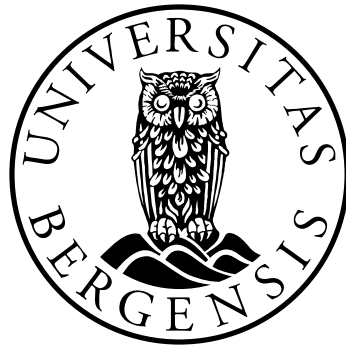# High Arctic Invertebrate Biogeography

Patterns and Colonization Processes since the Last Glacial Maximum

María Luisa Ávila Jiménez

Dissertation for the degree philosophiae doctor (PhD)

at the University of Bergen

2011

Dissertation date: 22nd September 2011

Scientific environment

This thesis is submitted in partial fulfilment of the requirements for the degree of Philosphiae Doctor (PhD). The study has been mainly funded by the University Centre in Svalbard (UNIS), and most of the work has been carried out at the Department of Biology at UNIS, co-supervised from the Department of Biology, University of Bergen. The project received additional support and funding from *Svalbard Science Forum Arctic Stipend*, *Svalbard Environmental Protection Fund* and *ARCFAC V*. Some of the laboratory work was performed at the British Antarctic Survey laboratory facilities in Cambridge, UK.

Supervisors:

Main Supervisor: Stephen J. Coulson.

Co- supervisor: Torstein Solhøy.

Acknowledgements

Now I am about to submit this dissertation, it is a real pleasure to look back and give a thought to all those whom without their help, this thesis would have never been possible (mostly when many lovely people has crossed my path, often with an amazingly helpful spirit). These acknowledgments are purely written as the thoughts are coming out of my mind, and the order of appearance does not imply anything (perhaps tells something on how my memory works, that's all).

The project counted with the help and support from a number of institutions: UNIS, University of Bergen, British Antarctic Survey, Swedish Polar Secretariat, Airlift, Lufttransport, Kings Bay and Norwegian Polar Institute. But this work would have never been possible without the samples I have got from many remote areas from many friends and colleges; the list is going to be long (I really hope I am not forgetting anyone!): Thank you Anatoly Babenko, Lech Iliszko (et al.), Katarzyna Zmudczyńska, Dorothee Ehrich, Eva Fuglei, Rolf Ims, Natalia Lebedeva, Cecilia Sandstrøm, Emilie Guegan, Martin Holmstrup, and many UNIS colleagues: Carl Bøggild, Seb, Louis, Lucie, Eike, Steffi Weege, Monika, Philip, Peter, Pernilla, and the AB201 students in 2008. My gratitude is also for those who tried but didn't succeed! Also thank you all who helped in the field and provided taxonomic expertise. Arne Fjellberg has done a magnificent job not only providing samples and taxonomic help when needed, but teaching me patiently few of his sampling, lab handling and identification tricks (as yet Collembola taxonomy seems to be a magic

he possess), and having always an answer for a question. Thank you Dariusz, your taxonomic help has been as wonderful as your everlasting happiness ☺. Thank you Stefanie Kaiser for proof reading the thesis!

There are no words that could express my gratitude to Steve, my main supervisor, a wonderful person, great mind and a brilliant researcher I am incredibly glad I have had the chance to work with. I should thank you not only for your support, time and patience (much needed when dealing with a student with selective hearing!), but for your seemingly endless confidence on me, leading to a piece of work which by today I am highly proud of. Thank you very much Torstein, for your support mainly at the end when it was most needed, and also for making each of my visits to Bergen a lovely experience. Thank you every one at the Zoology Department in Bergen, specially Argitxu and Marianne, and Tina, *Ricardo*, Sylvi and Hanne, for making me feel at home on my short visits to Bergen. It has been quite a pleasant experience to arrive each time to Ny-Ålesund to meet charming people like Doro, Nick Cox, Monica or my good friend Sylvi, all always happy to see you with a big smile ready. Cambridge really soon became a quite special place to me (and my home!), and the British Antarctic Survey an interesting place to work. Thank you guys from the *Uncharismatic Microfauna Research Group* office, for your welcoming spirit, and all this good office time. Thank you very much to my lab and coffee (and pub) mates at BAS, who were always ready and happy for a research discussion or answer any question, making me once again feel more than welcome. Again gratitude becomes

difficult to express, and I feel wordless trying to thank Chester Sands, my unofficial supervisor. Thank you Cheps not only for your effort unveiling few of the mysteries of molecular ecology to my untrained mind, the times working in the lab, the long conversations and discussions about past, present and future research prospects, but for your friendship, which made all this time not just a job but a live experience.

