperature of water directly influences the dissolved oxygen rate. Higher water temperatures are inevitably associated with less oxygenated waters which will impact species demanding high water oxygenation. Furthermore, the changes in precipitation correlated with the temperature shift will directly affect the availability of freshwater habitats. Therefore, climate induced shifts in these parameters will differentially alter the regions where successful reproduction is possible for each species, in particular their latitudinal limits.

We investigate potential impacts of climate change by modelling potential distributions of freshwater Basommatophora genera in response to two climate change scenarios for 2080. By comparing future vs. current potential distributions, we assess whether suitable climate space for freshwater Basommatophora is projected to increase or decrease with projected climate change in Europe under two extreme dispersal scenarios, unlimited dispersal or no dispersal. Furthermore, the importance of niche conservatism is also inferred through the analysis of correlation between phylogenetic distances and ecological distances in the Basommatophora group. Last, we infer which shifts of climatic variables (anomalies) will cause loss or gain of biodiversity by 2080.

Altogether, the analyses presented in this study should allow drawing reliable conclusions on the impact of climate change on freshwater gastropod biodiversity and hence on freshwater ecosystems. The following questions will be addressed in this study: i) which impact has the oncoming climate change on freshwater snail ranges? ii) what are the relationships between species niche characteristics and range size and -shifts? iii) which climatic factors influence the biodiversity in north-western Europe and to which extent do the climate change affects the biodiversity?

1.2 Materials and methods

Point occurrence data

Distributional data for Basommatophora genera were assembled from North Western Europe. This region, delimitated in the South by the Pyrenees and the Alps, is a homogeneous biogeographic area where the taxa are presumed to have reached ecological distribution equilibrium (Guisan & Zimmermann, 2005). The distribution data came from various sources, like natural history museums and public databases. The data from the museums in Brussels, Frankfurt, London and Vienna were gathered directly from the collection labels or copied from already existing inventories and subsequently georeferenced. Digital databases were provided by the curators of Budapest and Bern museums. The distribution data for Sweden was downloaded from the Swedish national monitoring databases at the Swedish University of Agricultural Sciences (SLU). The survey conducted in Norway by J. Økland (1990) was digitalized and georeferenced. We excluded occurrence data collected after 2000 to match the climatic data, as well as specimens with imprecise points of origin (e.g. Rhône delta, France).

Occurrence records are often biased towards areas that are easily accessible (along roads) or near cities or other areas of high population density (Hijmans *et al.*, 2000), and such a geographic bias can influence the result of the bioclimatic modelling. Our occurrence records showed indeed a more intense sampling around towns and the density was negatively correlated with the size of the country (e.g. Belgium was more densely sampled than

Germany, see Figure 1.1A). To remove this putative bias we created a grid of 0.5° cells and randomly selected a single point from each cell with one or more sampling points. This procedure was recommended by Graham *et al.* (2004) to handle museum data and applied for example in Ruegg *et al.* (2006). Such treatment also avoids high spatial autocorrelation which biases the results of ecological niche modelling. This reduced the number of records from 14506 to 4729 sites, more evenly distributed across the studied area.

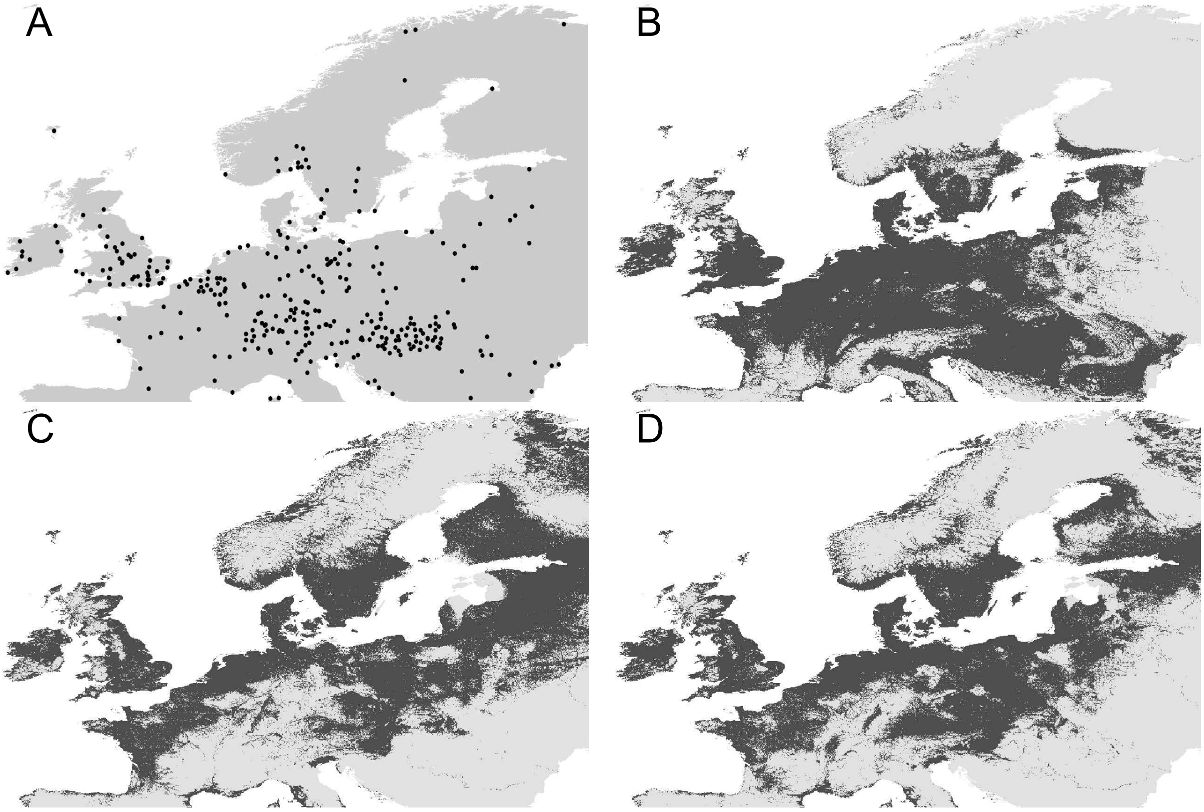

Figure 1.1: An example of the modelisation of a genus potential range, here for the *Stagnicola* genus. Maps of point occurrence data (A), predicted range for present climatic conditions (B), predicted range under climatic conditions for 2080 according to the B2 IPCC scenario (C), predicted range under climatic conditions for 2080 according to the A2 IPCC scenario (D), all at a 2.5 min resolution.

The taxonomy of the group is highly problematic. Species changed their names across time sometimes more than once (see Glöer & Meier-Brook, 1998; Glöer, 2002) and studies on the genera *Ancylus* and *Radix* revealed cryptic species and a poor taxonomic resolution based on morphological attributes (Pfenninger *et al.*, 2003b; Pfenninger *et al.*, 2006). Furthermore, the collections are composed of the shells only, not the entire organism, which makes the taxonomic revision of them difficult, if not impossible. Consequently, even some curators of the collections discouraged the use of species labelling. Therefore, we considered the unequivocal genus level rather than the often misleading species level.

Table 1.1: Variables used for the ecological modelling, from the Worldclim and Hydro1k datasets.

Original name	Variable	Variable calculation	Abbreviation in regression tree
BIO1	Annual mean Temperature		ann.mean.T
BIO2	Mean Monthly Temperature range		mean.M.T.Ra
BIO3	Isothermality	(BIO2/BIO7)(*100)	iso
BIO4	Temperature seasonality	(Standard deviation*100)	T.seas.
BIO5	Max Temperature Warmest month		max.T.warmM
BIO6	Min Temperature coldest month		min.T.coldM
BIO7	Temperature annual range	(5-6)	T.ann.ra
BIO8	Mean Temperature Wettest quarter		mean.T.wetQ
BIO9	Mean Temperature Driest quarter		mean.T.driQ
BIO10	Mean Temperature Warmest quarter		mean.T.warmQ
BIO11	Mean Temperature coldest quarter		mean.T.coldQ
BIO12	Annual Precipitation		ann.P.
BIO13	Precipitation Wettest month		P.wetM
BIO14	Precipitation Driest month		P.driM
BIO15	Precipitation seasonality	Coefficient of variation	P.seas.
BIO16	Precipitation Wettest quarter		P.wetQ
BIO17	Precipitation Driest quarter		P.driQ
BIO18	Precipitation Warmest quarter		P.warmQ
BIO19	Precipitation Coldest quarter		P.coldQ
h_dem	hydrologically correct DEM		
h_aspect	aspect		
h_flowdir	flow directions	direction of flow from each cell in the DEM to its steepest down-slope neighbor	
h_flowacc	flow accumulations	upstream catchment area	
h_slope	slope	direction of maximum rate of change in the elevations between each cell and its eight neighbors	
h_topoind	compound topographic (wetness) index	function of the upstream contributing area and the slope of the landscape	

Environmental data

A set of climate parameters were derived from a publicly available climate data base, downloaded from http://www.worldclim.org. The database provides monthly values for the years 1960–1990 in a 2.5 minutes grid resolution. Maximal and minimal monthly temperature and precipitation in grid cells covering the study area were used to calculate values of nineteen different climate parameters (Table 1.1) for the period 1960–1990 (referred to as 'baseline data'). Climate-change scenarios from HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model) were also downloaded from the same site for the period of 2050–2080 (referred to as the 2080 data), also in a 2.5 minutes grid resolution. We choose to use only one of the available models because a similar study on reptiles and amphibians by Araujo *et al.* (2006) revealed no significant differences between the climate models. Two scenarios for the General Circulation Model (GCM) HadCM3, reflecting different IPCC SRES (Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios) assumptions about demographic changes, socio-economic and technological development (Nakicenovic, 2000) were used. These scenarios present two storylines (A2 and B2), which reflect pessimal and optimal greenhouse gas emission pathways that might be taken during the 21st century. The climate data for 2080 was treated in the same way as the baseline data, to provide nineteen different climatic variables values for 2080.

We also included hydrological variables in the modelling. The Hydro1K variables are available at http://edc.usgs.gov/products/elevation/gtopo30/hydro/europe.html at a ~1km resolution and were resampled at 2,5 minutes resolution using cubic resampling in ArcView 9 (ESRI, Redlands, CA, USA) to match the climate grids. All six available variables (see Table 1.1) describe physical characteristics, such as slope, flow direction, catchment area or a derivation thereof. No significant change in these characteristics is likely to happen within the next 100 years. We therefore included the same values of these variables into both present and future environmental layers sets. All grids were clipped to a study region corresponding approximately to Europe (33°-80°N; 15°W-40°E).

Ecological Niche Modelling

The potential distributions of the genera were modelled with Maxent v3.1.0 (Phillips *et al.*, 2006). The maximum entropy algorithm estimates the distribution of a taxon (i.e the number of grid cells potentially suitable) by finding the probability distribution of maximum entropy (i.e. closest to uniform), subject to the constraint that the expected value of each of a set of environmental variables (or functions thereof) under this estimated distribution closely matches its empirical average (Phillips *et al.*, 2006). Maxent has been developed to address the problems associated with presence-only datasets (Phillips *et al.*, 2006) and has been shown to perform very well for species distribution modelling (Elith *et al.*, 2006).

For the projections we used the default convergence threshold (10^{-5}) and maximum number of iterations (500) values, using 25% of localities for model training. We let the program select both suitable regularisation values and functions of environmental variables automatically, which it achieved based on considerations of sample size. Maxent outputs a continuous probability value (cumulative values), which is an indicator of relative suitability for the species.

We chose a presence threshold to render each projection into a binary form. We considered grid cells with a cumulative probability of more than 10 (from a range of 0-100) as suitable, as suggested by Waltari *et al.* (2007) and Pearson *et al.* (2007). This threshold identified smaller areas than a lowest presence threshold that yielded zero omission error, thus resulting in more restricted pictures of potential distributions.

Evaluation of grids

The size of each genus' potential range was inferred from the number of suitable grid cells for three different climatic conditions: present, HadCM3_A2 and HadCM3_B2. We then calculated the shift in the genus potential range size under two dispersal scenarios. The Unlimited-Dispersal scenario (UD) assumed that the genus would be able to track its niche shift without any restriction, and the No-Dispersal scenario (ND) assumed the genus would survive only in the places where the present range and the future projected range overlap. For each distribution range modelled in Maxent, we also inferred the centroid of the range (i.e. center of mass) and calculated the absolute shift distance, as well as its latitudinal and longitudinal components, for each of the genera.

Niche definition of Basommatophoran genera

For all occurrence points, 19 biologically meaningful parameters (see Table 1.1) were extracted from present day climatic layers. All values falling outside the upper and lower 90% percentiles were excluded as outliers for further analysis. The lower and upper 90% percentiles values are referred to as Minimum and Maximum (Min and Max). The environmental range covered by each genus was calculated as the difference between Maximum and Minimum values for each of the 19 variables. The same procedure was applied to hydrological variables. In order to reduce the number of variables, Principal Components

Analysis (PCA) axes were extracted from each set of variables to examine the variation in environmental space within the freshwater Pulmonates. The coordinates of each genus on the three most important axes of each PCA were used as variables in comparative analyses. In total, 6 niche dimensions resulted from these PCAs (three axes times two variable sets).

Comparative analyses

In order to evaluate the influence of the species niche characteristics on the species ranges and their changes, we employed comparative methods that correct for the phylogenetic dependence of the data (Harvey & Pagel, 1991). We extended the method to a Bayesian approach, taking the uncertainty associated with the phylogenetic reconstruction of molecular clock trees into account. As no complete phylogeny of the taxa under scrutiny was publicly available, we used published mitochondrial COI and 16S sequences (see Appendix S1) to reconstruct the phylogenetic relations of the genera.

While the alignment of the protein coding COI sequences was straightforward and resulted in a data set of 1041 positions, the 16S ribosomal DNA sequences had to be aligned by hand according to the molluscan secondary structure model published by Lydeard *et al.* (2000). In particular, loop regions that could not be unambiguously aligned were excluded, leaving an alignment of 369 positions.

We used the program BEAST v.1.4.7 (Drummond & Rambaut, 2007) to obtain ultrametric trees required for comparative analyses. We analysed the data under a standard GTR + Γ + I model and an uncorrelated lognormal-distributed relaxed molecular clock (Drummond *et al.*, 2006). We used a Yule speciation model as the tree prior. For each model the MCMC was run for 10,000,000 steps and sampled every 1000 steps. The first 1,000,000 steps of each run were discarded as burn-in. This resulted in effective sample sizes for the posterior probability of much more than 500 for all parameters. We randomly sampled the posterior probability distribution of trees 1000 times after the Monte Carlo Markov Chain converged. This sample thus accounts for the uncertainty associated with phylogenetic reconstruction, choice of sequence evolution model parameters and molecular clock rate heterogeneity.

To test whether the niche characteristics and the ranges studied contained phylogenetic signal, i.e. whether closely related species tend to exhibit more similar traits than expected by chance, we conducted the permutation test on the variance of independent contrasts proposed in Blomberg *et al.* (2003). The null distribution was obtained by permuting the species trait values randomly 100 times over the 1000 phylogenies sampled. The *p* value was found by determining the quantile rank of the highest observed variance of each trait for the corresponding null distribution. The calculations were performed with COMPARE 4.6 (Martins, 2003).

To remove the phylogenetic non-independence from the data, we employed an independent-contrast approach, suggested by Felsenstein (1985), as implemented in the software COMPARE 4.6. This method assumes that the branch lengths of the phylogeny are known and proportional to the amount of evolutionary change. Relationships among species niche characteristics and range size and -shifts were explored using correlation analyses. To this end, we calculated correlation coefficients between the independent contrasts of the variables in question for all 1000 sampled trees. See Table 1.4 for a list of the variables tested for correlation.

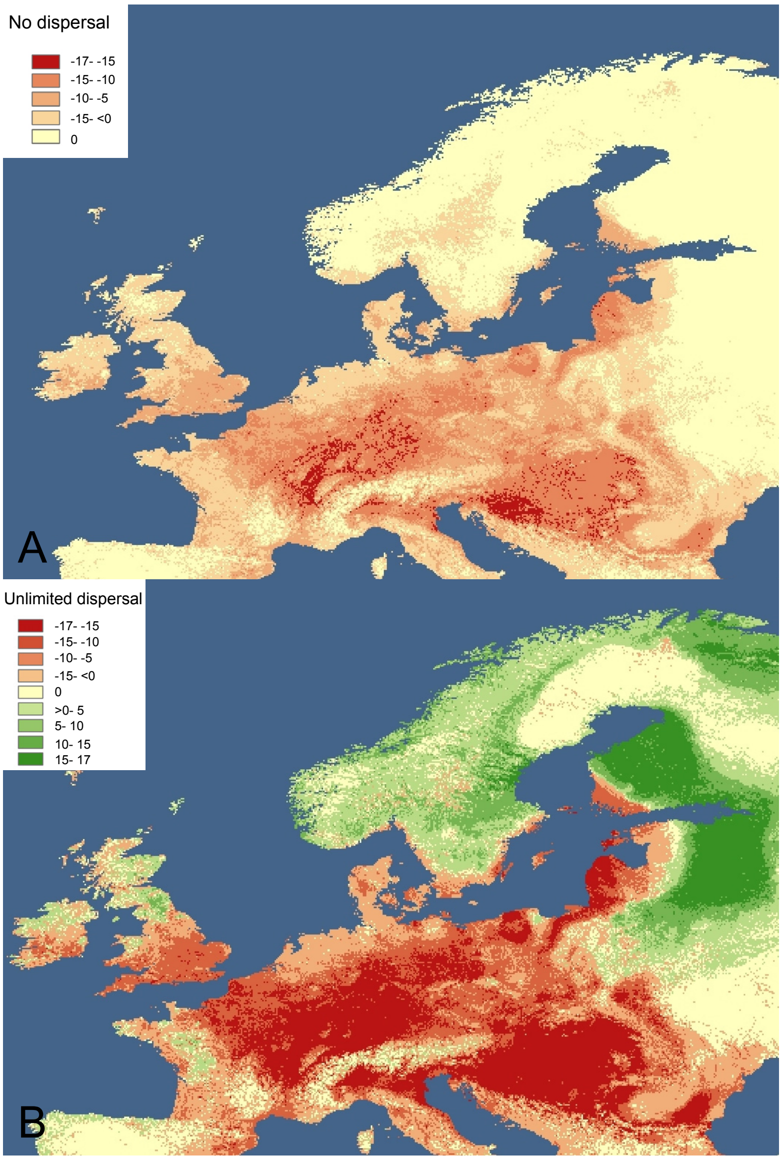

Figure 1.2: Maps of modelled biodiversity change under no dispersal hypothesis (A) and unlimited dispersal hypothesis (B), at a 5 minutes resolution. The value “biodiversity change” is calculated as the difference between the number of genera predicted to be present in a grid cell in 2080 (t_2) and the number of genera predicted to exist at present (t_1).

Climatic drivers of biodiversity change

To identify particular climatic factors causing changes in genera' richness within grid cells, we calculated and mapped two measures of range shifts for freshwater snail genera at a 5 minutes grid resolution. The resolution was downscaled compared to previous analyses because of software limitations. Biodiversity change with no dispersal (*BND*) was calculated as $BND=R(ND)_{t2}-R_{t1}$, where $R(ND)_{t2}$ was the projected genera richness for 2080 (scenario A2) and R_{t1} was the projected genera richness for present (see Figure 1.2A). Biodiversity change with unlimited dispersal (*BUD*) was calculated as $BUD=R(UD)_{t2}-R_{t1}$, where $R(UD)_{t2}$ was the projected genera richness for 2080 (see Figure 1.2B).

The relationships between biodiversity changes and climate anomalies (i.e. $\text{climate}_{t2}-\text{climate}_{t1}$) were inferred with a regression tree analysis (Breiman *et al.*, 1984). Regression-type problems are generally those where one attempts to predict the values of a continuous variable from one or more predictor variables. Here we attempt to predict the change in genera richness per grid cell from climate anomalies predictor variables. Roughly, regression tree analysis consists of recursively finding the variable and the bipartition of data combination that minimises the within-group variance. Tree methods are particularly well suited for data mining tasks, where there is only little a priori knowledge about causal relations. The use of regression trees analysis has many advantages, among them the simplicity of the interpretation and the possibility to uncover complex nonlinear relationships. The rpart library in R (R Development Core Team, 2008) was used to calculate the trees, with tenfold cross-validation and a Gaussian response model.

1.3. Results

Genera and their response to the climate change scenario

Losses in the total suitable area in northwestern Europe were predicted for most genera under both scenarios (Table 1.2). However, the predicted changes varied greatly among genera. Two out of 17 genera (*Planorbis* and *Stagnicola*) were predicted to have a larger suitable area by 2080, under the scenario A2. One more genus (*Myxas*) was also predicted to gain suitable area under the B2 scenario. Six out of the remaining fourteen genera were predicted to have a smaller suitable area under B2 than under A2. The stochasticity of change was greater under the A2 scenario: the area size loss ranged from 4 to 59% of the present suitable area, while this loss ranges from 13 to 46% under B2 (Table 1.2).

Table 1.2: Potential range size (number of grid cells) inferred in Maxent, for the HadCM3 Climatic model, under 2 dispersal hypothesis, and two IPCC scenario (A2 and B2). The percentage of area loss (number of grids cells in the future relative to the number of grid cell at present time) is also indicated on the right part of the table.

		Suitable area size (no. of grid cells)				Percentage of lost suitable area			
		Unlimited dispersal		No dispersal		Unlimited dispersal		No dispersal	
		A2	B2	A2	B2	A2	B2	A2	B2
Genus	Present	HadCM3	HadCM3	HadCM3	HadCM3	HadCM3	HadCM3	HadCM3	HadCM3
Acroloxus	103308	74866	75143	32107	42302	28	27	69	59
Ancylus	170677	149560	137179	85005	101073	12	20	50	41
Anisus	140570	102484	110419	40414	67884	27	21	71	52
Aplexa	112421	45839	60015	13225	36631	59	47	88	67
Bathyomphalus	172074	122710	133181	55801	78021	29	23	68	55
Galba	219206	191537	175806	124537	131770	13	20	43	40
Gyraulus	219206	192195	175806	119189	140525	12	20	46	36
Hippeutis	128789	109687	107228	36181	54273	15	17	72	58
Lymnea	169474	135602	140502	66393	92926	20	17	61	45
Myxas	122775	108659	**125457**	40274	66966	11	-2	67	45
Omphalaria	82212	45040	55149	35565	48301	45	33	57	41
Planorbis	126249	**140234**	**137554**	81754	99245	-11	-9	35	21
Planorbarius	126249	120602	109227	57044	70359	4	13	55	44
Radix	236681	214921	205735	135766	150466	9	13	43	36
Segmentina	106020	65274	74152	14851	41701	38	30	86	61
Stagnicola	195890	**227993**	**206132**	119806	129870	-16	-5	39	34
Physa	152212	123645	108199	65394	72198	19	29	57	53

A general change in location measured as the centroid shift of the suitable area was predicted, ranging from 631 km to 1304 km under A2, and from 390 km to 884 km under B2. Over the considered time span (roughly 100 years), it means the suitable area moved north-eastwards 4 to 13 km/year. The total suitable area will on average moved strongly northwards and moderately eastwards under B2, and more strongly so under A2.