It is not easy to be a supportive parent when your daughter lives over 3000 km away in the high Arctic; however, I have never lack the warmth of the family, not even in the distance. Warmth that has been coming with special intensity once a week, with clockwork accuracy, at each of those Grandpa's calls, which I have been missing since the day he left, and I will always do. Thank you Filla, for a beautiful friendship and an unforgettable field season ("*Veo casas y no es Longyearbyen*"!!). Thank you Jose, Yoli, mamá, papá, Nana, and my extended *brothers* and *sisters* (mis niñas y mis niños), for being there, os quiero una barbaridad. Thank you David, for knowing and understanding me, you must have won your little place in heaven for giving me constant and endlessly loving support all this time. You have shared my frustrations, my achievements are also yours.

I want to thank my friends and colleagues at UNIS, especially in the Biology Department, for nice times both at work and in leisure times. Thank you my friends in Longyearbyen, specially Margrete, Patricia & Per, Patricia & Tommy, Pernilla, Carlos & Emilia and all of you who left Longyearbyen too early (Steffi, Thor Inge and Alena, Åsmund, Ranghild, Jago, and once again Sylvi…) for great time together, help

me disconnect from work (and sometimes even help me to keep happy, fed, healthy and sane!).

Anywhere I have been, UNIS, BAS, Ny-Ålesund, Kinnvika, Horizont II… in the field, in the lab, in the office, out in the tundra… it is not always easy to keep your smile when you feel things are going wrong. Especially in those moments, thank you all who smiled back ☺

Svalbard will be always part of my life, where it will always remain a bit of my soul, my memories and my heart…

☺

A mi abuelo Pedro.

Photograph: Head of a *Megaphorura arctica* specimen, adult. Photographer: Pål Hermanssen ©

Abstract

The biogeography of Arctic terrestrial invertebrate species, and particularly processes creating and determining patterns of species distribution, have rarely been considered as a whole, but rather on a regional basis, resulting in a lack of an all- encompassing theory of invertebrate colonization of the Arctic. Additionally, dispersal and gene flow to high Arctic islands from populations already inhabiting warmer environments may enhance the survival of Arctic species under the warmer conditions forecasted by climate modellers. Hence there is a need for comprehensive phylogeographical, biodiversity and biogeographical studies to develop a deep understanding of the factors determining species distribution through time and space. Implementing a macroecological approach to this problem by combining community descriptions, field surveys, statistical biogeography and molecular ecology would provide an insight on the historical, geographical and environmental factors that define current invertebrate species distribution in the Arctic. I have tested the following hypothesis: 1) *Environmental factors, such as climatic regimes, restrain Arctic invertebrate species distribution at both the landscape and geographical scales.2) Recent glacial history, glacial survival and colonization, have a made a detectible contribution to current distribution of invertebrate species in the Arctic.* By addressing these key hypotheses, my research will unravel the history of colonization of the Arctic and develop a critical baseline knowledge from which predictions about potential future changes in biodiversity and geographic distribution of species can be made within the context of climate change. No indications of invertebrate glacial survival in the high

Arctic are found on the strength of this thesis However, for none of the scales considered can current environmental conditions provide an adequate explanation of the observed biogeographical patterns. The biogeographical patterns described illustrate the limitations of environmental factors *per se* in the determination of species distribution ranges and indicate dispersal, including long distance dispersal, as an essential element shaping invertebrate species distribution across all geographical scales.

List of publications

Core Publications

I: **Ávila-Jiménez, M.L.** & Coulson, S.J. Can snow depth be used to predict the distribution of the high Arctic aphid *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen? *BMC Ecology.* Submitted*.*

II: **Ávila-Jiménez, M.L**., Gwiazdowicz, D.J.,Solhøy, T.,Fjellberg, A., Dózsa-Farkas, K., Coulson, S.J., Ekrem T. Monson, F. The invertebrate fauna of the high Arctic island of Edgeøya, Svalbard: what can it tells us about the invertebrate colonization of the High Arctic? Manuscript.

III: **Ávila-Jiménez M.L.,** Sands, C.J, & Coulson S.J. First evidence of Arctic collembola dispersal patterns as inferred by COI sequencing in *Megaphorura arctica*. (Tullberg, 1876). Manuscript.

IV: **Ávila-Jiménez, M.L.** Coulson, S. J. A Holarctic biogeographical analysis unravels recent post- glacial colonization patterns. *Insects.* In press.