The two extreme dispersal scenario considered yielded as expected different outcomes. Under an unlimited dispersal hypothesis, the genera would track their suitable habitat and would therefore undergo the range changes as described above. Model projections assuming no dispersal predicted all species to contract, sometimes drastically. These reductions in the potential range are due to the fact that the overlap between present potential range and future potential range is often small. The contraction of the range was more important under the A2 scenario than under the B2 for all genera: 35 to 88% of the actual suitable habitat was lost (see Table 1.2).

Table 1.3: Test on phylogenetic signal

Test on phylogenetic signal	Mean variance of independent contrasts (over 1000 phylogenies)	Probability of finding lower than observed mean variance of independent contrasts by chance (randomly distributing trait values 1000 times over the 1000 phylogenies)	
Present	1.99E+10	0.406	
HadCM3_a	2.52E+10	0.560	
HadCM3_b	1.72E+10	0.698	
shift pres_a	3.87E+11	0.452	
shift_presb	2.51E+11	0.906	
PCA1	282.78	0.349	
PCA2	73.67	**0.000**	highly significant phylogenetic signal
PCA3	32.18	0.390	
hydro_PCA1	50.78	0.806	
hydro_PCA2	26.39	0.103	tendency for phylogenetic signal
hydro_PCA3	9.8	0.083	tendency for phylogenetic signal
longshift a	69.26	0.497	
latshift a	17.04	0.328	
longshift b	53.23	0.687	
latshift b	12.46	0.725	

Phylogenetic signal and mode of evolution

The presence of significant phylogenetic signal was detected in the trait PCA2 (Table 1.3). This axis explains 13% of the overall variance of the PCA. Additionally, the variables hydroPCA2 and hydroPCA3 were close to significance ($P<0.10$), suggesting that common phylogenetic history may have reduced variance in these traits, too.

No other phylogenetic signal was detected through this analysis, which may have two explanations: either the real absence of this signal for other variables than PCA2, or an irrelevant taxonomic level: the evolutionary retention took place rather at species level, within genera.

Niche definition and correlation analysis

The probability of observing a significant ($p <= 0.05$) correlation for $N=17$ is usually reached by a correlation coefficient (r) of 0.48. Once corrected for phylogenetic signal, the independent contrast analysis showed a significant negative correlation between the variables PCA1 and hydroPCA1 and the range size for all projections (present and both future scenario, Table 1.4). The variable PCA1 explained 61% of the overall variance in the PCA values of climatic variables for present (Table 1.5). The ranges covered by the genera for all of these climatic variables were negatively correlated with the axis of the PCA, with the exception of four variables expressing the homogeneity of precipitation or temperatures throughout the year (mean monthly temperature range, isothermality, temperature seasonality, temperature annual range and precipitation seasonality). One can therefore handle the scores of the genera on this PCA factor thus as a tolerance index. The higher its value, the lower the tolerance of the taxa towards climatic variation is. The variable hydro_PCA1 explained 40% of the overall variance in the PCA on values of hydrological variables. Minimum values for TopoInd were positively correlated with this axis, while maximum values and range for DEM and Slope were negatively correlated with it. Minimum values for TopoInd were positively correlated with this axis, while maximum values and range for DEM and Slope were negatively correlated with it.

This analyse revealed also a significant positive correlation between the variables PCA1 and hydro PCA1 and centroid and longitudinal shift of the suitable area. All the other variables failed to reach the significance level, and there were no other detected correlations between range shifts and environmental variables.

Table 1.4: Average correlation coefficients of phylogenetically independent contrasts (1000 phylogenies sampled from the posterior probability distribution, thus taking rate uncertainty, clock uncertainty and phylogenetic uncertainty into account) of climatic and hydrologic niche variables against range sizes and range shifts

		Area size			Shift of area centroid		Longitude shift		Latitude shift	
		Present	HadCM3_a	HadCM3_b	A2	B2	A2	B2	A2	B2
Present	PCA1	**-0.9**	**-0.84**	**-0.82**	**0.7**	0.46	**0.63**	**0,61**	0.21	0.19
	PCA2	0.46	0.19	0.28	0.04	0.24	0.03	0.17	0.02	0.29
	PCA3	-0.01	-0.16	-0.18	-0.20	-0.36	-0.17	-0.2	-0.19	-0.35
	hydro_PCA1	**-0.89**	**-0.73**	**-0.74**	**0.48**	0.25	**0.54**	**0.48**	0.21	0.07
Hydrologic niche	hydro_PCA2	-0.16	-0.04	-0.07	0.40	0.32	0.11	0.17	0.20	0.37
	hydro_PCA3	-0.28	-0.35	-0.41	0.04	-0.11	-0.25	-0.20	-0.44	-0.33

Table 1.5: Principal component analysis (PCA). Variables scores on the three first PCA axis account for 81% of total variance. The overall variance each axis explains is also showed.

		present		
		PCA1	PCA2	PCA3
	percentage of variation	61.4	13.25	6.89
range	rangeBio1	**-0.93**	0.22	-0.22
	rangeBio2	-0.78	-0.16	-0.05
	rangeBio3	-0.75	-0.13	0.21
	rangeBio4	-0.74	0.58	-0.13
	rangeBio5	**-0.93**	-0.15	0.00
	rangeBio6	**-0.85**	0.42	-0.24
	rangeBio7	-0.77	0.53	-0.20
	rangeBio8	**-0.86**	0.26	0.04
	rangeBio9	**-0.95**	-0.04	-0.17
	rangeBio10	**-0.92**	-0.09	-0.07
	rangeBio11	**-0.88**	0.33	-0.23
	rangeBio12	**-0.85**	0.00	0.51
	rangeBio13	**-0.83**	0.00	0.53
	rangeBio14	**-0.95**	-0.18	0.07
	rangeBio15	-0.78	-0.49	-0.17
	rangeBio16	**-0.83**	0.00	0.54
	rangeBio17	**-0.94**	-0.09	0.18
	rangeBio18	**-0.83**	-0.39	-0.15
	rangeBio19	**-0.90**	0.02	0.36
min	MinBio1	0.67	**-0.69**	0.18
	MinBio2	0.61	-0.17	-0.10
	MinBio3	0.49	-0.02	0.25
	MinBio4	0.54	-0.08	0.14
	MinBio5	0.78	-0.41	-0.11
	MinBio6	0.67	**-0.71**	0.20
	MinBio7	0.49	-0.11	0.19
	MinBio8	**0.80**	-0.29	-0.10
	MinBio9	0.75	**-0.60**	0.17
	MinBio10	0.76	-0.47	-0.06
	MinBio11	0.66	**-0.69**	0.22
	MinBio12	0.79	0.04	0.28
	MinBio13	0.66	0.09	0.35
	MinBio14	**0.83**	0.45	0.12
	MinBio15	0.73	0.36	0.16
	MinBio16	0.70	0.11	0.32
	MinBio17	0.82	0.42	0.13
	MinBio18	0.83	0.48	0.15
	MinBio19	0.78	-0.36	0.11
max	MaxBio1	**-0.85**	-0.44	-0.18
	MaxBio2	-0.69	-0.40	-0.17
	MaxBio3	-0.64	-0.16	0.34
	MaxBio4	-0.66	**0.69**	-0.10
	MaxBio5	-0.77	-0.57	-0.08
	MaxBio6	-0.76	-0.45	-0.19
	MaxBio7	-0.74	**0.63**	-0.15
	MaxBio8	-0.67	-0.02	-0.25
	MaxBio9	-0.79	-0.49	-0.12
	MaxBio10	-0.77	-0.54	-0.16
	MaxBio11	**-0.84**	-0.41	-0.15
	MaxBio12	-0.79	0.00	0.61
	MaxBio13	-0.77	0.02	0.62
	MaxBio14	**-0.90**	0.04	0.20
	MaxBio15	-0.78	-0.49	-0.17
	MaxBio16	-0.76	0.01	0.63
	MaxBio17	**-0.88**	0.10	0.32
	MaxBio18	-0.68	-0.26	-0.11
	MaxBio19	**-0.88**	-0.01	0.39

Regression trees

The regression tree obtained through the analysis of biodiversity change under the No-Dispersal hypothesis (BND) showed only genera loss (Figure 1.3A). The distribution of these projected losses over the area can be seen in Figure 1.2A.

The first splitting factor of the regression tree for BND was the summer precipitation, with a splitting value of -69.12 mm. The left part of the tree described the losses occurring in areas where the decline of summer precipitation was moderate (less than 69.12 mm). When combined with an increase in mean winter temperature above 0.49°C, there was almost no observed loss. In contrast, when the change in mean winter temperature was inferior to 0.49°C (i.e a small increase, or a decrease), the loss ranged from one to eleven genera, depending on the combination of other climatic factors. An increase between present and 2080s' mean temperature of driest quarter less than 1.4°C led to the loss of almost 5 genera. If the increase was larger (1.40°C and above), the variation in predicted loss is high. In areas showing a limited decrease of the annual precipitation, three genera were predicted to disappear. If the decline in annual precipitation was higher than 154.3 mm, in combination with a change in mean temperature of wettest quarter above -0.06°C (i.e. slight decrease or increase), seven genera would be lost. For areas where the decline in the wettest quarter temperature was greater than 0.06°C and the anomaly in mean monthly temperature range was higher than 0.04°C, more than 11 genera were predicted to disappear. However, if the mean monthly temperature range increased by less than 0.04°C, less than 2 genera were predicted to go extinct in these areas.

The right part of the tree described the anomalies leading to losses in areas where the summer drought due to climate change was more important (more than 69.12 mm decrease between today and 2080). In these areas, there was almost no loss when the anomaly for the temperature seasonality was less than -11.2. That is to say, when standard deviation of temperatures throughout the year was only slightly decreasing or even increasing between today and 2080. A decrease in temperature seasonality superior to 11.2 led to losses in most of the cases, whatever the variables combination was.

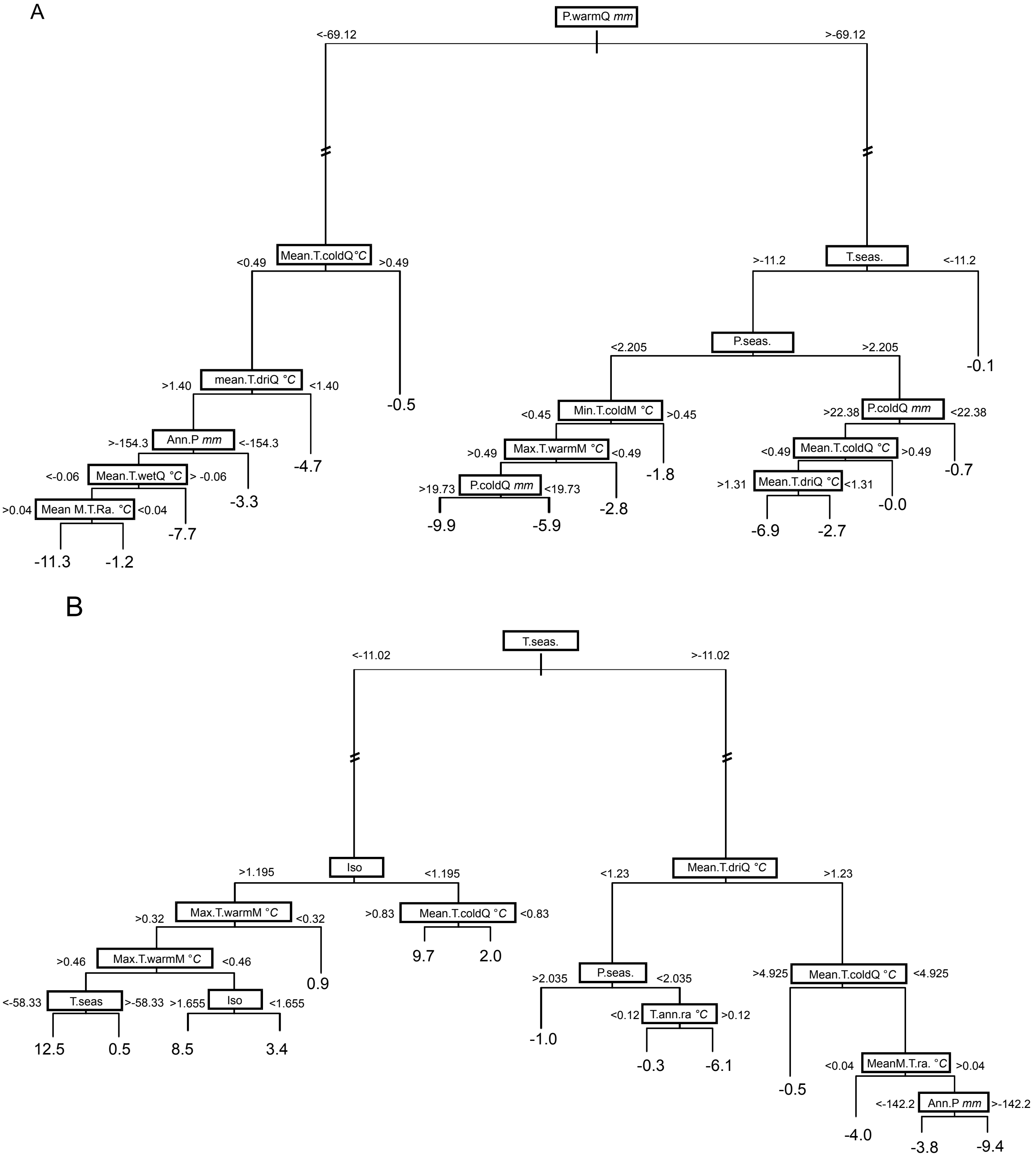

Figure 1.3: Regression tree for the predicted biodiversity variation (i.e. genera richness) per grid cell, at a 5 min resolution. Acronyms have the following meaning: **T**: temperature, **P**: precipitation, **warm**: warmest, **dri**: driest, **cold**: coldest, **wet**: wettest, **seas**: seasonality, **iso**: isothermality, **ann**: annual, **Q**: quarter, **M**: month. The units are associated with the variable name. The variable name is inserted in a box, framed with the threshold value. The terminal branches indicate the direction and the value of biodiversity change. Branch length is proportional to the error in the fit. A: under no dispersal hypothesis (ND), B: under unlimited dispersal hypothesis (UD). The branches for the first split are truncated

In areas with a precipitation seasonality increase less than 2.205, a too high increase of minimum winter temperature caused a mean loss of 1.8 genera. A moderate increase (less than 0.45°C) in winter minimum temperature led to losses from 3 to up to 10 genera. When associated with an increase in maximum summer temperature less than 0.5°C, nearly 3 genera were predicted to disappear, while at least 6 genera were predicted to go extinct when the anomaly for the maximum winter temperature was above 0.49°C. In this case, the anomaly in winter precipitations (threshold value 19.73) determined the severity of the losses.

In places where the precipitation seasonality increase exceeded 2.205, the genera loss ranges from 0 to 7. When winters became wetter with mean temperature anomaly not exceeding 0.49°C, the loss ranged from almost three to seven genera. On the opposite, moderate change in winter precipitation caused almost no losses.

A general feature of the regression tree under the ND hypothesis was the complexity of the interactions between the climatic anomalies leading to losses.

The distribution of the projected diversity changes is shown in Figure 1.2B. The southern part of the studied region was affected by losses, Germany and Poland being the most affected countries. At the opposite, Scandinavia was projected to gain genera under the unlimited dispersal hypothesis.

The regression tree obtained for the biodiversity change under the unlimited dispersal hypothesis (BUD) showed a first split (Figure 1.3B), segregating the gain of genera and the loss of genera. The direction of biodiversity change was therefore conditioned only by the value of the temperature seasonality anomaly. Temperature seasonality as defined in the Worldclim dataset is the standard deviation of temperature within a year. If the variation in this standard deviation between today and 2080 was above -11.02, then a loss in genera was predicted to occur in the grid cell. The severity of loss or gain was then determined by a combination of factors. On the left part of the tree the gains were ranging from 0 to 12 genera. A moderate increase (less than 1.19) or a decrease of the isothermality combined with a change in winter mean temperature less than 0.83°C (small increase or decrease) caused the gain of two genera. However, if the mean winter temperature increased by more than 0.83, the expected gain reached almost 10 genera. When isothermality increased for more than 1.195 but was combined with a limited augmentation of maximum summer temperature, less than one genus was predicted to establish. In areas where the previously cited isothermality increase was combined with an augmentation of the maximum summer temperature more than 0.32°C, the number of genera gain greatly varied, depending on the combination of temperature seasonality, isothermality and maximum summer temperature. In areas where the latter increased by more than 0.46°C and where the temperature seasonality decreased by more than -58.33, 12 genera were predicted to appear. If the temperature seasonality only slightly decreased, the gain stayed low (-0.5). In areas where the maximum summer temperature increased by less than 0.46°C and where the isothermality increased by more than 1.655, more than 8 genera were predicted to establish. When the change in isothermality was smaller, roughly 3 genera were predicted to be gained.

The gains predicted under the unlimited dispersal hypothesis were caused only by temperature factors; none of the precipitation variables played a role. The right part of the tree (Figure 1.3B) shows the predicted loss in biodiversity. At places where the temperature seasonality decreased by less than 11.02 or even increased, suitable areas were predicted to be lost. A slight increase (or a decrease) in mean temperature of driest quarter caused a loss ranging from almost 0 to six genera; if the precipitation seasonality at these places increased by more than 2.035, one genus was likely to disappear. For a precipitation seasonality changing by less than 2.035 and a temperature annual range rising for more than 0.12°C, the net loss was of 6 genera. By contrast, there was almost no loss (-0.3) when the temperature annual range change was less than 0.12°C (which implies not only moderate increase of this variable, but also decreases). An increase in the mean temperature of driest quarter for more than 1.23°C led to the most important predicted loss in biodiversity (minus nine genera), when combined with an increase in winter temperature under 4.9°C (or a decrease), an increase in monthly temperature range above 0.04°C, and a moderate decrease in annual precipitation (less than -142 mm). If the decrease in annual precipitation was more important (more than -142 mm), then the loss was of roughly 4 genera. At places where the winter temperature increased by more than 4.9°C, the predicted genera loss was limited (-0.5).

1.4. Discussion

Range size changes and shifts

Our study suggests that the climatic changes likely to occur over the next 80 years could have drastic consequences on the distribution of north-western European freshwater pulmonates. Even under a low carbon emission increase scenario (B2), the following consequences are predicted 1) Moderate to large losses of suitable habitat for most genera, 2) The centroids of the suitable areas will move substantially towards the northeast for most species, 3) If the genera are able to track their suitable habitat within ecological time, their new range will comprise areas in Scandinavia, but substantial southern parts of the range will be lost. When the dispersal is not possible, the size of the suitable area is predicted to become drastically reduced. Some studies suggested good dispersal abilities for freshwater snails (Cordellier &

Pfenninger, 2009; pers. comm. M. Salinger), but the necessary vectors - since active dispersal appears impossible over larger areas - are not well known. Previous studies revealed the influence of migratory waterfowl to freshwater invertebrates' dispersal (Bilton *et al.*, 2001; Figuerola *et al.*, 2005; Frisch *et al.*, 2007). From this preliminary knowledge, we suggest that the "no dispersal" hypothesis is rather unrealistic, and consider the unlimited dispersal hypothesis as closer to reality. The time factor may be determining: the last global warming event after the glacial maximum took place over a much longer period, and the pace of recolonisation and range expansion was therefore less constrained. Currently, the climate is projected to change more rapidly and with greater magnitude over the next century than has been experienced at least during the past 1000 years (Houghton *et al.*, 2001). Projected climate change rates thus might overstrain even the best migrants.

Even though the B2 scenario is based on less greenhouse gases emissions than A2, we found that the former does not have necessarily less severe consequences on the suitable area size. This may be due to the similar loss in southern parts of Europe both under A2 and B2, but a smaller extension of the suitable area in its northern part under B2 than under A2. Even if the absolute suitable area is larger under A2, it is also farther north, and the organisms may have difficulties to reach it.

Correlatives to present and predicted range size

The above described changes in suitable area and their consequences on the effective ranges assume that species occupy the same ecological niche over time (i.e. what could be termed anagenetic niche conservatism). Studies conducted on single gastropod species had variable outcomes in this regard: in the species *Ancylus fluviatilis*, an evolution of the occupied niche over time could not be excluded (Cordellier & Pfenninger, 2008), while in *Radix balthica* it appeared to be stable (Cordellier & Pfenninger, 2009).

However, a significant phylogenetic signal on the genus level was revealed for the winter temperatures the snails can endure, as well as the temperature variance throughout the year within the Basommatophora group, *i.e.* related genera had a greater ecological similarity in this regard than expected by chance (Table 1.3). This showed that on a cladogenetic level, the evolution of certain traits is phylogenetically constrained. It was therefore necessary to take this relation into account for valid correlation analyses (Harvey & Pagel, 1991).

The independent contrast correlation analysis showed a relationship between species niche characteristics and suitable area size. A low tolerance (narrow climatic range) was correlated with a small suitable area size at present (Table 1.4). This result is rather intuitive, and such a relationship was also shown for central European tree species (Köckemann *et al.*, 2009). However, this low tolerance also conditions the size of the future suitable area: the genera with a narrower niche will be *a priori* the most affected by climate change. The independent contrast correlation analysis also assessed the correlation between niche characteristics and suitable area shift. For low tolerance genera, the area shifts are eastwards rather than northwards. The direction of suitable area shifts is meaningful for organisms presumably relying on passive dispersal through birds. While switching between nesting and wintering places, migratory waterfowl follows south/north migration routes rather than west/east routes, thus possibly rendering bird mediated colonisation ineffective.

Changes in biodiversity

While the warmer temperatures enhance reproduction and growth rates (van der Schalie & Berry, 1973), this effect is counterbalanced by lower water oxygenation. The importance of temperature factors to biodiversity and even their prevalence (Gates, 1993) was confirmed by the regression tree analysis (Figure 1.3B). One would have expected precipitation changes to play a greater role in the survival of freshwater organisms, since precipitation determines to some extent the availability of habitats and their persistence. However, the factors predicting the diversity shift by 2080 are almost only temperature changes. In particular, the analysis of biodiversity change under the unlimited dispersal hypothesis revealed the striking influence of temperature seasonality, its value in the future determining the direction of change. A general outcome of this analysis is the complexity of the interactions of climatic factors; the interdependency has a strong influence on the biodiversity shift predicted between present and 2080. This biodiversity shift is predicted to be very important in countries such as Germany, France and Poland. The species of this group being generalist, the disappearance of one taxon at a time in a given area may be buffered by the replacement through other, ecologically similar taxa. However, the biodiversity loss in Germany is predicted to concern almost all of the genera taken into account in this study, which will have no longer suitable habitat by 2080. This excludes a replacement by local species. However, a similar shift of suitable habitat can be expected for the taxa currently inhabiting adjacent areas on the Southern European peninsulas, which may thus replace the current freshwater pulmonate biodiversity in the studied area.