V: **Ávila-Jiménez, M.L.** Coulson, S. J. Solhøy, T Sjöblom. A. 2010.Overwintering of terrestrial Arctic arthropods: the fauna of Svalbard now and in the future. *Polar Research* 29: 127- 137

Appendix publications

VI: **Ávila-Jiménez, M. L**., Fjellberg, A. & Coulson, S. J. 2008. First record of *Folsomia bisetosella* Fjellberg, 2005 (Hexapoda, Collembola) from High Arctic islands. *Norw. J. Entomol.* 56: 129-130.

VII: **Ávila Jiménez M.L.,** Gwiazdowicz, D.J., & Coulson, S.J. On the gamasid (Acari; Parasitiformes) mite fauna of Svalbard: a revised checklist of a High Arctic archipelago. *Zootaxa.* Submitted.

VIII: Gwiazdowicz, D., Coulson, S. J., **Ávila- Jiménez, M. L.** 2010. First records of *Zercon andrei* Sellnick, 1958 and *Zerconopsis muestairi* (Scheweizer, 1949) (Acari, Mesostigmata) from Bjørnøya. *Norw. J. Entomol* 56: 117- 119.

IX: Coulson, S. J., Fjellberg, A., Snazell, R., Gwiazdowicz, D.J., **Ávila-Jiménez, M.L.** On the Collembola, Araneae and Gamasida from the Kinnvika region of Nordaustlandet, Svalbard. *Geografiska Annaler Series A.* In press.

Declaration

Paper I: Ávila-Jiménez, M.L. & Coulson, S.J. Can snow depth be used to predict the distribution of the high Arctic aphid *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen?

Ávila-Jiménez, M.L. - Project conception, sourced funding, fieldwork, writing including statistics.

Coulson, S.J. - Fieldwork, editing and supervision.

Paper II: Ávila-Jiménez, M.L., Gwiazdowicz, D.J.,Solhøy, T.,Fjellberg, A., Dózsa-Farkas, K., .Ekrem T, Monson F., Coulson, S.J. The invertebrate fauna of the high Arctic island of Edgeøya, Svalbard: what can it tells us about the invertebrate colonization of the High Arctic?

Ávila-Jiménez, M.L. - Sourced funding for fieldwork, fieldwork, data analysis and manuscript writing and editing.

Gwiazdowicz, D.J. - Identification of gamasid mites and fieldwork

Solhøy, T. - Identification of oribatid mites and fieldwork

Fjellberg, A. - Identification of Collembola and fieldwork

Dózsa-Farkas, K. - Extraction and identification of Enchytraeidae

Monson F. - Identification of oribatid mites

Ekrem T. - Identification of Chironomidae

Coulson, S.J. - Fieldwork, editing and supervision.

Paper III: Ávila-Jiménez M.L., Sands, C.J, & Coulson S.J. First evidence of Arctic collembola dispersal patterns as inferred by COI sequencing in *Megaphorura arctica*. (Tullberg, 1876).

Ávila-Jiménez, M.L. - Lead the project, gathered the samples, ran the genetic sequencing, analysed the subsequent data, writing and editing.

Sands, C.J. - Supervision during molecular procedures, editing.

Coulson S.J. - Fieldwork, editing and supervision

Paper IV: Ávila-Jiménez, M.L. Coulson, S. J. A Holarctic biogeographical analysis unravels recent post- glacial colonization patterns.

Ávila-Jiménez, M.L. - Project conception and development. Data set analysis, writing and editing.

Coulson, S. J. - Editing and supervision

Paper V: Ávila-Jiménez, M.L. Coulson, S. J. Solhøy, T Sjöblom. A. 2010.Overwintering of terrestrial arctic arthropods: the fauna of Svalbard now and in the future.

Ávila-Jiménez, M.L. - Writing and editing

Coulson, S. J. - Editing and supervision

Solhøy, T. - Editing and supervision

Sjöblom. A. - Editing

Paper VI: Ávila-Jiménez, M. L., Fjellberg, A. & Coulson, S. J. 2008. First record of *Folsomia bisetosella* Fjellberg, 2005 (Hexapoda, Collembola) from High Arctic islands.

Ávila-Jiménez, M.L. - Writing and editing.