Conclusions

An important fauna shift is predicted to take place in Central Europe within the next decades: this area will no longer be climatically suitable for the present freshwater snail fauna. The most probable outcome is their replacement by related pulmonates presently inhabiting southern Europe, adapted to warmer climates. This replacement would assure the continuity of the existing food-webs. However, the colonisation by southern taxa can only take place if dispersal keeps pace with the suitable area shift. If not, the consequences of freshwater snail range changes on the freshwater ecosystems are difficult to predict, though some hypotheses can be formulated. The Basommatophora are generalists regarding their food resources, feeding on detritus and/or biofilm (Dillon, 2000). The reduction or the disappearance of these populations would mean less grazing pressure, and therefore the proliferation of organisms relying on the same food sources. No matter which scenario will actually take place, our study suggests that the consequences of the predicted climate change will be dramatic for the presence and composition of freshwater pulmonates in north-western Europe.

2ND CHAPTER

Climate-driven range dynamics of the freshwater limpet *Ancylus fluviatilis* (Pulmonata, Basommatophora)

Abstract

Aim

Our aim was to understand the processes that have shaped the present-day distribution of the freshwater limpet *Ancylus fluviatilis sensu stricto* in order to predict the consequences of global climate change on the geographic range of this species.

Location

North-western Europe.

Methods

We sampled populations of *A. fluviatilis s.s.* over the entire range of the species (north-western Europe) and sequenced 16S ribosomal RNA (16S) and cytochrome oxidase subunit I (COI) mitochondrial fragments to perform phylogenetic and phylogeographical analyses. Climatic niche modelling allowed us to infer the climatic preferences of the species. A Principal Component Analysis identified the most important climatic factors explaining the actual range of *Ancylus fluviatilis*. We also identified which climatic factor was the most limiting at range margins, and predicted the species' geographic range under a climate change scenario (Community Climate Model 3 – CCM3).

Results

By means of the phylogeographic analysis, we inferred that *A. fluviatilis s.s.* occupied northern refuges during the last glacial maximum. We showed that the climatic preferences of Baltic populations are significantly different from those of Central Europe populations. The projection of the occupied area under the CCM3 climate model predicts a moderate poleward shift of the northern range limits, but a dramatic loss of areas currently occupied, for instance in northern Germany and in southern Great Britain.

Main conclusions

Post-glacial range dynamics of *A. fluviatilis* were not governed by niche conservatism. Therefore, we must be cautious about bioclimatic model predictions: the expected impact of climate change could be tempered by the adaptive potential this species has already shown in its evolutionary history. Thus, modelling approaches should rather be seen as conservative forecasts of altered species ranges as long as the adaptive potential of the organisms in question cannot be predicted.

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2.1. Introduction

The realized geographical range of a species can be defined as the area where stably reproducing populations are found (Gaston, 1996). Thus, this area (1) offers the possibility for survival and reproduction; i.e abiotic and biotic conditions match the fundamental niche requirements of the species, and (2) was reached via dispersal during the species' history (Holt, 2003). The dynamics of a species' range can therefore be governed by the following two processes: (1) spatial tracking of the environmental niche without adaptation, including extinction if the niche vanishes, and (2) adaptation to ecological conditions outside the ancestral niche, either permitting colonization of areas not yet occupied or allowing the species to remain in the ancestral area despite changing conditions.

The cyclic climatic changes of the Pleistocene glaciations have been the most significant events in shaping the contemporary ranges of many extant lineages (Avise, 1998; Bernatchez & Wilson, 1998; Taberlet *et al.*, 1998; Hewitt, 1999, 2000). A close relationship between climatic conditions, such as temperature or precipitation, and species ranges has indeed been shown many times (Hugall *et al.*, 2002; Pfenninger *et al.*, 2007). The prevailing paradigm of species survival during the Pleistocene cold cycles consists of a retreat to southern European refuges, such as the Iberian Peninsula, Italy, the Balkans, areas near the Caucasus and the Caspian Sea (Taberlet *et al.*, 1998; Hewitt, 1999, 2004). However, there is growing evidence also for northern refuges for cold-adapted animals (e.g. Nesbo *et al.*, 1999; Stewart & Lister, 2001; Pinceel *et al.*, 2005; Kotlik *et al.*, 2006). Previous studies suggested that *Ancylus fluviatilis* might belong to this group (Pfenninger *et al.*, 2003b).

In this paper, we aim to understand the historical processes that have shaped the present day distribution of the freshwater limpet *A. fluviatilis* and subsequently assess the possible consequences of the oncoming global climate change for the species' range. A previous study conducted on *A. fluviatilis sensu lato* revealed the presence of four cryptic species (Pfenninger *et al.*, 2003b), one of which was identified as *A. fluviatilis* (O.F. Müller, 1774) *sensu stricto*. The range of the latter comprises north-western Europe and the north-western part of the Iberian Peninsula. The species occurs in most permanent lowland rivers, creeks, the shore zone of lakes, and even irrigation channels or fountains, without demanding high water quality (Økland, 1990; Glöer & Meier-Brook, 1998). High mountain ranges, such as the Alps or the Pyrenees, are not colonized by these limpets (Turner *et al.*, 1998; own observations), most likely because the considerable bed-load of high mountain streams does not allow the establishment of stable populations. The presence of a hard substrate, from which the limpets graze the biofilm and where the egg-clutches are deposited, is a necessary prerequisite for their occurrence. The life cycle is annual, with reproduction in spring after which most of the individuals die. *Ancylus fluviatilis* is highly selfing (Städler *et al.*, 1993) and local populations can consist of reproductively more or less isolated strains (Städler, 1997).

To understand the reactions of *A. fluviatilis* to past climate changes, we focused on the following questions. (1) Where were the refuges during the glaciations and how did the limpet re-colonize its present range? (2) Did the climatic niche evolve during expansions and can we plausibly forecast the species' range in a climate change scenario?

2.2 Materials and Methods

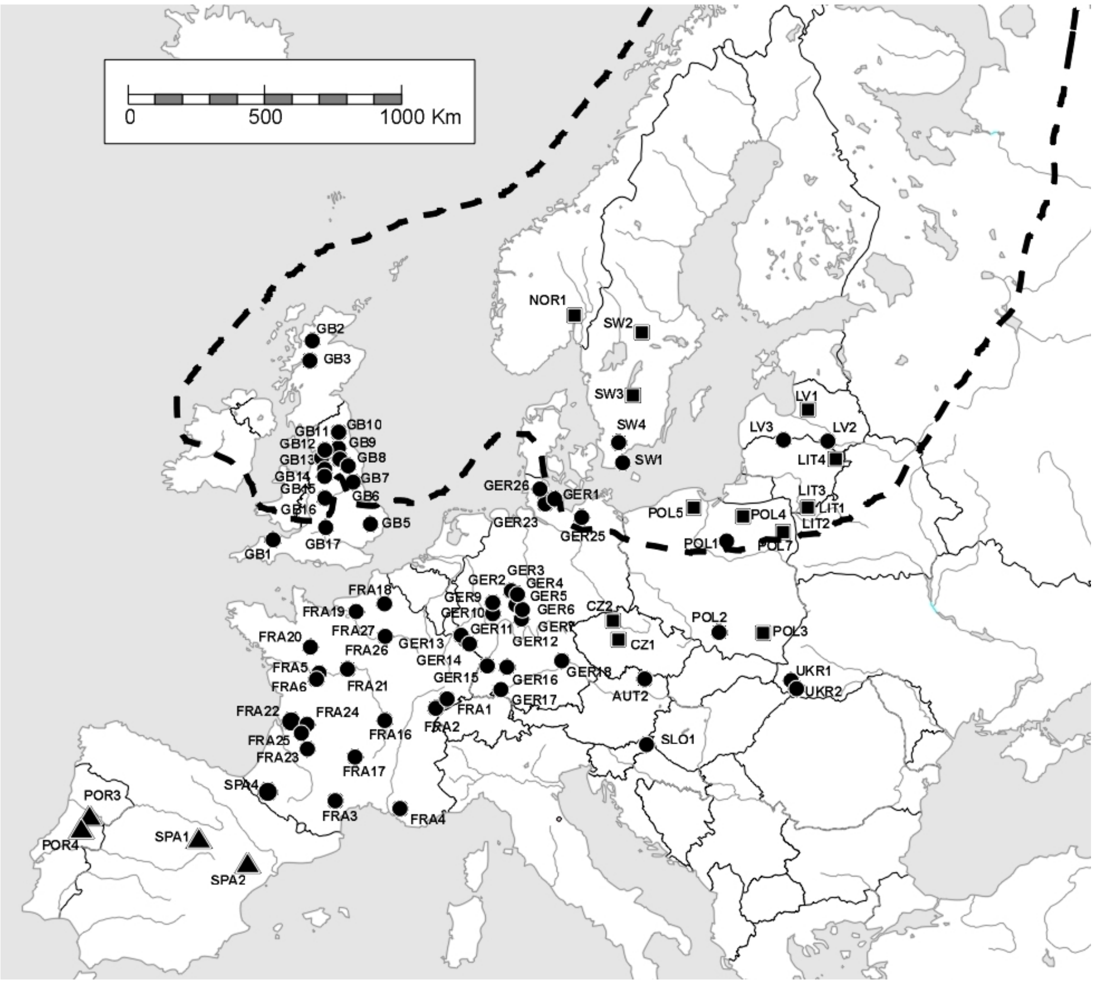

Figure 2.1: Map of Europe showing the range of *Ancylus fluviatilis s.s.* and the sampling localities. Squares stand for locations of the Baltic Area (BA) phylogroup, triangles for locations of the Iberian Peninsula phylogroup (IP) and circles for locations of the Central Europe (CE) phylogroup. Haplotypes from both phylogroups (CE and BA) were found at localities GB1 and POL1. The dashed line represents the ice cap extent at last glacial maximum (after Andersen & Borns, 1997).

Populations sampled and geographical distribution of the species

Forty-four populations across the geographical range of the species *Ancylus fluviatilis sensu stricto* were sampled, mainly from Sweden, France, Great Britain and Poland. Additionally, we included in this study the sequences of the 42 populations published in Pfenninger *et al.*, (2003b, Acc. Num. AY 238703-57), covering the remainder of the study area, making a total of 86 populations (Figure 2.1). Sampling sites and number of individuals sequenced are shown in Appendix S2.

DNA extraction, fragment amplification and sequencing

Specimens preserved in 70% ethanol were extracted from their shells and DNA was isolated following a slightly modified hexadecyltrimethylammonium bromide (CTAB) protocol published in Winnepennickx *et al.* (1993). A 5'-fragment of the 16S target-rRNA was amplified for all samples by polymerase chain reaction (PCR) with primers of the sequence 5'>CGCCTGTTTATCAAAAACAT<3' 16Sar and 16Sbr 5'>CCGGTCTGAACTCAGATCACGT<3' (Palumbi, 1996). Amplification was performed with Invitrogen *Taq* DNA polymerase in 25µL total reaction volume with standard reaction conditions. Samples were amplified for 10 cycles (90°C for 30 s, 46°C for 30 s and 72°C for 40 s) and 30 cycles (90°C for 30 s, 50°C for 40 s, ramp 0.3°C/s and 72°C for 40 s) after initial incubation at 92°C for 2 min 30 s. A 3-minute final elongation step at 72°C followed. PCR products were then cut out of a gel and cleaned with peqGOLD Gel Extraction Kit (Peqlab, Germany) following the protocol provided. Both strands of the purified amplification products were cycle-sequenced with ABI BigDye®Terminator v.3.1 Ready Reaction Sequencing mix (Applied Biosystems, USA), and read automatically on the ABI 3130xl sequencer from the same manufacturer. Sequences were deposited in GeneBank (Acc. Nos. EU000274-97). Sequences were initially aligned with ClustalW and adjusted manually, using the BioEdit software. After initial phylogeographic analysis (see below), one to four individuals for some of the haplotypes inferred with 16S sequences were chosen for additional analysis with partial cytochrome oxidase subunit I sequences (COI) (Appendix S2). The COI fragment was amplified with primers described in Folmer *et al.* (1994) and a group-designed reverse primer 5'>TGTTGATATAAAATAGGATC<3' (designed for Basommatophoran by K. Kuhn, pers. comm.) in 25µL reaction under the following conditions described in Pfenninger *et al.* (2006). PCR products were then cleaned using the Invitrogen kit. The sequences had been obtained following the same protocol as described above for 16S and also deposited in GenBank (Acc. Nos. EU376490-522).

Phylogeographic analyses

Phylogeographical patterns were inferred from the spatial distributions of sequences of two mitochondrial fragments. To distinguish recurrent population processes from historical events, we used nested clade analysis (NCA) (Templeton *et al.*, 1995). This statistical approach first tries to reject the null hypothesis of random association between haplotype variation and geography, and then interprets the significant patterns using explicit criteria that include an assessment of sampling adequacy. The NCA approach uses the temporal information contained in a haplotype network to partition historical (e.g. fragmentation, colonization) from recurrent (e.g. gene flow, drift, mating system) processes responsible for the observed pattern of genetic variation. The computer program TCS (Clement *et al.*, 2000) first compiled the sequences into haplotypes and constructed a network using statistical parsimony (SP), with the connection limit set at 95%. Due to multiple possible connections, we performed analysis on a subset of 16S haplotypes, which were additionally sequenced for COI, to increase phylogenetic resolution (see Appendix S2). The 16S network was modified accordingly, and the consensus network is shown in Figure 2.2. The nesting design was overlaid on this consensus network following the recommendations of Crandall (1996) and Templeton *et al.* (1995). Random association between geographical position of clades and nesting clades was tested by calculating the clade distance (D_c) and nested clade distance (D_n). The frequency of haplotypes/clades and the sample size per location were used to simulate and test the null hypothesis of random distribution of haplotypes and clades in Geodis 2.5 (Posada *et al.*, 2000). The biological inferences of the observed patterns were interpreted using the most recent inference key by Templeton (2004). Based on the phylogeographic inference, we defined three phylogroups, named according to their distribution centre: Iberian Peninsula (IP) populations from Spain and Portugal; Central Europe (CE) populations mainly from France, Germany, Austria and Great Britain; and Baltic Area (BA) populations from the Baltic Sea surroundings (Norway, Sweden, Poland, Lithuania and Latvia).

Estimating the variation of effective population size over time

To infer range expansion from the haplotype data, we relied on two conceptually different approaches, in addition to the phylogeographic analysis. The first approach was based on the assumption that geographic range expansions should be accompanied by a demographic population growth. This growth is expected to leave traces in the shape of gene-trees compared with neutral expectations in coalescent theory. Tajima's D (Tajima, 1989) and D^*

and F^* statistics (Fu & Li, 1993) examine the shape of gene-trees to test for deviation from a selectively neutral coalescent process in a population of constant effective size. The F-statistic (Fu, 1997) detects an excess of low-frequency alleles expected in the course of a population expansion (Schneider & Excoffier, 1999). Significant negative deviations of these indexes from zero are interpreted either as evidence of selective sweeps (Fu, 1997) or population expansions (Slatkin & Hudson, 1991; Fu, 1997). Positive deviations may indicate a long-lasting population subdivision (Slatkin & Hudson, 1991; Fu, 1997). All calculations were performed with DnaSP, version 4.0 (Rozas *et al.*, 2003).

Past demographic population dynamics were also estimated from the 16S dataset with a Bayesian skyline plot model of exponential growth implemented in BEAST v. 1.4 (Drummond *et al.*, 2005) for the joint CE and BA groups. The Bayesian skyline plot model generates a posterior distribution of effective population size through time using a Markov chain Monte Carlo (MCMC) sampling. These distributions are then used to generate credibility intervals of the desired parameter that represent both phylogenetic and coalescent uncertainty (Drummond *et al.*, 2005). It should be noted that coalescence analyses such as these assume there is no population subdivision. This assumption is certainly violated here, but it probably affects only the accuracy of the numerical parameters and not their general trend (Finlay *et al.*, 2007).

A lognormal model that relaxes the molecular clock hypothesis was used (Drummond *et al.*, 2006). We ran 30,000,000 generations (sampled every 1000 iterations), of which the first 10% were discarded as burn-in. The substitution model applied was GTR+Γ+I with no strong a priori parameter expectations, *i.e.* the parameters were also estimated by the MCMC. This model was chosen, because it makes best use of the Bayesian approach (Huelsenbeck & Rannala, 2004). Also, no a priori information on the mean substitution rate per year was available. We used a strong prior for the mutation rates, within a reasonable range for freshwater molluscs (DeJong *et al.*, 2001; Johnson, 2005; Bunje & Lindberg, 2007; Liu & Hershler, 2007) to all analyses (mean = 2×10^{-8} substitutions per site and year, lower bound = 5×10^{-9}, upper bound = 5×10^{-8}, corresponding to 0.5-5% nucleotide substitutions per one million years). The convergence and sampling efficacy of the Bayesian skyline plot were monitored using Tracer v. 1.2.1 (available at http://evolve.zoo.ox.ac.uk/software/).

Phylogeny

The 16S and COI sequences were concatenated for 33 individuals to perform a Bayesian analysis of phylogeny, with *Planorbarius corneus* and *Ferrissia* sp. as outgroup species, as well as representative sequences from *Ancylus* clades described in Pfenninger *et al.* (2003b). We performed the phylogenetic analyses based on Bayesian inference using MrBayes version 3.1 (Ronquist & Huelsenbeck, 2003). Based on the Akaike information criterion calculated with Modeltest (Posada & Crandall, 1998), we chose unlinked GTR+R+I models for both partitions, with no a priori parameter estimates. We ran four Metropolis coupled Monte Carlo Markov chains (MC^3) for 1,000,000 generations, sampling every 100 generations, and the first 1000 trees were discarded as burn-in. Bayesian inference of phylogeny is based upon a quantity called the posterior probability distribution of trees, which is the probability of a tree conditioned on the observations. Convergence of the MCMC chain was monitored by plotting maximum likelihood values of the trees against the number of runs.

Estimation of climatic niche and range prediction

Table 2.1: Description of the BIOCLIM variables and loadings on PCA axis. The four variables with the highest loadings on each PCA factor are shown in bold.

		Loadings of the variables on PCA factors		
Variable	Description	Factor 1	Factor 2	Factor 3
BIO1	Annual Mean Temperature	0.5977	**-0.7655**	0.0353
BIO2	Mean Monthly Temperature Range	0.0779	-0.7173	0.3453
BIO3	Isothermality	**0.8480**	-0.3669	-0.0841
BIO4	Temperature Seasonality	**-0.9026**	-0.0324	0.3434
BIO5	Max Temperature Warmest Month	-0.0305	**-0.9017**	0.3349
BIO6	Min Temperature Coldest Month	**0.8659**	-0.3557	-0.2485
BIO7	Temperature Annual Range	-0.7841	-0.2824	0.4407
BIO8	Mean Temperature Wettest Quarter	-0.8106	-0.1460	0.1055
BIO9	Mean Temperature Driest Quarter	0.7983	-0.4925	-0.0406
BIO10	Mean Temperature Warmest Quarter	-0.0128	**-0.9049**	0.2967
BIO11	Mean Temperature Coldest Quarter	0.8475	-0.4635	-0.1693
BIO12	Annual Precipitation	0.7741	0.4194	**0.4585**
BIO13	Precipitation Wettest Month	0.5883	0.2629	**0.7394**
BIO14	Precipitation Driest Month	0.6640	0.5828	-0.0600
BIO15	Precipitation Seasonality	-0.3639	-0.2078	**0.6836**
BIO16	Precipitation Wettest Quarter	0.5884	0.3116	**0.7163**
BIO17	Precipitation Driest Quarter	0.7338	0.4917	0.0189
BIO18	Precipitation Warmest Quarter	-0.1521	**0.7383**	0.3873
BIO19	Precipitation Coldest Quarter	**0.8887**	0.1537	0.3282
Eigenvalue		8.4916	5.0885	2.7421
Overall variance (%)		44.6929	26.7814	14.4319

The realized environmental niche can be estimated from presence-only data with high precision by extracting niche dimensions from spatial information on the distribution of environmental parameters (Nix, 1986). For the sites of each of the 86 populations of *A. fluviatilis* (effective-presence dataset), 19 biologically meaningful parameters (see Table 2.1) were extracted from the WorldClim (Hijmans *et al.*, 2005; http://www.worldclim.org) environmental layers with a spatial resolution of 2.5 min as implemented in the software DIVA-GIS 5.2 (Hijmans *et al.*, 2001). Principal components analysis (PCA) axes were extracted from the climatic variables to examine the variation in environmental space between populations of *A. fluviatilis*. Environmental niche dimension PCA factor values of the groups BA, CE and IP were compared by one way analysis of variance (ANOVAs).

A second data set was built from museum data from northern Europe. As a predictive niche modelling approach depends critically on unequivocal species identification, we only considered the area where the presence of *A. fluviatilis s.s.* was molecularly proven. The collections of the Senckenberg Museum, Frankfurt, the Naturkunde Museum, Bern, the Natural History Museum of London, the Natural History Museum of Budapest, the Naturhistorisches Museum of Wien, and the Royal Natural History Museum in Brussels, as well as the inventory of J. Økland (1990), were examined for *A. fluviatilis* samples, resulting in a database of 672 localities.

The BIOCLIM model (Nix, 1986; Busby, 1991) was used to predict the area where *A. fluviatilis* is likely to occur under current climatic conditions, using the 86 populations from the molecular dataset. We first inferred which climatic factor was the most limiting at range boundaries. To this end, the variable for which the percentile score was lowest (or highest) is mapped on the grid cells falling in the 95% percentile. It results in a map showing the most limiting factor for the distribution of the species. For the purpose of this study, areas that fell within the 5±95 percentiles of all climatic parameters of the profile were termed the ‘range’ of the predicted domain (true/false method). We evaluated the quality of this projection by matching the predicted range against the locations listed in the museum dataset.

The species’ bioclimatic niche was also projected on a future climate scenario for the year 2100, according to the publicly available Community Climate Model 3 (CCM3, double preindustrial CO_2 conditions, annual mean surface temperature 2K higher for the Northern Hemisphere; Govindasamy *et al.*, 2003). Future areas of climatic suitability were then compared with present day suitable areas and actual distribution.

The use of BIOCLIM for predictive niche modelling has recently received considerable criticism. For example, Elith *et al.* (2006) showed that newly developed models such as BRT, MAXENT and GDM perform better than the popular BIOCLIM and GARP models in predicting current ranges. However, Hijmans & Graham (2006) showed the superiority of BIOCLIM concerning the prediction of species’ distributions under climate change scenarios, which was our primary goal here.

A major point of criticism on the use of predictive niche modelling in general is that dispersal and interactions with other species, such as predation or competition, are not adequately taken into account (Davis *et al.*, 1998). While some studies have suggested that these factors are relatively negligible at large scales (e.g. Pearson *et al.*, 2002)), recent analyses by Araujo *et al.* (2005b) showed that strong fit between niche models and contemporary distributions is not necessarily a reliable guide to the ability of such models to predict changes in distribution under climate change. Notwithstanding, despite the inherent limitations of the approach, climate envelope models provide one of the few analytical means to study species' ranges (Beaumont *et al.*, 2005).

2.3 Results

MtDNA sequence variation and parsimony network

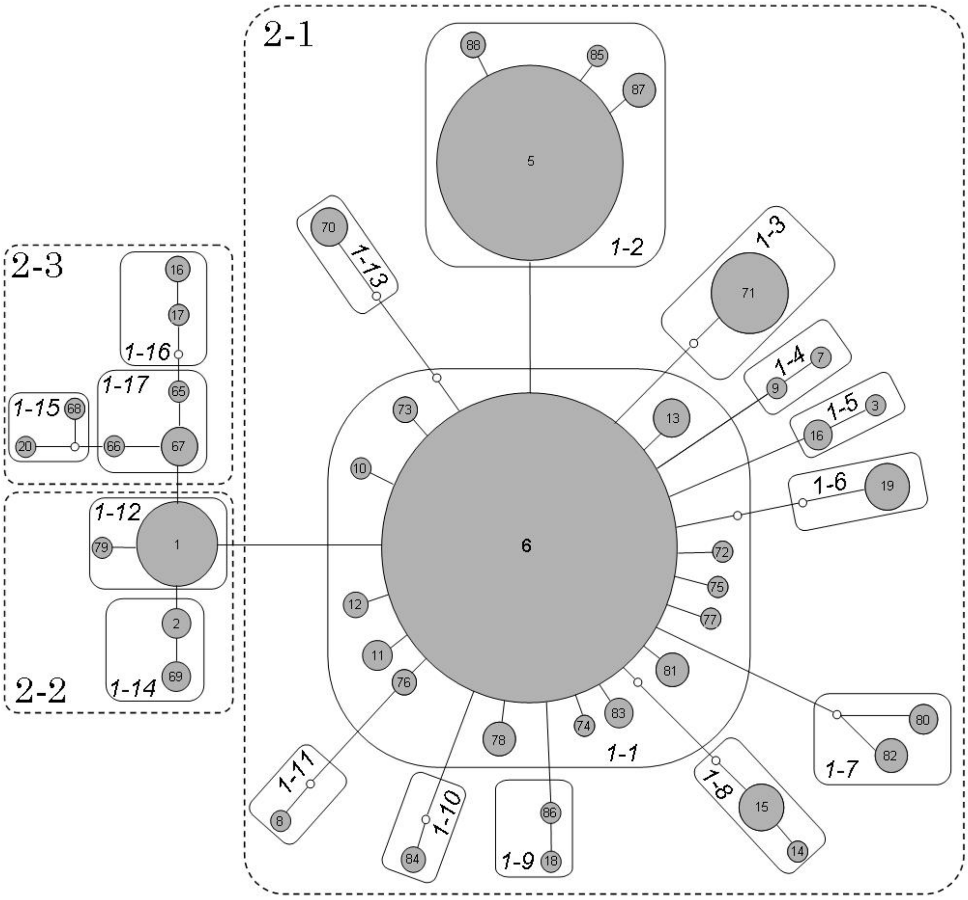

Figure 2.2: Statistical Parsimony consensus network. Circle sizes are proportional to the number of sequences in the represented haplotype. Small open circles are undetected haplotypes.

In total, 119 snails were sequenced from 44 populations (Appendix S2). 440 bp of the 16S fragment could be recovered and aligned and 17 polymorphic sites were observed, defining 24 new mtDNA haplotypes, in addition to 20 already described in Pfenninger *et al.* (2003b).

The haplotypes, their distributions among the populations and their affiliation to each phylogroup are presented in Appendix S2. For the additional COI sequences, 559 bp could be recovered for 33 individuals (Appendix S2). The resolved SP haplotype network is shown in Figure 2.2.

Nesting design is presented in Figure 2.2, while the results of the analysis performed in Geodis, as well as the inference reached by the key given in Templeton (2004), are presented in Table 2.2. Two of the three level-1 clades which had significant departures from the null hypothesis were characterized by restricted gene flow (1-2 and 1-1). NCA identified long distance movements for both 2-1 and 2-2 clades.

Table 2.2: Chi-squared test of geographical association of clades and biological inference from the NCA analysis of *Ancylus fluviatilis s.s.* Probability *p* is the probability of obtaining a χ^2 statistic larger than or equal to the observed statistic by randomly permuting the original contingency table 9999 times. Inferences were obtained following the key given in Templeton (1998). Abbreviations for the inferences are: CRE, contiguous range expansion; LDD, long distance dispersal; LDC, long distance colonization; IBD, isolation by distance; PF, past fragmentation; and RG, restricted gene flow.

Clades nested with	Permutational χ^2 statistic	*p*	Chain of inference	Inference
Clade 1-1	982.53	0.000	1-2-3-5-6-7-YES	RG/Dispersal with some LDD
Clade 1-2	111.22	0.0009	1-2-3-4-NO	RG with IBD
Clade 1-17	7.00	0.0485	1-2-11-12-13-14-YES	CRE or LDD or PF (inadequate sampling design)
Clade 2-1	1855.32	0.000	1-2-3-5-15-21-YES	LDC
Clade 2-2	23.00	0.0002	1-19-20-2-11-RE-12-13-YES	LDC with possible Subsequent Fragmentation
Clade 2-3	19.00	0.0083	1-19-20-NO	Inadequate sampling design
	or alternative explanation		1-2-11-RE-13-14	CRE, LDC
Total	448.73	0.0000	1-2-3-5-15-NO	PF and/or LDC

Identification of range expansions

Although Fu’s F_s (-0.28908, $p<0,001$) was highly significant, the other statistics failed to detect departures from the neutral expectation with values as follows: Tajima’s D, -0.05186; Fu & Li’s D^*, -0.02874; and F^*, -0.03227. The Bayesian demographic analysis showed a steady but slight increase in population sizes of *A. fluviatilis* over time (Figure 2.3).

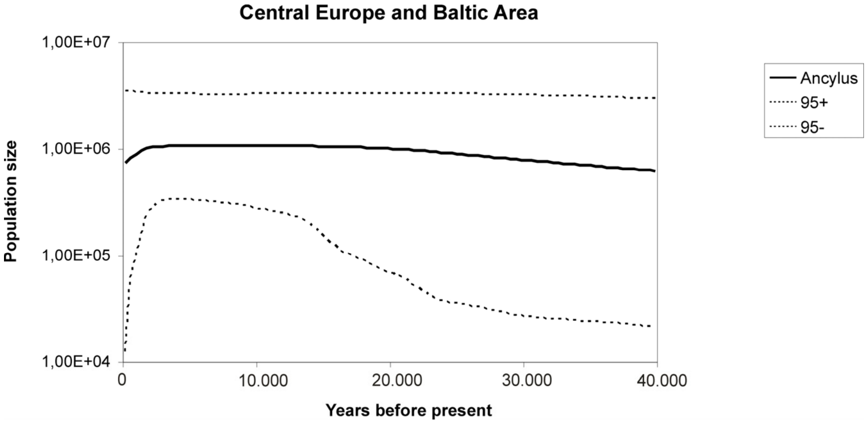

Figure 2.3: Bayesian skyline plot of the evolution of the effective population size of *Ancylus fluviatilis s.s.* through time for Central Europe and Baltic Area populations. The 95% highest posterior density (HPD) limits are shown as thin dashed lines.

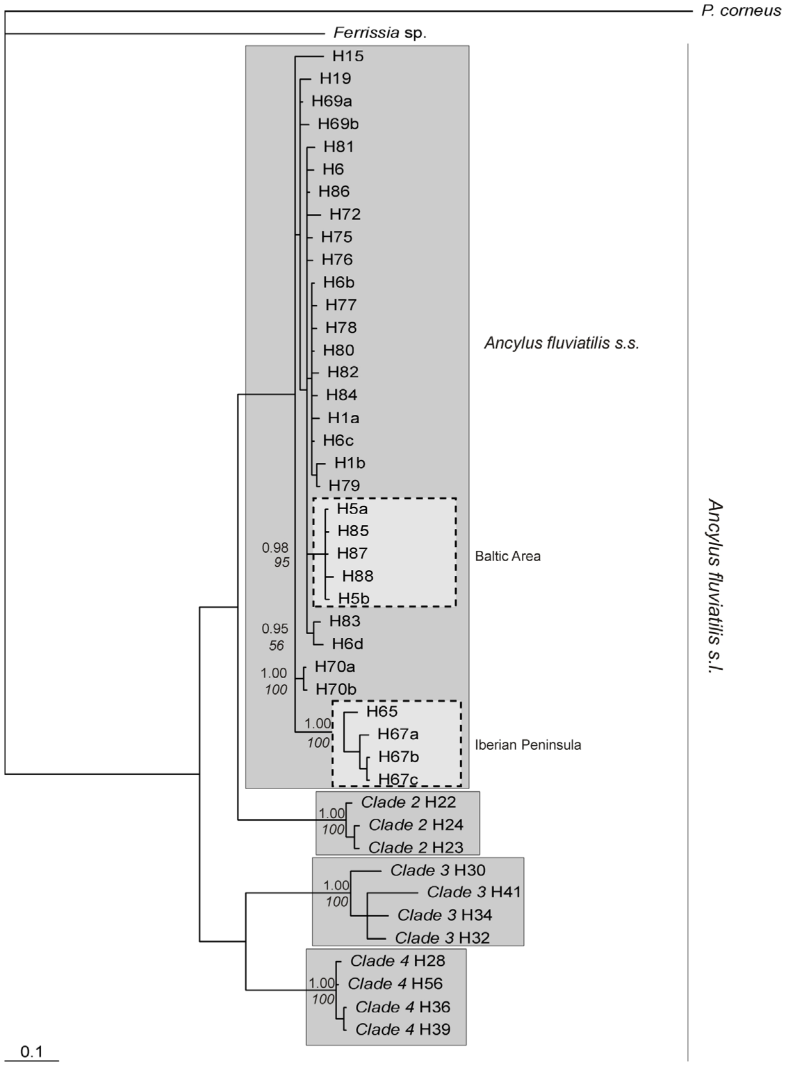

Figure 2.4: Bayesian inference tree of distance among *Ancylus fluviatilis s.s.* 16S haplotypes; cryptic species designation follows Pfenninger *et al.* (2003b). *Planorbarius corneus* and *Ferrissia* sp. were used as outgroups. Posterior probabilities from the Bayesian analysis are indicated above the branch, and the bootstrap values (from MP analyses) in italics, underneath. The phylogroups Iberian Peninsula and Baltic Area are accented with dashed lines.

Haplotype phylogeny

The Bayesian analysis of the *A. fluviatilis* sequences showed that all individuals belong to a well-supported monophyletic group equivalent to the other clades defined in Pfenninger *et al.* (2003b) (Figure 2.4). A maximum parsimony analysis yielded a congruent topology, regarding the major groups (data not shown).

Climatic niche

The PCA on climate variables retained three meaningful (larger than expected eigenvalues according to a broken-stick model) niche dimensions, accounting for 85.9% of the overall variance (Table 2.1). Axis 1, accounting for 44.7% of the total variation, opposed sites with cold and dry winters and annually variable temperatures, to populations in areas with warm and wet winters and more uniform temperatures. Axis 2 (26.8%) was a climatic gradient from warm and dry to cool and wet summers. The third axis (14.4%) distinguished between locations experiencing a wet summer and seasonally varying precipitations and a dry summer and a uniform precipitation regime throughout the year. Because the number of samples in each class was highly unbalanced (81 North Europe vs. five Iberian Peninsula, and 65 Central Europe vs. 16 Baltic Area), we performed new ANOVAs with subsets of the larger groups. Twenty random sub samples of size five were draw from North Europe locations and twenty random sub samples of size 16 from Central Europe populations as well. We then compared these new smaller groups to Iberian Peninsula and Baltic Area, respectively. It could be shown that the significant difference on Axis 3 observed between North and Iberian groups is due to some extreme values. The other results did not differ qualitatively from those presented here.

The realized climatic niche of the Iberian Peninsula populations differed significantly from those of the remaining populations for the second axis (Figure 2.5). Populations from the Iberian Peninsula experience a significantly warmer and drier summer than the northern populations. The Central Europe and Baltic sites also differed significantly from each other for the other two niche dimensions (Figure 2.5). While populations from the Baltic area endure relatively wet summers and seasonally strongly varying precipitations, those from Central Europe face drier summers and a more uniform precipitation regime throughout the year. The annual mean temperature was the most limiting of the climatic factors to account for the northern boundary of the range of *A. fluviatilis*.

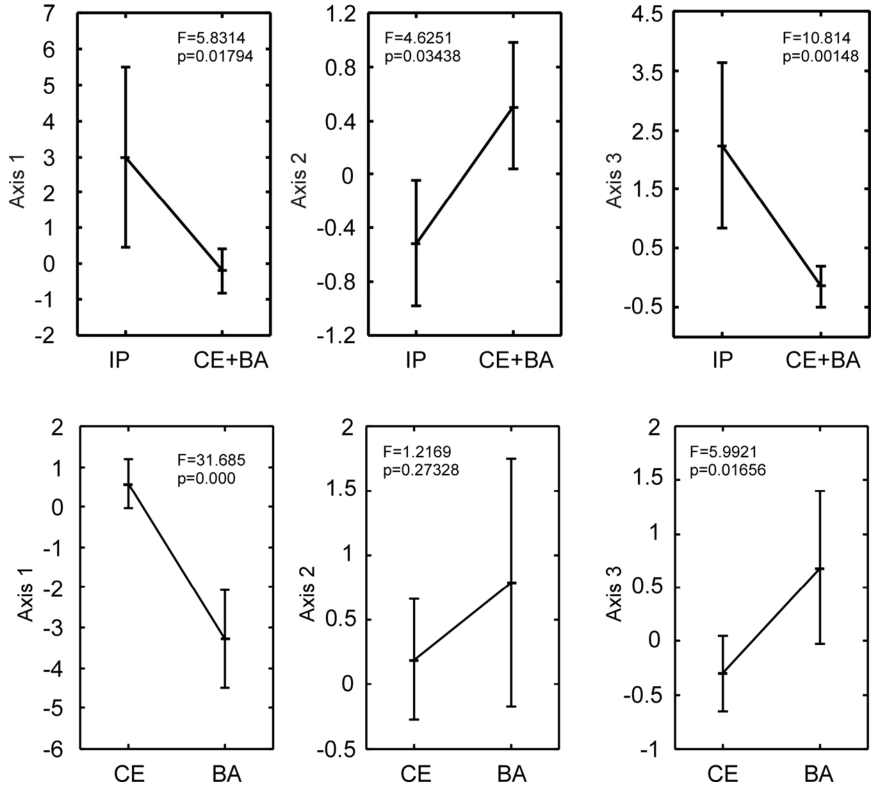

Figure 2.5: ANOVAs of Principal Components Analysis (PCA) factor values among phylogroups of *Ancylus fluviatilis s.s.* Error bars indicate 95% confidence intervals. IP, Iberian Peninsula; CE, Central Europe; BA, Baltic Area.

Species range prediction

The results of climate niche modelling are shown in Figure 2.6A. From the 672 point localities of the museum data set used to evaluate the quality of the modelling approach, 81% were included in the predicted area. We therefore assume that our sampling data set provides an adequate basis on which to model the area that would be occupied under a climate change scenario. The examination of predicted areas of climatic suitability at the end of the 21st century indicated a range shift of *A. fluviatilis s.s.* to the north and a dramatic loss of habitat in Central Europe (Figure 2.6B). In total, a loss of 43.6% of the area currently occupied by *A. fluviatilis* is predicted. Modelling predicted areas for the different phylogroups separately yielded very similar results (data not shown).

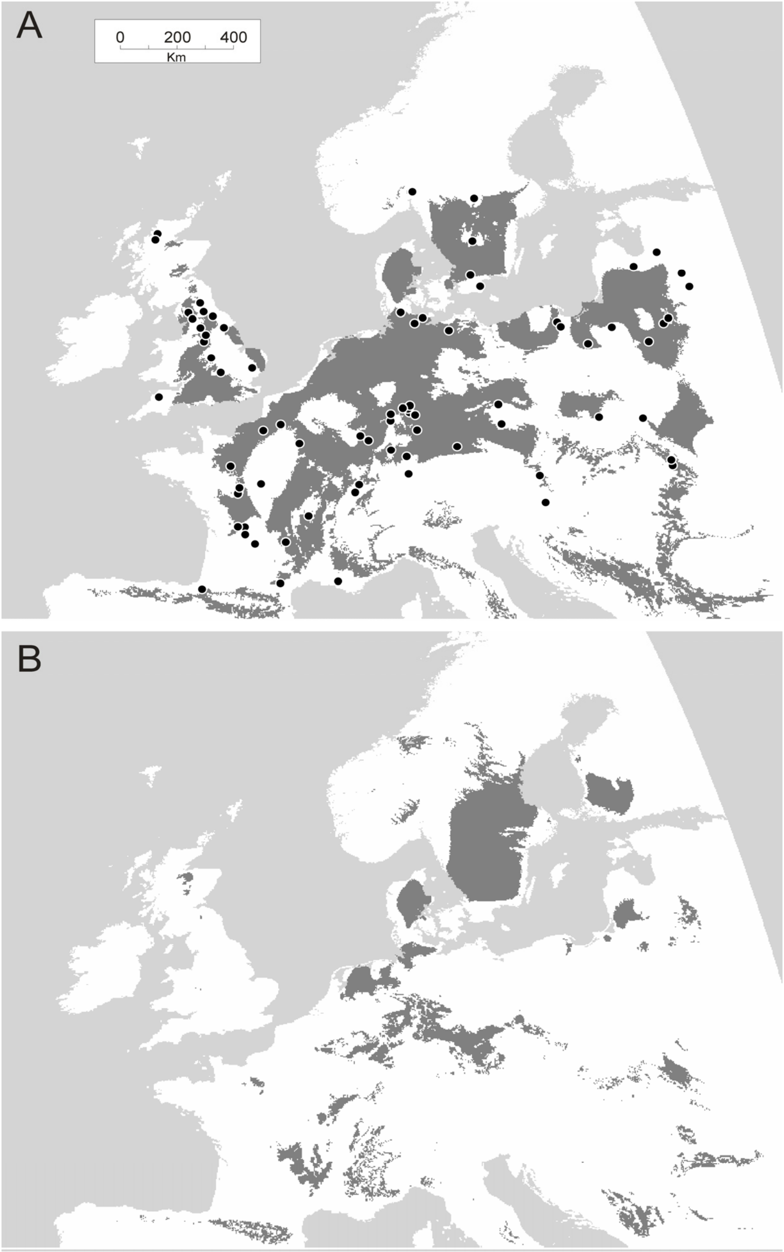

Figure 2.6: Predicted bioclimatic area, inferred with a BIOCLIM model from the effective presence data, showing the area occupied by *Ancylus fluviatilis s.s.* (light grey). (A) Map showing the potential present area (inferred with WorldClim climate data), with the sampling locations. (B) Map showing the potential future area, under the niche conservatism assumption (inferred with modelled climate data for year 2100, CCM3 model).

2.4 Discussion

Evidence for Central European refugium

Bayesian demographic analysis indicated that the most recent common ancestor of the northern clade, gathering populations from Central Europe and Baltic Area, lived at least 40,000 yr BP (Figure 2.3, lower 95% posterior density margin). The past fragmentation of the Iberian clade must therefore have taken place before that period. We can thus assume that the northern clade already existed during the last glacial maximum (LGM) and was never present on the Iberian Peninsula. Moreover, southern French populations (FRA3, FRA4) resulted more recently from a long distance colonization event. Southern France is therefore unlikely to have been a potential refuge. The current distribution of the most likely ancestral haplotype 6 is Central Europe. Survival through the LGM in Central Europe therefore seems to be the most parsimonious explanation for the observed phylogeographical pattern.

Although the nested clade analysis showed a range expansion of the species, other analyses of the molecular data (Fu's, Bayesian inference) did not yield clear evidence for an increase in effective population size in the past. An explanation could be the relatively small size of the expansion area compared with the refuge area. The colonisation of the expansion area, thus not requiring exponential demographic growth, didn't left traces in the shape of the gene tree.

Fossil records of *A. fluviatilis* (Baltic Ice Lake stage, 10,000-11,000 yr BP, Yoldia Sea stage, 9500 yr BP) in the Baltic area (Bennike & Lemke, 2001) strengthen the inference of this species' presence in Central Europe at early stages of deglaciation. Evidence for similar northern refuges for freshwater fishes of the genus *Cottus* (Hänfling *et al.*, 2002; Volckaert *et al.*, 2002), *Perca* (Nesbo *et al.*, 1999) and *Lota* (Van Houdt *et al.*, 2005) also reinforce the possibility of northern refugia for a freshwater gastropod.

Evidence for central or northern European refugia has also been found for several woodland tree species (Stewart & Lister, 2001) and voles and other small mammals (Bilton *et al.*, 1998; Brunhoff *et al.*, 2003; Kotlik *et al.*, 2006). High alpine plant species survived the glaciations either by 'nunatak' survival or survival at the periphery of the Alps (Schonswetter *et al.*, 2003; Tribsch & Schonswetter, 2003). All previous phylogeographical studies on land snails with a Palaearctic distribution (Haase *et al.*, 2003; Pfenninger *et al.*, 2003a; Wilke & Duncan, 2004, Pinceel, 2005 #55) suggest relatively northern refugia. Thus, the pattern of Pleistocene survival in southern refuges may be more complicated than proposed in Taberlet *et al.* (1998) and Hewitt (1999).

Taxonomic considerations

Both phylogeographic and phylogenetic analysis revealed the presence of a well-supported distinct lineage on the Iberian Peninsula that differed significantly in realized climatic niche and occupied a distinct geographical area. BIOCLIM analysis has already contributed substantially to the identification of two distinct species, for example in the Australian brown *Antechinus* species complex (Sumner & Dickman, 1998). However, the sequence divergence (Figure 2.4) between the monophyletic group located on the Iberian Peninsula and the other populations of *A. fluviatilis s.s.* is lower than the sequence divergence observed between *A.*

fluviatilis s.s. and the cryptic species described in Pfenninger *et al.* (2003b). Moreover, the lineage has no sister taxon relationship to the rest of the species. Further investigations with increased sampling in particular on the Iberian Peninsula are still necessary to determine if this clade represents a case of incipient speciation.

Climatic niche evolution

Most populations in the northern part of the current species range were sampled in previously glaciated areas in the Baltic area. We show that the realized niche of these populations differs significantly from the niche of Central Europe populations. Putatively living in waters of the tundra and steppe of the periglacial area during the LGM (Andersen & Borns, 1997), the species may have followed the northern shift of its habitat during the retreat of the ice cap. The populations that stayed in Central Europe experienced warming conditions, but rather than disappearing from this area they adapted to the new conditions. Even though a certain variation in environmental conditions may be expected over larger latitudinal distribution ranges, as in the present case, the non-overlapping confidence intervals and low internal heterogeneity on climate PCA axis 1 (Figure 2.5) suggested that the Central Europe populations now experience climatic conditions completely outside the ancestral climatic range. This large niche shift suggests adaptive evolution rather than phenotypic plasticity, the more so since Central European individuals of *A. fluviatilis* are relatively vulnerable to water temperature changes (unpublished data).

With few exceptions (Davis & Shaw, 2001), phylogeographical studies have relied on the tacit or explicit assumption of niche conservatism to explain inferred range expansions (Taberlet *et al.*, 1998; Hewitt, 2004). However, several well-known examples show that local adaptation is possible in very short evolutionary time, if the selection pressure is strong enough, even in the face of gene-flow (Grant & Grant, 1993; Carvalho *et al.*, 1996; Schluter *et al.*, 2001; Hoekstra *et al.*, 2004; van Heerwaarden & Hoffmann, 2007), and this might be also the case with *A. fluviatilis*.

Temperature was found to be the most limiting factor for *A. fluviatilis* on its actual northern range margin, low annual average temperature probably preventing the species from expanding its range further. However, it is possible that *A. fluviatilis* has not reached the limits of its potential range simply because of limited dispersal capacities (i.e. historical reasons). However, the generally good dispersal ability of small freshwater organisms (Bilton *et al.*, 2001), also studied for several snails (Brönmark, 1985; Myers *et al.*, 2000), indicates that this species has rather reached its physiological limits.

The approach we chose to assess the validity of the species' distribution allowed us to draw well-supported conclusions about the evolution of the range of *A. fluviatilis* through time. We also showed the ability of *A. fluviatilis* to adapt, in a relatively short evolutionary time, to changing bioclimatic conditions. We must therefore be cautious about the predictions of the model. We have to consider the hypothesis that this species is able to adapt to the new conditions, as it did in the past. The crucial question is whether the species can cope with the speed of the oncoming global change. If not, this species may experience a dramatic decrease in its distribution range if the model itself is reliable. In such an event, this may affect the entire ecosystem, because grazing pressure on the biofilm by *Ancylus fluviatilis* would probably be reduced. However, some of the climatically differently adapted cryptic species described in Pfenninger *et al.* (2003b) may colonize the vacant niche.

Bioclimatic models often represent the most feasible method of examining potential distributions of species (Beaumont *et al.*, 2005). However, bioclimatic model predictions based on the same data but derived from different algorithms can produce widely divergent outcomes and even when consistent in their predictions have a high probability of being wrong (Araujo *et al.*, 2005b). This paper adds a supplementary cautionary note to the predictive power of such approaches that do not consider evolutionary processes. Once the frequency of niche evolution, as well as its speed and extent are better understood, it might be possible to include this uncertainty in predictive modelling.

3RD CHAPTER

Inferring the past to predict the future: climate modelling predictions and phylogeography for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora)

Abstract

Understanding the impact of past climatic events on species may facilitate predictions of how species will respond to future climate change. To this end, we sampled populations of the common pond snail *Radix balthica* over the entire species range (NW Europe). Using a recently developed analytical framework that employs ecological niche modelling to obtain hypotheses that are subsequently tested with statistical phylogeography, we inferred the range dynamics of *R. balthica* over time. A Maxent modelling for present-day conditions was performed to infer the climate envelope for the species, and the modelled niche was used to hindcast climatically suitable range at the last glacial maximum (LGM) ca 21 kyr ago. Ecological Niche Modelling predicted two suitable areas at LGM within the present species range. Phylogeographic model selection on a COI mtDNA dataset confirmed that *R. balthica* most likely spread from these two disjunct refuges after the last glacial maximum. The match observed between the potential range of the species at LGM given its present climatic requirements and the phylogeographically inferred refugial areas was a clear argument in favour of niche conservatism in *R. balthica*, allowing thus to predict the future range. The subsequent projection of the potential range under a global change scenario predicts a moderate pole-ward shift of the northern range limits, but a dramatic loss of areas currently occupied in France, western Great Britain and southern Germany.

Molecular Ecology (2009), ***18****, 534-544, together with M. Pfenninger*

3.1. Introduction

The evidence for a rapid and profound climate change within the next century is now largely undisputed. Temperatures are predicted to rise by up to 4 °C by 2100, associated with changes in precipitation patterns. Ecologists already observed poleward and upward shifts of the species ranges (Thuiller *et al.*, 2005). It is therefore a major challenge for ecology to estimate and predict the consequences of global warming on biodiversity.

One means to achieve such predictions is Ecological Niche Modelling (ENM). This method predicts potential distributions for species by deriving an environmental envelope from known distribution points and projecting this envelope onto a spatially interpolated climate surface of an area. Ecological modelling has been used to accurately model the present distribution of many species (e.g. Peterson, 2001; Anderson *et al.*, 2002; Hijmans & Graham, 2006). However, it can be used to predict past and future distributions under the assumption that a species' climatic niche (the set of abiotic condition under which surviving and reproduction are possible) is constant over time. Many studies (Bakkenes *et al.*, 2002; Berry *et al.*, 2002; Humphries *et al.*, 2002; Skov & Svenning, 2004; Thuiller *et al.*, 2006) assumed such niche conservatism to predict the future potential geographical distributions of plants and animal species, resulting in many cases in dramatically reduced species ranges (Thomas *et al.*, 2004). However, the degree to which geographical distribution shifts follow consistent climate regimes is poorly known. Evidence for niche conservatism has been shown for several taxa (Peterson *et al.*, 1999; Peterson & Holt, 2003; Martinez-Meyer *et al.*, 2004), but it may not be a general pattern (Rice *et al.*, 2003; Ruegg *et al.*, 2006; Pfenninger *et al.*, 2007). Thus, it appears advisable to test the assumption of niche conservatism before reasonable predictions about the future distribution of a particular species can be made.

The comparison of inferences obtained through phylogeographic analysis and ENM provides a test of the niche conservatism assumption. Phylogeography was successfully used in the past two decades to reconstruct refugial distributions at the last glacial maximum (LGM) and the subsequent range dynamics from the current distribution pattern of genes across landscapes (Hewitt, 2001). A match between phylogeographically inferred refugial areas and the potential range of the species at LGM given its present climatic requirements can be considered as a clear argument in favour of niche conservatism. This in turn justifies the use of ENM for future predictions. A mismatch between both inferences, however, can have several explanations, beginning with methodological errors either in phylogeographic inference, ENM modelling, or barriers to dispersal. If such errors can be ruled out, a possible alternative explanation is that the species' climatic niche has indeed evolved, as has been suggested e.g. for the land snail *Candidula* (Pfenninger *et al.*, 2007).

The genus *Radix* Montfort 1810, formerly included in *Lymnaea*, is part of the Lymnaeidae family (Basommatophora). A previous study conducted on the genus *Radix* revealed the presence of at least five reproductively isolated Molecularly defined Operational Taxonomic Units (MOTU) in north-western Europe, whose taxonomic affiliation remain uncertain (Pfenninger *et al.*, 2006). MOTU 2 was found exclusively in north-western Europe and fits therefore the assumed distribution of the described species *Radix balthica* (L., 1758). Although no formal taxonomic attribution to this name has yet been made, we will use this name hereafter.

The species occurs in many permanent slow-flowing rivers, the shore zone of lowland lakes and ponds, and even irrigation channels or fountains, without demanding a particular substrate or high water quality (Økland, 1990; Glöer & Meier-Brook, 1998). Though prone to fossilisation like all shell-bearing molluscs, a reconstruction of its historical distribution by the fossil record is not possible, because the shell shape is not species specific in *Radix* and allows thus no unequivocal assignment (Wullschleger & Jokela, 2002; Pfenninger *et al.*, 2006).

Here we used a recently developed analytical framework, drawing both on phylogeography and ENM (Dépraz *et al.*, 2008) to analyse the past range dynamics of a *Radix* species and make reliable predictions about the influence of global warming on its range. We achieved this by first inferring possible LGM refugia of *R. balthica* through projection of the present niche requirements of the species onto climatic surface data for the LGM. We then tested the resulting and alternative hypotheses with statistical phylogeography methods. This proceeding allowed the evaluation of niche conservatism in *R. balthica*, in order to reasonably predict the future range of the species in the oncoming climate change.

3.2. Materials and Methods

Populations sampled and distribution of the species

One hundred seventy-two individuals from 49 populations covering the entire range of *R. balthica* were sampled and immediately stored in 95% ethanol. Additionally, we included in this study the sequences of 60 individuals from 29 populations published in Pfenninger *et al.* (2006) (Acc. Num. DQ980030-0193), making a total of 232 individuals from 78 populations.

Sampling sites and number of individuals sequenced are shown in Appendix S3, and are mapped in Figure 3.1.

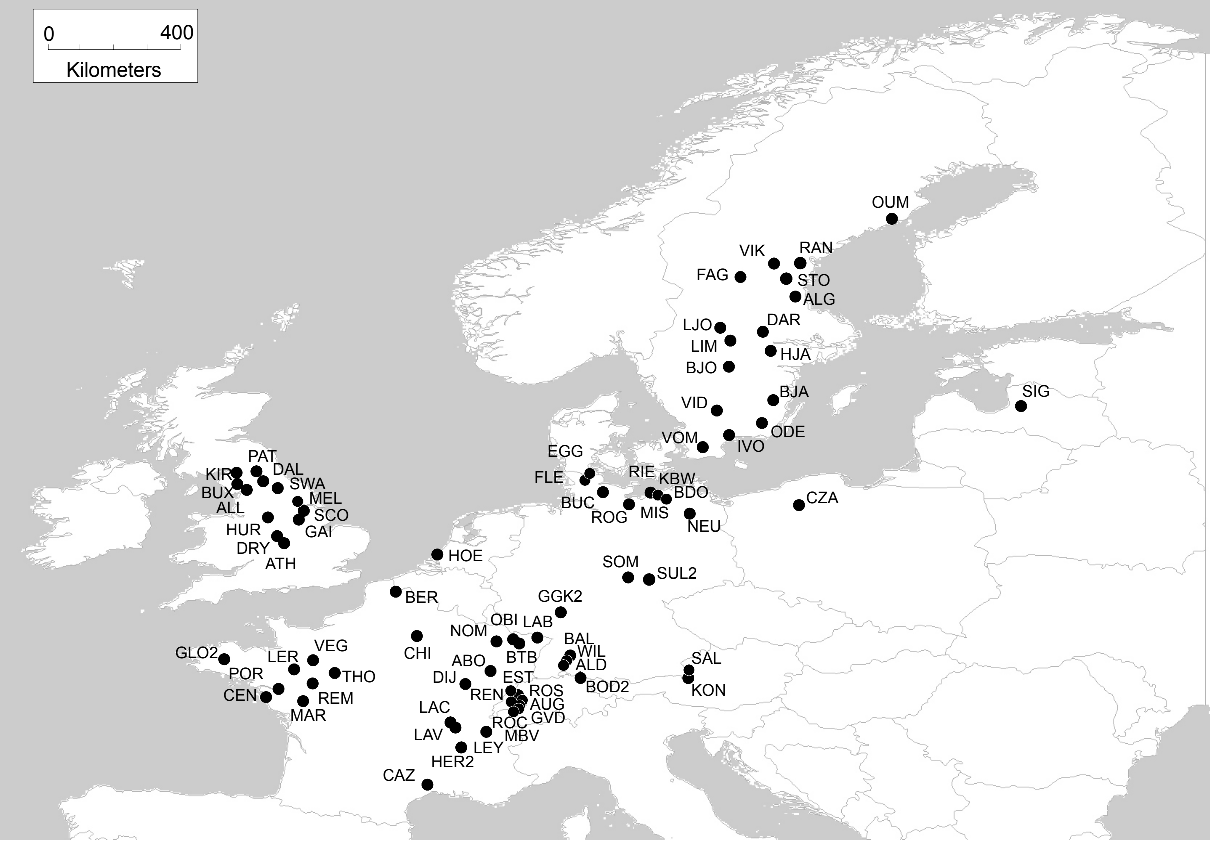

Figure 3.1: Map of the sampled populations of molecularly identified *R. balthica*. This represents the most accurate estimation of the species range given the problems with morphological species identification in the genus (Pfenninger *et al.*, 2006).

Climatic data

The climatic envelope occupied by the species is described through 19 environmental variables, listed in Table 3.1. These 19 bioclimatic variables likely summarise dimensions of climate particularly relevant in determining species distributions (Waltari *et al.*, 2007). We have not taken hydrological variables into account, because they are not available at a relevant scale. Since the grid cells of climatic layers are about 5x5 kilometres, the presence of principally suitable habitats (drainages ditches, small creeks, ponds, etc…) can be assumed for all cells considered. For Last Glacial Maximum (LGM), present and future climate conditions, we used three sets of monthly climate data (precipitation and temperature). For current conditions (means 1950-2000) we used WorldClim, a global climate database with a spatial resolution of 2.5 minutes (Hijmans *et al.*, 2005), available at http://www.worldclim.org. The LGM climate layers were kindly provided by E. Waltari and R. Hijmans, described in Waltari *et al.* (2007) and created as follows. Data for LGM were drawn from general circulation model (GCM) simulations from the Model for Interdisciplinary Research on Climate (MIROC) (Hasumi & Emori, 2004). The original MIROC3.2 data were obtained from the PMIP2 website (http://pmip2.lsce.ipsl.fr, 01-25-2008) with a spatial resolution of 2.8°, and downscaled to a definition of 2.5 minutes. To obtain past climatic data with this resolution, the differences between LGM and recent (pre-industrial) MIROC climate data were first calculated at the native coarse resolution. The interpolated difference maps were then added to the WorldClim current climate data which has a spatial resolution of 2.5 minutes. This established procedure (Ruegg *et al.*, 2006; Waltari *et al.*, 2007) has the double advantage of producing data at a resolution relevant to the spatial scale of analysis, and of calibrating the downscaled LGM climate data to actual observed climate conditions. The species' bioclimatic niche was also projected on a future climate scenario for the end of 21nd century, according to the GCM HadCM3, with a scenario reflecting an important increase in CO_2 concentration as a result of non-restricted CO_2 emission (Intergovernmental Panel on Climate Change, Special Report on Emission Scenarios, scenario A2; Nakicenovic, 2000).

Table 3.1: Bioclimatic variables used for the ecological niche modelling

	Name	Variable definition
BIO1	Annual mean Temperature	
BIO2	Mean Monthly Temperature range	
BIO3	Isothermality	(BIO2/BIO7)(*100)
BIO4	Temperature seasonality	(Standard deviation*100)
BIO5	Max Temperature Warmest month	
BIO6	Min Temperature coldest month	
BIO7	Temperature annual range	(BIO5-BIO6)
BIO8	Mean Temperature Wettest quarter	
BIO9	Mean Temperature Driest quarter	
BIO10	Mean Temperature Warmest quarter	
BIO11	Mean Temperature coldest quarter	
BIO12	Annual Precipitation	
BIO13	Precipitation Wettest month	
BIO14	Precipitation Driest month	
BIO15	Precipitation seasonality	Coefficient of variation
BIO16	Precipitation Wettest quarter	
BIO17	Precipitation Driest quarter	
BIO18	Precipitation Warmest quarter	
BIO19	Precipitation Coldest quarter	

Estimation of climatic niche and range prediction

The realised environmental niche can be estimated from presence-only data with high precision by extracting niche dimensions from spatial information on the distribution of environmental parameters (Nix, 1986). From the multitude of available ecological niche modelling methods, the Maximum entropy model (Maxent, Phillips *et al.*, 2004; Phillips *et al.*, 2006) was used to predict where *R. balthica* is likely to occur under current climatic conditions. We chose the maximum entropy approach because of its good performance with presence only data, as shown in Elith *et al.* (2006). Maxent generates ENM using presence-only records, contrasting them with pseudo-absence data sampled from the remainder of the study area. The present day ENM was developed based on the 78 molecularly confirmed occurrence points of the species. The species' bioclimatic niche was then projected on past climate layers to predict the species potential range at LGM. The species' bioclimatic niche was also projected on future climate layers. Future areas of climatic suitability were compared with present day suitable areas and present distribution, by calculating the percentage of area lost under two dispersal scenarios: no dispersal and unlimited dispersal. The no dispersal scenario assumed that the species is incapable of dispersal, in which case the new suitable area is the overlap between current and future potential range, while the unlimited dispersal assumed that the future species suitable area becomes the entire potential future range projected with ENM.

We used the default convergence threshold (10^{-5}) and maximum number of iterations (500) values, using 25% of localities for model testing. We let the program select both suitable regularisation values and functions of environmental variables automatically, which it achieves based on considerations of sample size. Maxent outputs a continuous probability value (cumulative values), which is an indicator of relative suitability for the species. We chose a presence threshold to render each projection into a binary form. We considered grid cells with a cumulative probability of more than 10 (from a range of 0-100) as suitable, as suggested by Waltari *et al.* (2007) and Pearson *et al.* (2007). This threshold identified smaller areas than a lowest presence threshold that yielded zero omission error, thus resulting in a more restricted picture of the potential distribution. The area under the ROC curve (AUC) gave an evaluation of the projections' overall quality. An AUC score above 0.7 is considered good model performance (Fielding & Bell, 1997).

DNA extraction, fragment amplification and sequencing

Individuals preserved in 95% ethanol were extracted from their shell and DNA isolated following a slightly modified CTAB protocol published in Winnepennickx *et al.* (1993). A 5'-fragment of the COI target mtDNA was amplified for all samples by PCR with universal primers described in Folmer *et al.* (1994). Amplification was performed with Invitrogen *Taq* DNA polymerase in 25µL total reaction volume with standard reaction conditions. Samples were amplified for 40 cycles (90°C for 30 s, 48°C for 1 min, ramp 0.3°C/s to 72°C, and 72°C for 1:30 min) after initial incubation at 94°C for 2 min 30 s. PCR products were purified using the PureLink PCR Purification Kit (Invitrogen, USA) and directly cycle-sequenced with ABI BigDye®Terminator v.3.1 Ready Reaction Sequencing mix (Applied Biosystems, USA) on the ABI 3130xl capillary sequencer. Sequences were deposited in GenBank (Acc. Nos. FJ470328–93). All the sequences were initially aligned with CLUSTALW as implemented in BIOEDIT and adjusted manually.

Phylogenetic relation of haplotypes

A minimum-spanning network among mtDNA haplotypes was constructed using ARLEQUIN (Excoffier *et al.*, 2005). The minimum-spanning network represents all possible minimum length connections among the genotypes.

Estimating variation in effective population size over time

To infer range expansion from haplotype data, we relied on two conceptually different approaches. The first approach is based on the assumption that geographic range expansions should be accompanied by a demographic population growth. This growth is expected to leave traces in the shape of gene-trees compared to neutral expectations in coalescent theory. Tajima's *D* (Tajima, 1989) examines the shape of gene-trees to test for deviation from a selectively neutral coalescent process in a population of constant effective size. The *F*-statistic (Fu, 1997) detects an excess of low-frequency alleles expected in the course of a population expansion (Schneider & Excoffier, 1999). Significant negative deviations of these indexes from zero are interpreted either as evidence of selective sweeps (Fu, 1997) or population expansions (Slatkin & Hudson, 1991; Fu, 1997). Positive deviations may indicate a long lasting population subdivision (Slatkin & Hudson, 1991; Fu, 1997). All calculations were performed on the entire dataset with ARLEQUIN (Excoffier *et al.*, 2005).

The second approach is based on the assumption that episodes of population growth and decline may also leave characteristic signatures in the distribution of pairwise nucleotide differences of populations (mismatch distribution; Rogers & Harpending, 1992). The validity of the demographic expansion hypothesis was tested using a parametric bootstrap approach, in which the sum of squared deviation (SSD) among the observed distribution and the expected distribution was compared to the SSD among the simulated distributions and the expected distribution. This test was conducted in ARLEQUIN v. 3.1 (Excoffier *et al.*, 2005). Since we are aware of limitations of this approach (different processes may produce similar mismatch patterns resulting in partially unrealistic assumptions (Rogers & Harpending, 1992; Excoffier, 2004), we simply use it as additive arguments for inferred phylogeographical scenarios.

Refugial model selection

To evaluate different explicit refugial hypotheses simultaneously, we applied a model selection approach (Johnson & Omland, 2004; Stephens *et al.*, 2007), which was first introduced in phylogeography in Pfenninger & Posada (2002) and extended in Dépraz *et al.*, (2008) and Jesse *et al.* (2008). We formulated twelve hypotheses reflecting potential spatial settings and processes governing the initial postglacial colonisation. These hypotheses combined three colonisation modes (stepping-stone, direct and passive waterfowl migration) with four refugial area scenarios (*Central*, *Southern*, *Western* and "*two-refugia*"). The latter reflected the hypothesis gained from ENM. The passive waterfowl migration pathways are derived from personal communication of K. Schwenk.

In order to find general patterns and to keep computations feasible, the 78 sampling sites were pooled into geographically coherent clusters. This clustering was performed with a spatially restricted k-means approach modified from Guiller *et al.* (2006). The k-means clustering was first performed 10 times on the average pairwise population sequence divergence matrix for k values between 4 and 10. To obtain geographically coherent clusters, the algorithm was constrained by the connections of the Delaunay triangulation network among sampling sites. The k-means software was kindly provided by A. Guiller. For each clustering result, an AMOVA (Excoffier *et al.*, 2005) was then performed, grouping the populations according to the obtained clusters. We retained the configuration that maximised the variance among groups for further analyses. The different hypotheses were translated into corresponding migration matrices. It should be noted that the migration matrices contrasted different hypothesis on the initial colonisation rather than the probably more complex current gene-flow patterns. The maximum likelihood migration rates among these clusters and associated thetas for all models were then estimated using Migrate-n version 3.0 (Beerli & Felsenstein, 2001).

The first genealogy was started with a random tree. Initial theta and migrant values were generated from an F_{ST} calculation. A static heating scheme with four different temperatures was applied. We ran ten short chains with 40,000 generations each, from which 1000 trees were recorded in regular intervals after a burn in phase of 20,000 generations. These were followed by three long chains of 1,000,000 generations each from which 10,000 trees were sampled after a burn in period of 20,000 generations. Parameter estimates were gained from the last chain. Log-likelihood estimates cannot be compared over different runs with Migrate-n. We ran therefore a final analysis with an unconstrained migration model. Using the likelihood-ratio-test option, we gained comparable log-likelihood estimates for the previously estimated parameter sets under this model. We used these estimates and the number of free parameters in each model to calculate the Akaike Information Criterion (AIC, Akaike, 1974) and resulting Akaike weights to obtain measures of relative model support.

3.3. Results

Maxent modelling of current, paleo- and future distribution

The present range of *R. balthica* predicted through the projection of its bioclimatic niche on present climate is shown on Figure 3.2A. The AUC score for this modelisation was high (0.94). The niche projection on climatic layers for Last Glacial Maximum (Figure 3.2B) predicted a substantial reduction in range during the drier and cooler conditions of the LGM. One major refuge area, stretching from central France to central Germany was suggested. The modelling additionally predicted small discrete refugees north of the eastern Alps (area around Salzburg, Austria), south-western France and the eastern Pyrenees, in northern Spain, in the now Venetian Gulf and Slovenia, and in northern Balkans. Except for the first, however, these small predicted refuges are presently not inhabited by *R. balthica* and could therefore not be considered in the phylogeographic analysis.

The projection of the future bioclimatically suitable area of the snail showed a general shift of the present predicted range to the north (Figure 3.2C). Northern Great Britain was predicted to become suitable, as well as northern parts of Scandinavia (Norway and Finland). In the centre of the range, France and south-western Germany become unsuitable, as well as Poland. The area predicted to be suitable decreases by 30% between today and 2080 under the unlimited dispersal scenario. Under the no dispersal scenario, the area predicted to be suitable decreases by almost 60%.

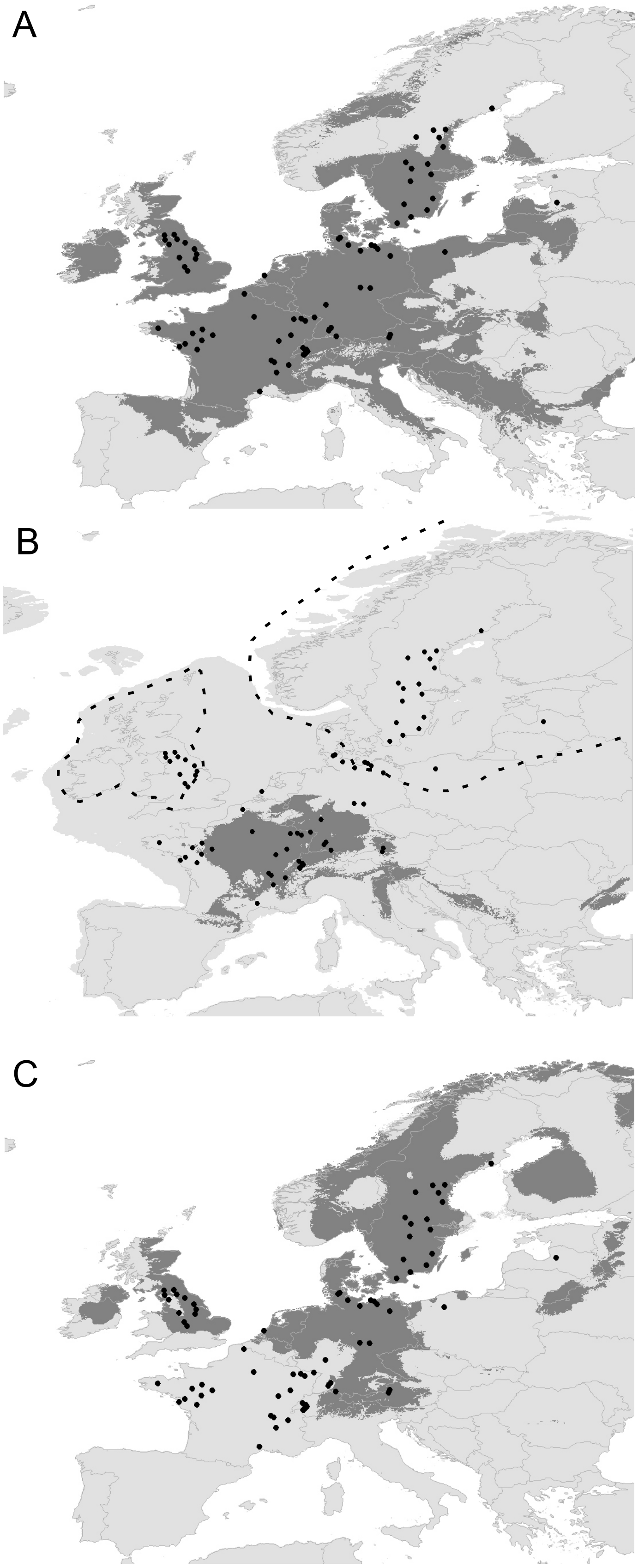

Figure 3.2: Prediction of present (A), past (B) and future (C) range of *R. balthica*, as inferred from respectively WorldClim, MIROC3.2 and HadCM3_A2 climatic datasets (equal area projection). Unsuitable areas are light grey, suitable dark grey and white represent the areas without data. The dashed line indicates the approximate limits of ice sheets (Peltier, 1994; Ray & Adams, 2001). Black dots represent locations where *Radix balthica* was sampled.

MtDNA sequence variation and parsimony network

In total 232 individuals from 78 populations were available for analysis (Appendix S3). We could recover and align 405 bp of the COI fragment. Eighty-two polymorphic sites were observed, defining 95 mtDNA haplotypes. The haplotypes and their distribution among the populations are presented in Appendix S3. The Minimum Spanning Network is shown in Figure 3.3.

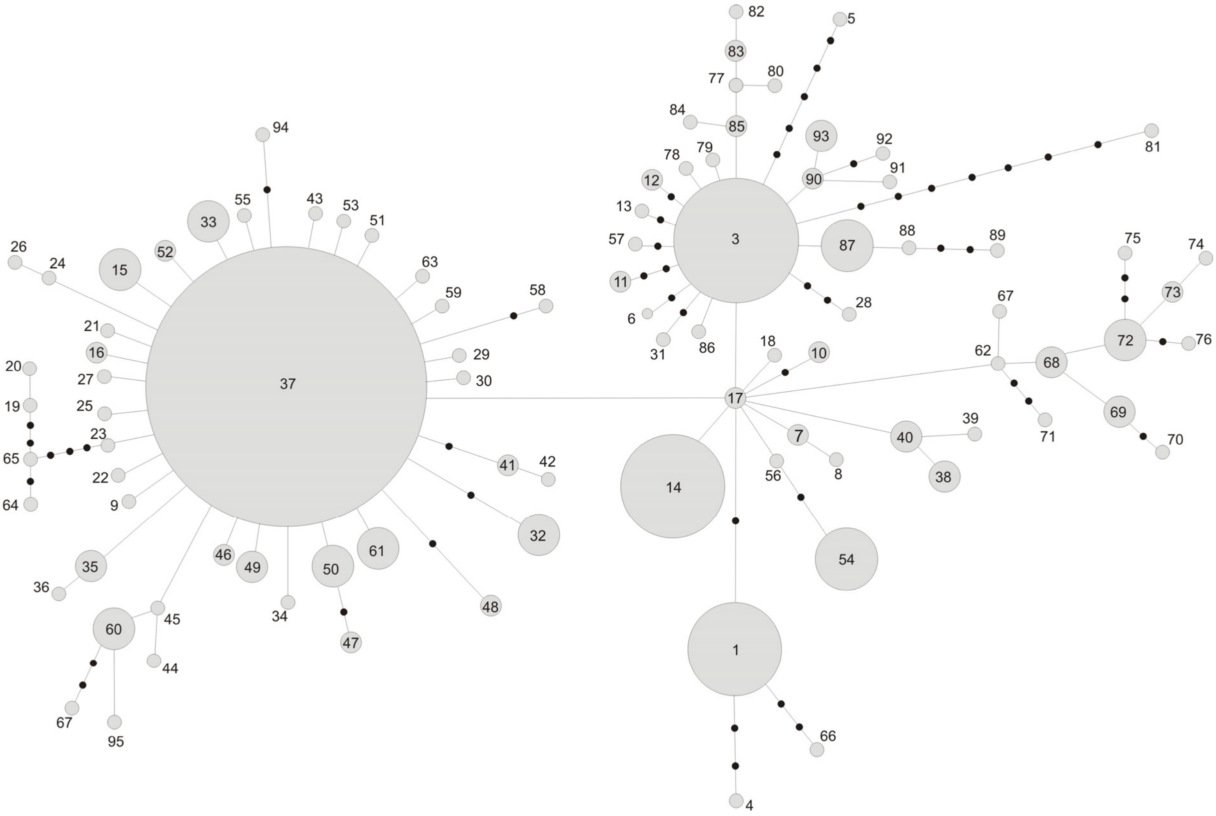

Figure 3.3: Minimum Spanning Network. Each circle represents a haplotype, its size being proportional to the frequency of occurrence of a certain haplotype. Small plain circles represent haplotypes that where not sampled. Connecting lines represent one mutational step.

Changes in population size

Fu's F_s (-25,49813 ***) was highly significant. This suggests a population expansion (Slatkin & Hudson, 1991; Fu, 1997; Ray *et al.*, 2003). This is confirmed by Tajima's D (-2,136***), also significant. Neither a sudden expansion model nor a spatial expansion model could be rejected by the match-mismatch distribution analysis (Figure 3.4).

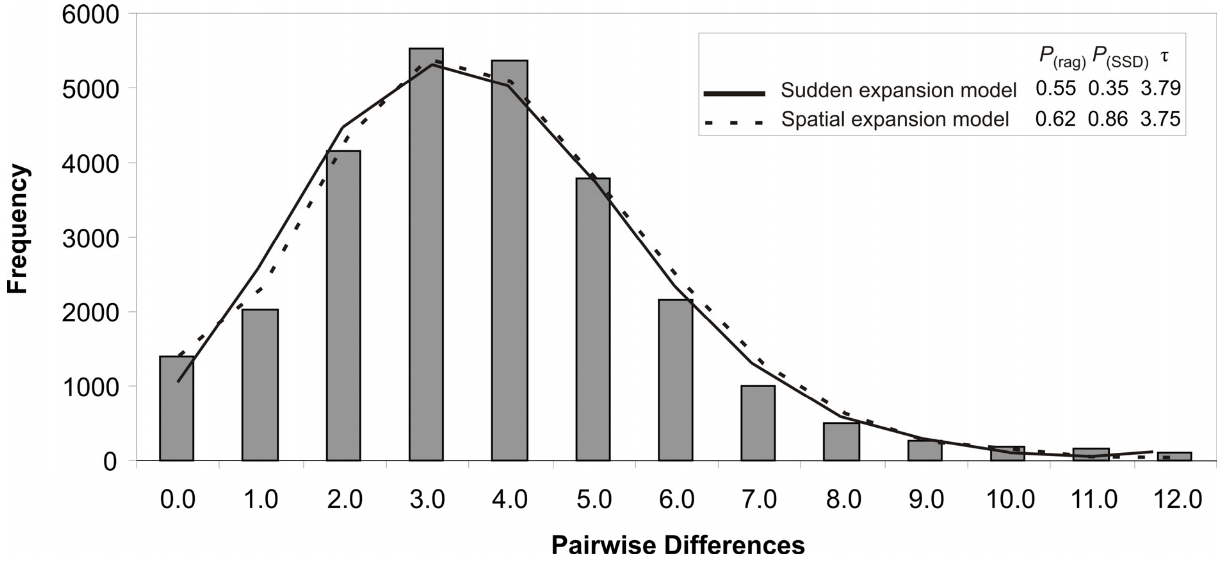

Figure 3.4: Results of mismatch distribution analysis. Bars represent the frequency of observed pairwise differences among *R. balthica* haplotypes. The black line depicts the theoretical distribution as expected under the hypothesis of sudden expansion, the dotted line the distribution under of spatial expansion hypothesis. Various demographic parameters are also shown: τ the expansion parameter expressed in units of mutational time; $P_{(rag)}$ the probability of observing by chance a higher value of the raggedness index than the observed one under the hypothesis of population expansion and $P_{(SSD)}$ the probability of observing by chance a higher value of the sum of squared deviations than the observed one under the hypothesis of population expansion.

Model selection

A maximum of among group variance (23.8%) was found with eight clusters, containing 2 to 21 populations. The population pooling scheme is given in Figure 3.5A. Two of the inferred population cluster (*Central* and *East*) matched two predicted LGM refugia. Model selection criteria supported two dispersal scenarios, both within the *two-refugia* hypothesis. The "stepping-stone" dispersal scenario had an AIC of 7979, with an Akaike weight of 0.82, while the "migratory waterfowl" dispersal scenario yields an AIC of 7982 with an Akaike weight of 0.17. The other scenarios were not supported by the data (cumulative Akaike weight < .0.01, Figure 3.5B). The supported model implied at least two LGM refugia (*Central* and *East*) in central Europe, one spanning from north-eastern France to south-western Germany, the other north of the eastern Alps (area around Salzburg, Austria).

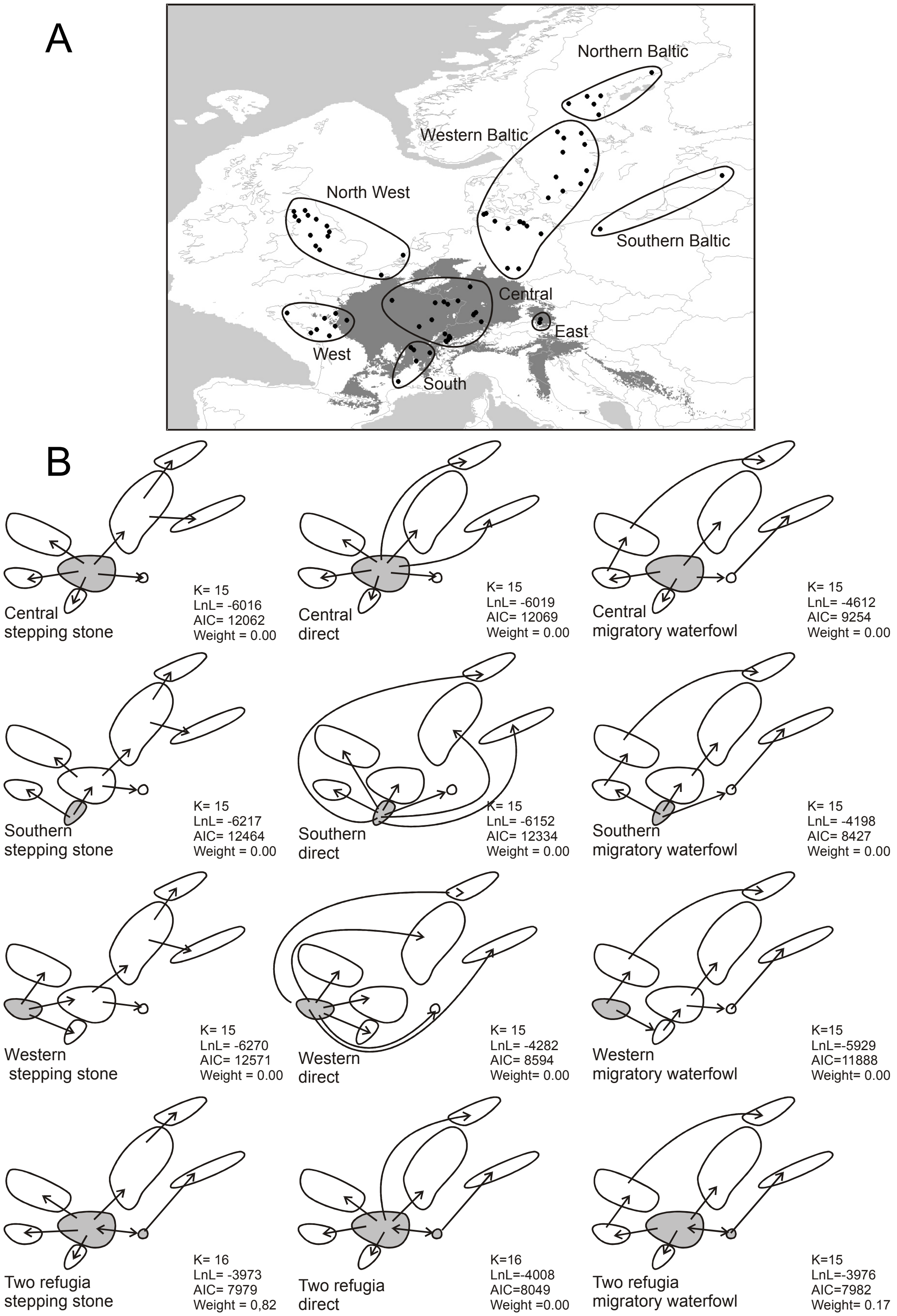

Figure 3.5: Design and results of migration model selection approach. A: Population pooling scheme, derived from spatial clustering for Migrate-analysis. The grey shaded area correspond to the Maxent predicted suitable area. B: Migration models applied. Grey areas denote source populations; arrows indicate assumed direction of gene-flow. LnL denotes the log-likelihood of the parameter set, K gives the number of free parameters in the model. AIC values measure the fit of the models to the data, taking different parameterisation into account. Note that smaller AIC values indicate better fit. The Akaike weight informs about relative model support.

3.4. Discussion

Climate modelling of the present range

Ecological niche modelling has been extensively used to deduce species potential ranges from known occurrence data. However, its very nature makes ENM prone to range overestimation, because it uses only a limited number of all possible biotic and abiotic factors. For instance, ENM has been criticised for not including historical factors such as dispersal processes (Davis *et al.*, 1998). However, given the good dispersal capacities of small freshwater animals (Bilton *et al.*, 2001), we assume that the snail could reach all potentially suitable areas since the last glaciation event. Other factors not taken into account by current ENM are biotic interactions. These may explain some discrepancies between the predicted area and our knowledge of the species range. We know from previous studies that *R. balthica* does not occur in eastern Europe, more precisely the Balkans (Pfenninger *et al.*, 2006), where substantial areas are predicted as suitable in the ENM (Figure 3.2A). However, a closely related species of *R. balthica* occurs in the eastern predicted range (Pfenninger *et al.*, 2006). Indeed, suitable area for a species can be occupied by sister species having similar requirements (Peterson *et al.*, 1999; Cook *et al.*, 2004; Waltari *et al.*, 2007). Nevertheless, the performance indicator (AUC, area under the curve) used to estimate the quality of the projection scored high (0.94).

Paleoclimate modelling and hindcasting LGM refugia

Until recently, precise climatic data for LGM were available only for restricted regions. Concerted efforts of climatologists have recently provided climatic data for LGM based on various sources (pollen, glaciology). Despite the considerable amount of work such databases represent, their use in ecology is still deemed difficult, mainly because of their very coarse scale. The downscaling method used here is aimed at overcoming this difficulty, but relies on assumptions in need of further validation (Waltari *et al.*, 2007).

In this study, the projection of the current climatic requirements of *R. balthica* onto LGM climatic layers yielded several potentially suitable areas across Europe (Figure 3.2B). Two of them lay within the current species range and could thus be used to generate hypotheses for the model selection analyses (Figure 3.2A). The other areas also defined as climatically suitable might as well have served as LGM refugia. However, since the populations from these hypothetical refugia are extinct (if they ever existed in the first place), their contribution to the current genetic diversity is at best indirect via existing populations.

Phylogeographic test of ENM derived hypotheses

The retreat of the ice sheet was followed by the emergence of suitable habitat for *R. balthica*. The resulting species range expansion, tracking its habitat, must have been logically associated with a demographic expansion. This was supported by the results of the match-mismatch distribution analysis (Figure 3.4), even though it was not possible to make a distinction between a sudden and a spatial expansion model. The indices D and F_s also deliver results concordant with an expansion event.

The model selection approach permitted testing relative support of the different plausible refugial/colonisation scenario (Figure 3.5B). An advantage of model selection is that it allows testing simultaneously different competing models, instead of testing each of them against a null model (Johnson & Omland, 2004). This allows the inclusion of prior information to the model, such as a gene flow direction consistent with the direction of the ice sheet retreat, and refugial areas outside the ice sheet at LGM. Model selection clearly showed that two dispersal scenarios within the "*two-refugia*" hypothesis received overwhelming support by the data, compared to the competing models (Figure 3.5). Their isolation in the Pleistocene was also supported by the match of the population grouping inferred by spatial clustering with proposed ENM refugias at LGM. According to the analyses conducted on mitochondrial data, *R. balthica* was thus isolated in at least two distinct refugia in north-western Europe during LGM, and expanded then its range to areas south-, north- and westward. This species joins the currently growing group of species inferred to have had cryptic refugia (for reviews see Provan & Bennett, 2008 and Stewart & Lister, 2001). The model selection approach also allowed assessing the relative support of different dispersal scenarios. The "migratory waterfowl" dispersal scenario gained some support by the data, which suggested that this process played a role in the post glacial colonisation, as already suspected by Darwin for freshwater invertebrates in general (1859). However, the better support of the stepping stone scenario indicated that short scale dispersal played a more important role in tracking the emerging habitat. Altogether, our analyses suggested that the post glacial colonisation succeeded through complex processes, where diverse dispersal modes had their part.

The match between statistical phylogeography analysis and ecological niche modelling argues for niche conservatism in *R. balthica.* This finding adds the snail to several animal and plant species where such an absence of niche evolution has been demonstrated (Prinzing *et al.*, 2001; Martinez-Meyer *et al.*, 2004; Martinez-Meyer & Peterson, 2006; Waltari *et al.*, 2007;

Dépraz *et al.*, 2008). We could thus put some confidence into the future range prediction under a global warming scenario (Figure 3.2C). The northward shift of the range as a predicted consequence of doubled CO_2 level in atmosphere matches the general trend: species are moving polewards as already shown for example in Araujo *et al.* (2005a); for more references see Parmesan (2006). This predicted northward expansion of the species has already been observed in Sweden as a consequence of increasing lake temperatures (Pfenninger, pers. com.). *R. balthica,* however, was predicted to be also affected in other parts of its range. The projection predicted considerable loss of suitable area in central Europe. This does not necessarily mean that these habitats will remain unoccupied. With a lower competition pressure, these areas will be possibly colonised by sister species presently inhabiting southern Europe (Pfenninger *et al.*, 2006). The MOTUs 3 and 5 described there potentially have greater tolerance to drought and higher water temperatures. The impacts of such a replacement alone on an ecosystem are difficult to predict, but likely limited. On the contrary, the arrival of *R. balthica* in habitats of newly emerging suitable areas in northern Europe will probably affect the ecosystem there. The arrival of a new detritus feeder might affect the existing food web structure. The increase of the snail population could also allow the proliferation of their predators and parasites.

The possible extinction of *R. balthica* from its former range (central Europe) is also likely to have an impact the overall genetic variability of the species. This is illustrated by the potential loss of the 40 haplotypes occurring exclusively in populations of the predicted unsuitable area out of the total 95 haplotypes (42%). *Per se*, refugial areas are hosting the highest variability. The disappearance of those populations could influence the overall survival of the species as a whole by enhancing its genetic impoverishment and thus potential adaptability.

Conclusions

ENM and phylogeography have already been used together for cross validation (Hugall *et al.*, 2002; Waltari *et al.*, 2007). However, the recently developed approach (Dépraz *et al.*, 2008) applied here has the advantage of combining both approaches in a rigorous statistical framework and thus constitutes an attractive prospect for the field (Provan & Bennett, 2008). It is particularly suited to test the assumption of niche conservatism which is a necessary prerequisite for reliable prediction on future ranges under climate change scenarios.

General discussion

In this last part of my thesis, I will develop a general view on the effects of global climate change on the ranges of freshwater pulmonates. Initially, I will summarize the main answers to the questions I asked at the onset of this project: 1) What are the relationships between species niche characteristics and range size and -shifts? 2) What was the species reaction to past climate changes such as the LGM? 3) What impact has the oncoming climate change on freshwater snail ranges? 4) Did the climatic niche evolve during expansions and can we plausibly forecast the species' range in a climate change scenario? I describe the general findings of my study hereafter and show how prediction of ranges changes can benefit from our knowledge of past ranges changes. Furthermore, I discuss the implications of predicted range changes on the population structure. Finally, I will suggest future research directions to improve predictions of the future ranges and infer the role of range shifts in the species evolutionary history.

Forecasting the ranges of species is frequently achieved with climate envelope models (ecological niche modelling). Bioclimate envelope models use associations between environmental variables and known distributions of species to define environmental requirements (niche) that can be projected under other climate scenarios (past and future). I used this approach in Chapter 1 to infer the changes in the climatically suitable area for Basommatophora genera. I showed that for a great proportion of European Basommatophora genera the suitable areas were projected to contract by 2080. The forecasted warming in the cooler northern ranges predicted the emergence of new suitable habitats, but also reduced drastically the available habitat in the southern part of the studied region.

It is hypothesised that widespread species are more likely to cope with environmental change than smaller range species, because of their putative phenotypic plasticity. In Chapter 1, I showed through comparative analyses a positive correlation between the niche width of Basommatophora genera (i.e. the climatic range covered by the species) and the suitable area size at present, assessed through ecological niche modelling. A similar result was found for trees by Köckemann *et al.* (2009). I also showed that there was a significant positive correlation between the niche width and the future area suitable to the genera, putting the less widespread genera at increased risk.

However, before translating the changes in suitable area modelled through ecological modelling into range changes predictions, one has to consider several factors. The use of ENM relies on many assumptions (Araujo & Guisan, 2006); in particular, the absence of change in climate preferences throughout time, also called phylogenetic niche conservatism (PNC). But the degree to which geographical distribution shifts follow consistent climate regimes (an evidence for niche conservatism, at least at coarse scales) is poorly known.

Therefore, I first assessed the impact of past climate change on the species range. Species are likely to move in response to climate change primarily by leading-edge range shifts (Hewitt, 1999), but also by jump dispersal and corridors. As such, the lessons from postglaciation should often apply to predicting climate change response (Wilson *et al.*, 2009). In chapters 2 and 3, I showed that past climate changes had an effect on the ranges of two species of European Basommatophora. The projection of *R. balthica* current climatic preferences on Last Glacial Maximum data showed a small suitable area in central Europe (Chapter 3). This result was confirmed by the phylogeographic analyses. The same refugial pattern was observed for *A. fluviatilis* (Chapter 2). Both of these cold adapted species had a narrower range and occupied central European refuges during the Last Glacial Maximum. The survival of species in small northern cryptic refuges has been shown to be more widespread among taxa (reviewed in Stewart & Lister, 2001; Provan & Bennett, 2008) than previously thought, challenging the classical refugia hypothesis (Balkans, Iberic Peninsula, Italy; Taberlet *et al.*, 1998). In particular, cold adapted species seems to have survived the last glaciations at places that were previously not considered suitable (citations in Provan & Bennett, 2008).

As stated in a recent review by Losos (2008), PNC is not ubiquitous among all taxa (see citations therein). Niche conservatism applies for several taxa (Peterson *et al.*, 1999; Peterson & Holt, 2003; Martinez-Meyer *et al.*, 2004), but may not be a general pattern (Rice *et al.*, 2003; Ruegg *et al.*, 2006; Pfenninger *et al.*, 2007). This variability in PNC is well reflected in the results of my thesis. In Chapter 2, I exposed the case of *A. fluviatilis*, which exhibits a high variability in climatic preferences. Furthermore, the clades inferred through the phylogeographic analyses corresponded to the populations exhibiting significantly different climatic preferences, which speak for a possible ongoing speciation. However, the analyses conducted do not allow a conclusive outcome. In chapter 3, on the other hand, *R. balthica* has been shown to keep the same climatic preferences within (at least) the last 20,000 years. In this case, the concordance of two independent analyses allows putting a high confidence in this inference of niche conservatism. Given these results, outlining the differences within the Basommatophora groups in regard to PNC, one should be careful when assuming PNC to predict future ranges. All the more, it appears advisable to test the assumption of niche conservatism before predictions about the future distribution of a particular species can be reasonably made. The use of ENM without quantifying the phylogenetic niche conservatism could be misleading, predicting drastic reductions in ranges although the species adaptive potential is very high.

However, an important issue in this case is the time frame considered. Species which exhibit a high adaptive potential (i.e. limited PNC) would nevertheless need time. As emphasised at the beginning of my thesis, the rate of the present change is much higher than the one of the warming event which followed, for example, the last glacial maximum. The climate warming following the last glacial maximum had a slower pace, since conditions similar to today's climate were reached approximatively 8000 years ago (Andersen & Borns, 1997)(stabilisation within roughly 10000 years). In chapter 3, it was showed that *R. balthica* exhibited niche conservatism during the last 20,000 years. This speaks for stability throughout time of the species climatic preferences. On the other hand, *A. fluviatilis* as well as *R. balthica* now occupy a wide range in Europe. This supposes a wide climatic tolerance and a high phenotypic variability within the species, since present populations are found in significantly different climatic spaces (Chapter 2). This phenotypic variability, if not counterbalanced by genetic local adaptation, could allow the populations to survive the ongoing global change.

An alternative for a species to adapt to the new conditions in its historical range is to disperse, following its climatic niche. The importance of dispersal to the species persistence should not be underestimated, as the analyses conducted in Chapter 1 considering two extreme dispersal scenario yielded drastically different results. Species not able to disperse are deemed to have their range considerably reduced, while under an unlimited dispersal scenario, some genera are predicted to have an even larger range by 2080. Species exhibit various dispersal capacities, and this has an impact on their expansion in the newly suitable areas. Translating the predicted changes in the suitable area into changes in the effective ranges thus requires measuring dispersal ability. The interplay of this trait with the adaptive potential determines the survival chances of the populations/species in areas subjected to environmental changes (Gaston, 1996).

The influence of migratory waterfowl on dispersal of freshwater organisms have been hypothesised in several studies (Malone, 1965; Rees, 1965; Frisch *et al.*, 2007), and (Boag, 1986) tested its feasibility. Waterfowl-mediated passive dispersal has been shown to play a role in inter-population gene flow in small invertebrates (Figuerola *et al.*, 2005). The results presented in the chapter 3, inferring the post LGM recolonisation of Europe by *R. balthica*, although supporting a stepping stone model as the main expansion way, also supported this hypothesis. However, the prerequisite for this type of migration is a successful hitchhiking event, where the living snail or egg masses stick to the legs or feathers, and whose likelihood has not been yet measured. Furthermore (Dillon, 2000) stressed: “On a coarse geographic scale, one must figure high the likelihood that freshwater mollusc distributions derive from vagaries of chance colonization”, the dispersal of freshwater snail is highly dependent on random events. Very little is known about the frequency of these events and its measurement is not an easy task. Nevertheless, hitchhiking is presumably not species-specific. Numerous species of waterfowl are very widespread in Europe, and fly daily between water bodies. One can therefore presume that dispersal, though random, is frequent enough to ensure the colonisation of new habitats.

Independently from the dispersal rate of the studied taxa, I showed in chapter 1 that there will be a profound faunal shift for Central Europe. This is reinforced by the species-specific projections in chapters 2 and 3. Following the projections, this area is no longer suitable for the species currently living in central European habitats. The consequences of such a change are difficult to predict because the many factors discussed above (dispersal, adaptation, phenotypic plasticity) are intertwined. In the case of dispersal abilities which match the rate of climate change, the areas in central Europe could be colonised by species currently living south of the studied region and/or by populations that were locally adapted to warmer climatic conditions. In the case of either no arrival of migrants or no adaptation of the present populations to new conditions, the populations occupying these habitats will suffer a fitness decrease and eventually die out, and their niche left vacant. This would permit the proliferation of organisms relying on the same food resources, but also likely affect their predators’ fitness.

The establishment of Basommatophora populations in newly suitable habitats is also likely to have consequences on local communities. The arrival of new detritus feeders will have an impact on the food web as a whole. However, global change is also affecting the ranges of other organisms that where not included in my study. Northern Europe could constitute a newly suitable area for eastern European species as well. For example, the suitable area of the *Radix* taxon presently inhabiting eastern Poland (Pfenninger *et al.*, 2006) could also shift to northern Europe, increasing the competition there. Northern Europe is thus likely to host completely new communities, composed of organisms that were until now not in contact with each other. Ecological Niche Modelling indeed delivers a rather optimistic point a view, since competition and predation are not included in the predictions.

While central Europe may become climatically challenging for local populations, it is also likely to become suitable for marginal populations at the warmer distributional border of widespread taxa such as *R. balthica* and *A. fluviatilis*, facilitating their establishment. These migrants may be a source of adaptive alleles to central parts of the range. Traditionally, gene flow has been viewed as an antagonistic process opposing local adaptation by introducing locally maladaptive variants, but its role may change when the environment changes. In spatially shifting climatic areas, gene flow may provide novel alleles from warm adapted populations (Davis & Shaw, 2001; Ayre & Hughes, 2004; Hewitt & Nichols, 2005). Such beneficial alleles are expected to spread faster than neutral alleles. In this case, the gene flow may prevent central European populations to disappear. However, the introgression of “better genes” may be negatively correlated with the degree of selfing, which should not be underestimated in freshwater snails. They are hermaphroditic and capable of self fertilisation. For example, *A. fluviatilis* has a very high selfing rate, while others such as *Radix* or *Lymnea* exhibit extremely variable mating strategies (from complete outcrossing to selfing, but see (Meunier *et al.*, 2004; Wullschleger & Jokela, 2002; Jarne & Städler, 1995)).

Selfing is a double-edged sword: on one hand, a high amount of selfing may prevent gene-flow at the centre of the range, thus preventing the local populations from benefiting from novel alleles that would eventually allow maintaining the populations’ fitness. Furthermore, self-fertilisation increases the homozygosity level. The newly established populations may suffer from inbreeding depression, as deleterious alleles have a higher probability to be found at a homozygous state. On the other hand, a single founder event is enough to create a population in newly suitable habitats at the northern margin. The mixed mating system of freshwater snails could prove being a very advantageous trait, in the case of rapid environmental change. The fact that founders can reproduce without needing a sexual partner is likely to favour a rapid expansion of their range. For a given habitat, the probability that a second colonisation event (two independent arrival of a living individual) occurs is probably quite low. The results of chapter 3 also indicate a low gene-flow between established populations, thus reinforcing this inference. Freshwater snails, though not able to disperse by themselves over large distances, may be considered as good colonisers, thanks to their ability to self-fertilise.

Perspectives

The insights I gained on adaptive potential and climate niche of Basommatophora allow confidence in the projection of species ranges in the future. However, they also open a wide range of questions to answer, in order to better understand the processes governing range dynamics and its consequences on the genetic structure of the species.

What we would like to know is whether and how evolution will play out in the near future, and whether it would be fast enough to keep track with environmental change (Gomulkiewicz & Holt, 1995; Reusch & Wood, 2007). To this end, the use of increasingly inexpensive genomics tools will allow systematic identification of key genes and traits critical for population persistence under global change. These traits range from factors favouring and enhancing dispersal (resistance to desiccation, behavioural traits), to heat shock proteins (HSP), whose expression level is under selection and varies in a pattern consistent with a thermal environment (Sørensen *et al.*, 2003).

For the taxa studied here, the area where a faunal shift is predicted to occur is also the core of the range, with the highest genetic variability *per se*. The extinction of these populations is likely to have profound effects in the overall genetic diversity of the species. Likewise, if the dispersal abilities match the rate of climate change, the series of founder events this dispersal at the northern range margin represents would lead to a loss of alleles and to homozygosity, possibly enhanced in this case by the mating system of freshwater snails; rapid continued expansion would produce large areas of reduced genetic diversity in Northern Europe (Hewitt, 1999). Whether or not the resulting loss of genetic diversity plays a role for the survival of these species needs further assessment.

Finally, I underlined the importance of dispersal both for the prediction of range shifts and as a way to gain new alleles allowing the persistence of populations. The modes of dispersal, its speed in terms of km/year therefore need to be further assessed. Furthermore, very little is known about birds (or other animals) species which may transport freshwater snails from one location to another. Further investigations on this dispersal factor are therefore necessary. Whether the migrants arriving at a site dispersed from a neighbouring location (stepping stone model) or from more distant sites (long distance colonisation) has a non-negligible influence on the composition of the new populations and hence on their fitness.

Summary

Global warming is expected to be associated with diverse changes in freshwater habitats in north-western Europe. Increasing evaporation, lower oxygen concentration due to increased water temperature and changes in precipitation pattern are likely to affect the survival ratio and reproduction rate of freshwater gastropods (Pulmonata, Basommatophora). This work is a comprehensive analyse of the climatic factors influencing their ranges both in the past and in the near future. A macroecological approach showed that for a great proportion of genera the ranges were projected to contract by 2080, even if unlimited dispersal was assumed. The forecasted warming in the cooler northern ranges predicted the emergence of new suitable areas, but also reduced drastically the available habitat in the southern part of the studied region. In order to better understand the ranges dynamics in the past and the post glacial colonisation patterns, an approach combining ecological niche modelling and phylogeography was used for two model species, *Radix balthica* and *Ancylus fluviatilis*. Phylogeographic model selection on a COI mtDNA dataset confirmed that *R. balthica* most likely spread from two central European disjunct refuges after the last glacial maximum. The phylogeographic analysis of *A. fluviatilis,* using 16S and COI mtDNA datasets, also inferred central European refugia. The absence of niche conservatism (adaptive potential) inferred for *A. fluviatilis* puts a cautionary note on the use of climate envelope models to predict the future ranges of this species. However, the other model species exhibited strong niche conservatism, which allow putting confidence into such predictions. A profound faunal shift will take place in Central Europe within the next century, either permitting the establishment of species currently living south of the studied region or the proliferation of organisms relying on the same food resources. This study points out the need for further investigations on the dispersal modes of freshwaters snails, since the future range size of the species depend on their ability to establish in newly available habitats. Likewise, the mixed mating system of these organisms gives them the possibility to fund a new population from a single individual. It will probably affect the colonisation success and needs further investigation.

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Zusammenfassung (German summary)

Was genau die Grenzen eines Artverbreitungsgebiets bestimmt, ist eine Frage, mit der sich Biologen seit der Veröffentlichung von Wallaces Werk „*Geographical distribution of animals*“ im Jahre 1876 beschäftigen. Das Verbreitungsgebiet einer Art kann als der Bereich definiert werden, in dem sich fortpflanzungfähige Populationen befinden. Zwei Bedingungen sind in diesem Bereich erfüllt: (1) abiotische und biotische Bedingungen stimmen mit den fundamentalen ökologischen Anforderungen der Art überein, so dass die Populationen überleben und sich erfolgreich fortpflanzen können und (2) die Art hat tatsächlich in ihrer Verbreitungsgeschichte diese Region erreicht und eine Population etabliert. Für eine Population gibt es drei Wege auf Umweltveränderungen zu reagieren: Plastizität, Migration oder Anpassung. Drei Prozesse steuern die Dynamik der Verbreitungsgebiete: phänotypische Plastizität, Anpassungs- und Verbreitungsfähigkeit. Das Zusammenspiel dieser Prozesse bestimmt die Veränderungen der Verbreitungsgebiete und schließlich das Schicksal einer Art.

Es liegen unbestrittene Beweise für einen schnellen und tief greifenden Klimawandel innerhalb des nächsten Jahrhunderts vor. Die Temperaturen werden voraussichtlich kontinuierlich ansteigen und unter anderem Veränderungen der Niederschlagsmuster mit sich bringen. In Süßwasserhabitaten wird der prognostizierte Klimawandel vor allem Einfluss auf das Durchflussregime, die saisonale Wasserverfügbarkeit und die durchschnittliche Temperatur haben. Dies wiederum wird voraussichtlich die Fortpflanzung und das Wachstum vieler im Wasser lebender Organismen beeinflussen. Während einige der auftretenden Habitatveränderungen durch phänotypische Plastizität und / oder lokale Anpassung gepuffert werden können, kann man davon ausgehen, dass sich Artverbreitungsgebiete wesentlich verändern werden. Dies war schon in der Vergangenheit der Fall. Die ersten zu erwartenden Auswirkungen in der nördlichen Hemisphäre sind Arealverkleinerungen und Artenaussterben. Solche Veränderungen in den Artverbreitungsgebieten, zum Beispiel das Verschwinden von Schlüsselarten oder die Invasion nicht heimischer Arten, werden das Ökosystem als Ganzes beeinflussen.

Pulmonaten stellen einen wesentlichen Teil der Süßwasserbiodiversität dar und bewohnen eine Vielzahl von Ökosystemen. Sie ernähren sich hauptsächlich von Periphyton und Detritus und sind eine wichtige Nahrungsquelle für Fische und andere Arten des Makrozoobenthos. Daher spielen sie eine herausragende Rolle in der Nahrungskette der aquatischen

Ökosysteme. Jede Änderung innerhalb der Gastropodengemeinschaft hat daher tief greifende Auswirkungen auf diese Ökosysteme. Es gibt Grund zu der Annahme, dass die Klimaveränderung eine deutliche Auswirkung auf die Verbreitungsgebiete von Süßwasserschnecken haben wird. Die Erhöhung der Verdunstungsrate aufgrund der globalen Erwärmung und die Veränderung von Niederschlagsmengen führt zu Trockenperioden, vor allem in niederen Breitengraden, was zu einem teilweisen Lebensraumverlust führt. Überleben, Fruchtbarkeit und Generationsdauer von Süßwassermollusken sind von der Umgebungstemperatur abhängig; die Erhöhung der Wassertemperatur wird deswegen eine Verschiebung der Areale induzieren, in denen Vermehrung möglich ist. Letztlich kann die Fitness der Arten durch Verringerung der Sauerstoffkonzentration im Wasser reduziert werden.

Das Ziel dieser Arbeit war es, die Auswirkungen der vergangenen und zukünftigen Klimaveränderungen auf die Verbreitungsareale der Süßwasserpulmonaten zu bewerten. Konkret sollten die folgenden Fragen beantwortet werden:
1) Welche Auswirkungen hat der bevorstehende Klimawandel auf die Verbreitungsgebiete von Süßwasserschnecken?
2) Was sind die Zusammenhänge zwischen den Eigenschaften der Nische einer Art und ihrer Arealgröße und -verschiebungen?
3) Welche klimatischen Faktoren beeinflussen die Artenvielfalt in Nord-Westeuropa und in welchem Umfang hat der Klimawandel Auswirkungen auf die Biodiversität?
4) Wo waren die Refugien während der letzten Eiszeit und wie haben die Arten ihre jetzigen Verbreitungsgebiete besiedelt?
5) Verändert sich die klimatische Nische einer Art und können wir die zukünftigen Verbreitungsgebiete von Süßwassermollusken prognostizieren?

Zunächst wurde eine makroökologische Analyse an den nordeuropäischen Gattungen durchgeführt. Dabei wurde die Korrelation zwischen heutigen Verbreitungsgebieten und abiotische Faktoren (hydrologisch und klimatisch), unter Berücksichtigung phylogenetischer Distanzen, untersucht. Diese Untersuchung gab einen Einblick in die relative Bedeutung der klimatischen Faktoren, die die Verteilung des Taxons beeinflussen und ermöglichte den Nachweis eines phylogenetischen Signals. Dadurch ließ sich das evolutionäre Potenzial der Kladen zur Anpassung an veränderte Umweltbedingungen abschätzen. Anschließend wurden die gesammelten Informationen über die besetzte ökologische Nische, mithilfe *Ecological*

Niche Modelling (ENM), zur Beurteilung der Auswirkungen des Klimawandels auf die Verbreitungsgebiete der Gattungen benutzt. Da sich erhebliche Unterschiede in den relevanten Merkmalen (Reproduktion und Überleben) auf intraspezifischer Ebene zeigen, wurde ein zweiter Ansatz mit zwei Modell-Arten benutzt. Dieser Ansatz stützte sich auf die phylogeographische Analyse der Arten *Ancylus fluviatilis* und *Radix balthica* und diese erlaubte Schlussfolgerungen über die Auswirkungen der vergangenen Klimaänderungen auf die Verbreitungsgebiete. Darüber hinaus, ermöglichen die so gewonnenen Kenntnisse über vergangene Kolonisationsmuster und ihre Geschwindigkeit eine Prognose über Reaktionen auf die aktuelle globale Erwärmung zu stellen.

In den Kapiteln 2 und 3 wurde gezeigt, dass frühere Klimaveränderungen einen Einfluss auf die Verbreitungsareale von den zwei Modell-Arten hatten. Kombinierte ENM und phylogeographische Analysen zeigten, dass *A. fluviatilis* (Kapitel 2) und *R. balthica* (Kapitel 3) während der letzten Eiszeit ein engeres Verbreitungsgebiet besetzten und ähnliche Refugien in Mitteleuropa hatten.

Für einen großen Teil der europäischen Basommatophora-Gattungen, wurde modelliert dass sich die geeigneten Areale bis 2080 verkleinert haben werden (Kapitel 1). Die prognostizierte Erwärmung resultiert im kühleren Norden Europas in einer Entstehung neuer geeigneter Habitate, gleichzeitig führt sie zu einer drastischen Verkleinerung des verfügbaren Lebensraums im südlichen Teil der untersuchten Region. Durch vergleichende Analysen, wurde eine positive Korrelation zwischen der Nischenbreite von Basommatophora-Gattungen und der Größe ihrer aktuellen bewohnten Gebiete gezeigt. Es wurde des Weiteren eine signifikante positive Korrelation zwischen der Nischenbreite und der Größe des zukünftigen klimatisch geeigneten Gebiets festgestellt. Somit erhöht sich das Aussterberisiko für weniger weit verbreitete Gattungen.

Wenn Arten anpassungsfähig sind, also geringen *Phylogenetic Niche Conservatism* (PNC) zeigen, wird das zukünftige Artverbreitungsareal nicht mit dem modellierten geeigneten Gebiet übereinstimmen. PNC gibt es nicht in allen Taxa, was auch in dieser Arbeit nachgewiesen werden konnte. In Kapitel 1 wurde ein schwaches phylogenetische Signal erkannt, womöglich verursacht durch die niedrige taxonomische Auflösung. Wenn die Analyse sich auf Artebene beschränkt, gibt es Unterschiede in der Größe des PNC. Die heutigen Populationen von *A. fluviatilis* besetzen Habitate, die sich klimatisch signifikant von ihrem Refugiumsgebiet unterscheiden (Kapitel 2). Dies weist auf einen relativ niedrigen PNC hin. *R balthica* zeigt im Gegensatz dazu einen starken PNC, da diese Art dieselbe klimatische Nische seit 20.000 Jahren besetzt (Kapitel 3). Angesichts dieser gegensätzlichen Ergebnisse, erscheint es ratsam, den PNC genau zu prüfen bevor man eine Prognose über die Artverbreitungsgebiete mithilfe *Ecological Niche Modelling* macht.

Die Verwendung von ENM ohne vorherige Quantifizierung des PNC könnte irreführend sein, weil es zu einer Vorhersage von drastischen Verengungen des Artverbreitungsareals führen könnte, obwohl das adaptive Potenzial der Art hoch ist. Dennoch, auch für solche Arten ist die Geschwindigkeit des aktuellen Wandels, die viel höher ist als die bisheriger klimatischer Ereignisse, ein wichtiger Faktor. Andererseits gibt es heute Populationen beider Arten, *A. fluviatilis* und *R. balthica,* in klimatisch unterschiedlichen Habitaten in Europa, was eine große klimatische Toleranz und eine hohe phänotypische Variabilität innerhalb der Arten voraussetzt (Kapitel 2). Diese phänotypische Variabilität könnte dazu führen, dass die Süßwassermollusken den globalen Wandel besser überstehen könnten, als die ENM-Projizierungen vorhersagen.

Die hier vorgestellte Arbeit hat gezeigt, dass die Verbreitung eine große Bedeutung für die Persistenz von Arten in Zeiten von Umweltveränderungen hat. Die Wichtigkeit diese nicht zu unterschätzen, zeigten die Analysen in Kapitel 1: zwei extreme Verbreitungsszenarien ergaben drastisch unterschiedliche Ergebnisse. Arten, die nicht in der Lage sind, sich effektiv auszubreiten, haben deutlich verkleinerte Verbreitungsgebiete in 2080. Im Rahmen eines unbegrenzten Verbreitungsszenarios, wird für einige Gattungen vorhergesagt, dass sie 2080 ein größeres Verbreitungsgebiet als heute erreichen könnten. Die Verbreitung von Süßwasserschnecken ist in hohem Maße abhängig von zufälligen Ereignissen; es wird vermutet, dass diese Organismen zum Beispiel von Wasservögeln transportiert werden können. Sehr wenig ist bekannt über die Häufigkeit dieser Ereignisse und deren Messung ist keine leichte Aufgabe. Die Ergebnisse aus Kapitel 3, in welchem Kolonisationsrouten analysiert wurden, verstärken die Wasservogel-Hypothese. Zahlreiche Arten von Wasservögeln sind weit verbreitet in Europa, und ziehen täglich zwischen Gewässern. Man kann daher davon ausgehen, dass Verbreitungsereignisse häufig genug stattfinden, um die Besiedelung neuer Lebensräume zu sichern.

Die Konsequenzen der prognostizierten Änderungen der Verbreitungsgebiete auf die gesamte Biodiversität in Europa sind schwer vorhersehbar. Dieser Arbeit zeigt, dass es eine erhebliche

Veränderung der mitteleuropäischen Fauna geben wird. Wenn die Verbreitungsfähigkeit einer Art der Geschwindigkeit des Klimawandels entspricht, könnte Mitteleuropa von Arten besiedelt werden, die derzeit in Südeuropa leben und / oder von Populationen, die vor Ort an wärmere klimatische Bedingungen angepasst sind. Im Falle, dass keine Migranten ankommen oder keine Anpassung der derzeitigen Populationen an die neuen Umweltbedingungen stattfindet, werden die Populationen einen Fitness-Rückgang erleiden und schließlich aussterben. Dies würde die starke Vermehrung von konkurrierenden Arten, welche auf die gleichen Ressourcen zugreifen, fördern. Gleichzeitig wird die Gründung neuer Populationen von Süßwassermollusken in den nordeuropäischen Habitaten Auswirkungen auf die lokalen Lebensgemeinschaften haben. Globaler Wandel betrifft auch die Artverbreitungsgebiete von anderen Organismen, die möglicherweise auch neue geeignete Lebensräume in Nordeuropa besiedeln werden. In Nordeuropa werden sich daher wahrscheinlich völlig neue Artgemeinschaften bilden von Organismen, die bisher nicht in Kontakt miteinander waren und um das neue Territorium konkurrieren werden.

Der Hermaphroditismus der Basommatophora, mit der Möglichkeit zur Selbstbefruchtung und Auszuchtung, spielt wahrscheinlich auch eine Rolle bei der Ausweitung ihrer Verbreitungsareale. Aber Selbstbefruchtung ist ein zweischneidiges Schwert: ein hohes Maß an Selbstbefruchtung kann den Genfluss zwischen Populationen, trotz einer hohen Verbreitungsrate, behindern. Dadurch können mitteleuropäische Populationen von vorteilhaften Allelen eingewanderter, wärmeangepasster Individuen nicht profitieren. Selbstbefruchtung erhöht auch die Homozygotiefrequenz: die neu gegründeten Populationen könnten dadurch unter Inzuchtdepression leiden. Andererseits reicht ein einziges Individuum aus, um eine Population in einem neuen geeigneten Habitat zu gründen. Dies könnte bei raschen Veränderungen der Umwelt eine sehr vorteilhafte Eigenschaft sein. Süßwasserschnecken, die passiv verbreitet werden, könnten aufgrund ihrer Fähigkeit zur Selbstbefruchtung gute Erstbesiedler sein.

Durch Weiterentwicklung der Kombination von ENM und Phylogeographie könnten die Ergebnisse dieser Arbeit in Zukunft vertieft werden. Dies würde erlauben, die Wirkungen von vergangenen Klimaveränderungen an mehreren Arten zu vergleichen. Zudem könnte man auf genetischer Ebene untersuchen, welche Gene eine Rolle bei der Temperaturanpassung spielen, und ob diese Gene schnell genug evolvieren können, um die Anpassung der Arten zu gewähren.

Appendixes

Appendix S1: DNA sequences for COI and 16S fragments used in the Basommatophora phylogeny

Species	NCBI sequence COI	NCBI sequence 16S
Acroloxus lacustris	AY282581	EF489311
Ancylus fluviatilis	AY282582	EF489312
Aplexa hypnorum	AY577504	AY577464
Bathyomphalus contortus	EF012166	EF012184
Galba truncatula	DQ980189	Acc. Numb to be provided
Gyraulus albus	Y14710	AY577480
Hippeutis complanatus	EF012170	EF012187
Lymnea stagnalis	EF489390	EF489314
Myxas glutinosa	DQ980191	Acc. Numb to be provided
Omphalaria gla	DQ980192	
Physa acuta	AY282589	AY651219
Physa fontinalis	AY577505	AY577465
Planorbarius corneus	AY282590	AY577473
Planorbis planorbis	EF012175	AY350568
Segmentina nitida	EF012178	AY577481
Stagnicola palustris		U82082
Radix sp. 1	DQ980134	Acc. Numb to be provided
Radix sp. 2	DQ980142	Acc. Numb to be provided
Radix sp. 3	DQ980120	Acc. Numb to be provided
Radix sp. 4	DQ980141	Acc. Numb to be provided
Radix sp. 5	DQ980082	Acc. Numb to be provided
Radix sp. 6	DQ980125	Acc. Numb to be provided
Siphonaria serrata	EF489380	EF489302
Anisus vortex	AY577518	AY577478
Anisus leucostoma	AY577517	AY577477

Appendix S2: Sampling localities, geographical position, distribution of *A. fluviatilis* haplotypes (columns) at each sampling location (rows), number of 16S and COI sequences for each locality and phylogeographical group of each haplotype.

			Haplotypes																																													
SL	Lat	Long	16	17	20	65	66	67	68	1	4	2	19	69	70	6	7	9	3	12	10	11	13	18	8	5	71	14	15	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	*N* 16S	*N* COI
AUT2	48.69	16.00																					4																								4	
CZ1	49.90	14.37																								4																					4	
CZ2	50.67	14.17																								1																					1	1
FRA1	47.32	6.43								2	1																																				3	
FRA2	47.06	6.22								2																																					2	
FRA3	43.46	2.44										3	2																																		5	
FRA4	43.53	5.29												3																																	3	2
FRA5	47.22	0.31													1																																1	2
FRA6	47.04	0.19													4																																4	
FRA16	46.13	3.85														1														1																	2	1
FRA17	45.06	2.69																											3																		3	1
FRA18	49.82	2.39								2																																					2	
FRA19	49.57	1.49								3																																					3	
FRA20	48.15	-0.23																															1														1	1
FRA21	47.36	1.41														1																		2													3	1
FRA22	45.66	0.24											4																																		4	1
FRA23	45.01	1.09														2																															2	
FRA24	45.67	0.59														3																															3	
FRA25	45.37	0.65											1			2																												1			4	2
FRA26	49.04	3.43														4																															4	
FRA27	49.03	3.38														3																															3	
GB1	50.96	-3.72														1										1																					2	
GB2	57.90	-4.84																				3																									3	
GB3	57.47	-5.01														5																															5	
GB5	52.11	0.74								2																											1										3	2
GB6	53.89	-0.83														3																															3	
GB7	54.32	-1.51														1																						3									4	1
GB8	54.53	-2.01																																					4								4	1
GB9	54.57	-2.05																																						1							1	1
GB10	54.89	-2.26														3																															3	
GB11	54.51	-2.92																																						1	2						3	1
GB12	54.21	-2.65																																							1						1	
GB13	53.87	-2.23																																						1							1	
GB14	53.54	-1.85														4																															4	1
GB15	53.26	-1.90								1						1																								1							3	
GB16	52.61	-1.52																																								2					2	1
GB17	51.96	-0.92								4																																					4	1
GER1	54.28	10.58														6																															6	
GER2	50.55	9.19														1		1																													2	
GER3	50.57	9.23														2	1																														3	
GER4	50.54	9.27														1																															1	
GER5	50.47	9.16														1																															1	

GER6	50.44	9.20																	1																													1	
GER7	50.40	9.28																		1																												1	
GER8	50.27	9.41														1																																1	
GER9	50.23	8.36														2					1	1																										4	
GER10	49.99	8.29																					1																									1	
GER11	49.99	8.30														2																																2	
GER12	49.62	9.65														1																																1	
GER13	49.35	6.71														2																																2	
GER14	49.15	7.04														2																																2	
GER15	48.79	8.24																		1																												1	
GER16	48.53	9.05									2																																					2	
GER17	47.76	9.13																							1																							1	
GER18	48.95	11.73														1								1																								2	
GER23	54.17	10.07														2																																2	1
GER24	54.29	10.59														3																																3	
GER25	53.72	11.89																													2	1															3	
GER26	54.61	9.37														1																																1	
LV1	57.13	24.92																								2																	1				3	1
LV2	56.20	26.05																									5																			5	
LV3	56.46	23.24																									5																			5	
LIT1	54.11	24.32																								2																				2	
LIT2	54.08	24.27																																											4		4	1
LIT3	54.12	24.30																								1																				1	
LIT4	55.58	26.25																																												2	2	1
NOR1	59.92	10.71																								6																				6	
POL1	53.24	19.83																								1		1																		2	
POL2	50.16	19.63														4																																4	
POL3	50.08	21.96																								5																				5	
POL4	53.85	21.15																								2																				2	
POL5	54.07	18.45																								1																				1	
POL6	54.11	18.41																								3																				3	
POL7	53.27	23.03																								4																				4	
POR3	40.55	-7.84				1	1																																							2	1
POR4	40.22	-7.85						5																																						5	3
SLO1	46.65	16.09																											4																		4	
SPA1	40.86	-2.54	2																																												2	
SPA2	40.68	-0.12		1	1																																										2	
SPA4	43.19	-0.55							1																																							1	
SW1	55.72	14.16														1																			1											2	2
SW2	59.59	14.55																								4																				4	1
SW3	57.73	14.13																								3																				3	
SW4	56.20	13.66																																		4										4	1
UKR1	48.31	23.05														2																																2	
UKR2	48.16	23.11																									5																			5	
		∑	2	1	1	1	1	5	1	16	3	3	7	3	5	69	1	1	1	2	1	4	5	1	1	40	15	1	7	1	2	1	1	2	1	4	1	3	4	4	3	2	1	1	4	2	235	33
Phylogeo. Group			IP	IP	IP	IP	IP	IP	IP	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	BA	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	CE	BA	CE	BA	BA		

Appendix S3: Sampling localities, geographical position, distribution of *Radix balthica* haplotypes (columns) at each sampled location (rows), number of COI sequences for each locality

			Haplotype																																																
Name	Latitude	Longitude	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
GVD2	46,554	7,074	3																																																
ROS	46,720	7,109	3		2																																														
EST	46,856	6,840			1																																		4												
AUG	46,615	7,181			6																																														
GVD1	46,555	7,072				1																																													
GGK2	49,935	8,479					1																																												
SUL2	51,087	11,625						1																																											
MBV	46,492	7,047	3																																																
REN	46,385	6,895							1										1																																
RIE	54,149	11,689																																			2												
ROC	46,364	6,938							1	1																																									
CAZ	43,769	3,798									1																																								
BDO	54,075	11,936																																			1												
KBW	54,149	11,725																																			1												
GLO2	48,225	-3,404										2	1																																				
HER2	45,117	4,974												1	1																																		
LAV	45,830	4,804			1											3																																	
OUM	63,845	20,259															3	1																															
VEG	48,179	-0,265																	1	1																													
CZA	53,682	16,925																			1	1																											
MIS	53,884	12,175																					1																2												
EGG	54,614	9,372																						1																									
FLE	54,699	9,505																							1																								
BUC	54,172	10,073																																			1												
ROG	53,729	10,94																								1	1	1																					
BER	50,673	2,704																											1										2												
NEU	53,362	13,071																												1																					
SOM	51,130	10,916																																			1												
BOD2	47,667	9,213											1	1		7	1	1													1	1																			
IVO	56,152	14,509																															1																		
ODE	56,623	15,673																																4																	
BJA	57,462	16,055																																	4																
HJA	59,169	15,928																																		1			2												
DAR	59,896	15,688																																			3	1													
ALG	61,105	16,819																																					4												
STO	61,778	16,518																																						3											
RAN	62,337	16,973																																							1	3									
VIK	62,295	16,090																																									2	1							
FAG	61,825	14,876																																					2						1						

			Haplotype																																																
Name	Latitude	Longitude	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
LJO	60,004	14,156																																					4												
LIM	59,586	14,555																																												1					
BJO	58,663	14,483																																					4												
VID	57,067	14,042																																					3								1				
VOM	55,698	13,554																																					1									2			
HOE	51,989	4,128																																					2												
GAI	53,195	-0,769																																															1	2	
SCO	53,498	-0,664																																					2										1		
MEL	53,887	-0,828																																																	2
SWA	54,32	-1,512																																					1												1
DAL	54,829	-2,981																																					1												
PAT	54,513	-2,924																																																	
KIR	54,214	-2,652																																																	
BUX	53,258	-1,905																																					3												
ALL	54,896	-2,259																																																	
HUR	54,571	-2,050																																					4												
DRY	52,319	-1,318																																																	
ATH	52,591	-1,548																																					1												
CHI	49,049	3,403																																																	
SIG	57,155	24,854																																																	
SAL	47,816	13,054																																																	
KON	47,581	12,99																																																	
POR	47,159	-1,482																																																	
DIJ	47,3568	5,1459			1																																														
ABO	47,7718	5,9847																																																	
LAB	48,6473	7,69																																																	
OBI	48,9501	6,7556			2																																														
NOM	48,89	6,215																																																	
BTB	48,7928	7,0216																																																	
CEN	46,9378	-1,884																																					2												
LAC	45,9758	4,6366																																																	
REM	47,3742	-0,3011																																																	
THO	47,7427	0,452																																																	
MAR	46,7399	-0,6581																																																	
LER	47,8765	-0,9758																																																	
ALD	48,1	8,703																																																	
BAL	48,273	8,86																																																	
LEY	45,642	5,859																																																	
WILL	48,166	8,737																																																	
N individuals			9	0	13	1	1	1	2	1	1	2	2	2	1	10	4	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	4	1	3	1	50	3	1	3	2	1	1	1	1	2	2	2	3

			Haplotype																																												*N*
Name	Latitude	Longitude	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	COI
GVD2	46,554	7,074																																											3
ROS	46,72	7,109																																											5
EST	46,856	6,84																																											5
AUG	46,615	7,181																																											6
GVD1	46,555	7,072																																											1
GGK2	49,935	8,479																																											1
SUL2	51,087	11,625																																											1
MBV	46,492	7,047																																											3
REN	46,385	6,895																																											2
RIE	54,149	11,689																																											2
ROC	46,364	6,938																																											2
CAZ	43,769	3,798																																											1
BDO	54,075	11,936																																											1
KBW	54,149	11,725																																											1
GLO2	48,225	-3,404																																											3
HER2	45,117	4,974																																											2
LAV	45,83	4,804																																											4
OUM	63,845	20,259																																											4
VEG	48,179	-0,265																																											2
CZA	53,682	16,925																																											2
MIS	53,884	12,175																																											3
EGG	54,614	9,372																																											1
FLE	54,699	9,505																																											1
BUC	54,172	10,073																																											1
ROG	53,729	10,94																																											3
BER	50,673	2,704																																											3
NEU	53,362	13,071																																											1
SOM	51,13	10,916																																											1
BOD2	47,667	9,213																																											13
IVO	56,152	14,509																																											1
ODE	56,623	15,673																																											4
BJA	57,462	16,055																																											4
HJA	59,169	15,928																																											3
DAR	59,896	15,688																																											4
ALG	61,105	16,819																																											4
STO	61,778	16,518																																											3
RAN	62,337	16,973																																											4
VIK	62,295	16,09																																											3
FAG	61,825	14,876																																											3

			Haplotype																																											N
Name	Latitude	Longitude	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	COI
LJO	60,004	14,156																																													4
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VID	57,067	14,042																																													4
VOM	55,698	13,554																																													3
HOE	51,989	4,128																																													2
GAI	53,195	-0,769				1																																									4
SCO	53,498	-0,664																																													3
MEL	53,887	-0,828	1	1																																											4
SWA	54,32	-1,512			2																																										4
DAL	54,829	-2,981					3																																								4
PAT	54,513	-2,924					3	1																																							4
KIR	54,214	-2,652							2	1	1																																				4
BUX	53,258	-1,905										1																																			4
ALL	54,896	-2,259											4																																		4
HUR	54,571	-2,050																																													4
DRY	52,319	-1,318	3											1																																	4
ATH	52,591	-1,548												3																																	4
CHI	49,049	3,403													1																																1
SIG	57,155	24,854														1	1																														2
SAL	47,816	13,054																1																													1
KON	47,581	12,99																	1																												1
POR	47,159	-1,482																							1			1						1													3
DIJ	47,3568	5,1459																						1								1															3
ABO	47,7718	5,9847																																	1										3			4
LAB	48,6473	7,69																																						2	1								3
OBI	48,9501	6,7556																																				1											3
NOM	48,89	6,215																		1																			1										2
BTB	48,7928	7,0216																												1										2									3
CEN	46,9378	-1,884																																													2
LAC	45,9758	4,6366																																		2	1						2	1	1				7
REM	47,3742	-0,3011																			3	3	1																								7
THO	47,7427	0,452																							2	1			1																		4
MAR	46,7399	-0,6581																							1	1	1																				3
LER	47,8765	-0,9758																																								1							1
ALD	48,1	8,703																																												1	1
BAL	48,273	8,86																																						1							1		2
LEY	45,642	5,859																															1														1
WILL	48,166	8,737																													1							1											2
N individuals			4	1	2	1	6	1	2	1	1	1	4	4	1	1	1	1	1	1	3	3	1	1	4	2	1	1	1	1	1	1	1	1	1	2	1	2	1	5	1	1	2	1	1	3	1	1	232

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EMPLOYMENT

From 02/2008 on	Postdoctoral research associate, BiK-Forschungszentrum, "Biological Archives", Frankfurt am Main
08/2008-12/2008	Research associate, BiK-Forschungszentrum, "Molecular Ecology Lab", Frankfurt am Main
2005-07/2007	Research associate, Ecology and Evolution Department, Institute of Ecology, Evolution and Diversity, Frankfurt am Main

EDUCATION AND RESEARCH EXPERIENCE

January 2005	**PhD student** at the Ecology and Evolution Department, Institute of Ecology, Evolution and Diversity, Frankfurt, Germany *Impact of the climate change on freshwater Pulmonates in Europe.* Supervisor: PhD. M. Pfenninger, Priority program "Aquashift", DFG
2004	**DEA** (MSc.) Biodiversity and Ecosystems, University of Lille. *Dissertation: Structure and gene flow in weed beet* (Beta vulgaris*, L.*) *populations in northern France.* Supervisor: PhD Jean-François Arnaud "Plant Populations Genetics and Evolution" Laboratory (GEPV), University of Lille 1.
2003	**Maîtrise** in Populations and Ecosystems Biology, University of Montpellier. *Dissertation: Genetic diversity of an invasive species:* Varroa destructor *(Acarii), honey-bee's parasite.* Supervisor: PhD Maria Navajas Center for Biology and Management of Populations (CBGP), Montpellier.
2002	**Licence** in Populations and Ecosystems Biology, University of Montpellier.
2001	**DEUG** in Biology, University of Nantes
1999	**Baccalauréat** in Sciences, Lycée Jean Perrin, Rezé

PUBLICATIONS (PEER-REVIEWED)

M. Pfenninger, **M. Cordellier** & B. Streit (2006) Comparing the efficacy of morphologic and DNA-based taxonomy in the freshwater gastropod genus *Radix* (Basommatophora, Pulmonata). *BMC Evolutionary Biology*, **6**:100.

M. Cordellier & M. Pfenninger (2008) Climate-driven range dynamics in the freshwater limpet *Ancylus fluviatilis* (Pulmonata, Basommatophora). *Journal of Biogeography*, **35** (9), 1580-1592.

A. Dépraz, **M. Cordellier**, J. Hausser and M. Pfenninger (2008) Postglacial recolonisation at a snail's pace (*Trochulus villosus*): confronting competing refugia hypotheses using model selection, *Molecular Ecology*, **17**, 2449-2462.

M. Cordellier & M. Pfenninger (2009) Inferring the past to predict the future: phylogeography and climate modelling predictions for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora), *Molecular Ecology,* **18***,* 534-544.

M. Cordellier, A. Pfenninger, B. Streit, M. Pfenninger (2009) Assessing the effects of climate change on the distribution of pulmonate freshwater snail biodiversity, *in revision.*

COMMUNICATIONS

M. Cordellier, S. Fénart, J.-F. Arnaud & J. Cuguen (2004) Structure génétique intra- et inter-parcellaire des populations de betterave mauvaise herbe dans la zone de production de betterave sucrière.
Poster, XXVIIème Petit Pois Deridé, Paris

M. Cordellier & M. Pfenninger (2005) The impact of climate variability on the species ranges of European freshwater Pulmonates, progress and preliminary results.
Oral presentation, Aquashift workshop, Kiel.

M. Cordellier & M. Pfenninger (2006) Influence des variations climatiques sur les aires de répartition des Pulmonés d'eau douce en Europe
Oral presentation. XXIXème Petit Pois Déridé, Lille.

M. Cordellier & M. Pfenninger (2006) The impact of climate variability on the species ranges of European freshwater Pulmonates.
Oral presentation, Aquashift workshop, Kiel.

M. Cordellier (2007) Ecological modelling and phylogeography of European freshwater snails: can we predict the impact of climate change?
Oral presentation, Population Genetics Group Meeting, Warwick.

M. Cordellier & M. Pfenninger (2008) Inferring the past to predict the future: phylogeography and climate modelling predictions for the freshwater gastropod *Radix balthica* (Pulmonata, Basommatophora).
Poster, DanBIF Conference "Biodiversity Informatics and Climate Change Impacts on Life", Aarhus.

TEACHING ABILITIES

Teaching assistant for diverse practical courses (Soil ecology, Molecular Biology) at Frankfurt's University.

Training of undergraduate students: R. Kraus, S. Trumic, C. Arnold, C. Judith.

LANGUAGES

French: mother language
English: fluent
German: fluent

GRANTS

Freunde und Förderer Frankfurt University (2007) 600€ Travel grant for participation to the PopGroup meeting in Warwick, UK.

Freunde und Förderer Frankfurt University (2008) 300€ Travel grant for participation to DanBIF Conference "Biodiversity Informatics and Climate Change Impacts on Life", Aarhus, DK.

REVIEWS

Molecular Ecology

Frankfurt am Main, March 10. 2009

Erklärung

Ich erkläre hiermit, dass ich mich bisher keiner Doktorprüfung unterzogen habe.

Frankfurt am Main, den

……………………………….
(Unterschrift)

Eidesstattliche Versicherung

Ich erkläre hiermit an Eides Statt, dass ich die vorgelegte Dissertation über

Impact of climate change on freshwater snail species' ranges

selbständig angefertigt und mich anderer Hilfsmittel als der in ihr angegebenen nicht bedient habe, insbesondere, dass aus Schriften Entlehnungen, soweit sie in der Dissertation nicht ausdrücklich als solche mit Angabe der betreffenden Schrift bezeichnet sind, nicht stattgefunden haben.

Frankfurt am Main, den 10.03.2009 …………………………..(Unterschrift)

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