Fjellberg, A. - Taxonomic advice and suggestions

Coulson, S. J. - Editing and supervision

Paper VII: Ávila Jiménez M.L., Gwiazdowicz, D.J., & Coulson, S.J. On the gamasid (Acari; Parasitiformes) mite fauna of Svalbard: a revised checklist of a High Arctic archipelago. *Zootaxa.*

Ávila-Jiménez, M.L. - Fieldwork, analysis, writing and editing

Gwiazdowicz, D.J. - Mite identification

Coulson, S.J. - Fieldwork, editing and supervision

Paper VIII: Gwiazdowicz, D., Coulson, S. J., Ávila- Jiménez, M. L. 2010. First records of *Zercon andrei* Sellnick, 1958 and *Zerconopsis muestairi* (Scheweizer, 1949) (Acari, Mesostigmata) from Bjørnøya.

Gwiazdowicz, D. - Mite identification, writing and editing

Coulson, S. J. - Fieldwork, editing and supervision

Ávila- Jiménez, - M. L. Fieldwork and editing

Paper IX: Coulson, S. J., Fjellberg, A., Snazell, R., Gwiazdowicz, D.J., Ávila-Jiménez, M.L. On the Collembola, Araneae and Gamasida from the Kinnvika region of Nordaustlandet, Svalbard.

Coulson, S. J. - Fieldwork, analysis, writing, editing and supervision

Fjellberg, A. - Collembola identification and editing

Snazell, R. - Araneae identification and editing

Gwiazdowicz, D.J. - Gamasida identification and editing

Ávila-Jiménez, M.L. - Fieldwork, identification of Collembola and editing

Contents

1. On the structure of the thesis

A general context for biogeography, macroecology, and the present thesis is given in the introduction. This is followed by a brief discussion of the recent glacial history of the Arctic, providing the historical framework where patterns described in the present thesis are shaped. The main study areas are then presented. After this each of the main subjects considered in the thesis appear in order of increasing geographical scope, developing the theme of the thesis, and finally the conclusions. Thus the first project described deals with the effects of snow depth on the local distribution of the endemic aphid *Acyrthosiphon svalbardicum* in Kongsfjorden, Svalbard (Paper I).This is followed by a comprehensive biodiversity survey of the Svalbard archipelago (Papers II, VI, VII, VIII, IX), focused on the least described areas to date in eastern and northern Svalbard. The first evidence of dispersal, population interconnectivity and source for populations colonizing the high Arctic archipelago of Svalbard are given through a phylogeographical study in Arctic collembolan species *Megaphorura arctica* (Paper III*)*, and finally a description on the biogeographical pattern in the Holarctic area, including descriptions of the main dispersal routes, areas of recent colonization and potential glacial refugia, is given in an analytical biogeography study (Paper IV). A final discussion summarizes and evaluates the major outcomes of this thesis. The scientific articles produced from this thesis work are enclosed at the end of the thesis and are referred to within the text by roman numerals.

2. Introduction

The lands […] are full of trees of a thousand kinds, so lofty that they seem to reach the sky. […] And the nightingale was singing, and other birds of thousand sorts […]. There are palm-trees of six or eight species, wondrous to see for their beautiful variety […] wrote Christopher Columbus in 1492 about what is today known as the Dominican Republic, impressed not just by the variety of living forms, but by the number of species he was gazing at for the first time. Differences in species distributions have puzzled the human race since the awareness of the world (Linnaeus 1781, Darwin 1859, Hultén 1937, Blackburn & Gaston 2002). Carl Linnaeus wrote in his Dissertation *On the Increase of the Habitable Earth* (Linnaeus 1781) the need of a high mountain in the *Gardens of Paradise* to hold all the cold adapted species created by *God*, and the distribution *a posteriori* of the *Creation* led his interest not only in classifying species and describing their distribution, but to ponder concerning dispersal vectors, about what he wondered *If a lake have a force to move stones of a weight that many yokes of oxen are unable to draw, what must we expect from the ocean?* Darwin himself tackled the question of dispersal and colonization, giving a series of examples of long distance and accidental dispersal, defining sources and dispersal barriers, and the relationship between the level of differentiation and the time since species drifted apart (Darwin 1859). The importance of dispersal in determining biogeographical patterns is increasingly recognized. Hultén (1937) finely described, based on plant distribution data, biogeographical patterns, glacial refugia, and colonization patterns which yet today are largely supported by molecular methods

(Abbott & Brochmann 2003, Brochmann *et al.* 2003, Skrede *et al.* 2006, Alsos *et al.* 2007). A common picture emerging from a number of Arctic phylogeographical studies in different taxa is that nunatak survival in the high Arctic rarely needs to be invoked to explain observed patterns (Schneeweiss 2011).That leaves recent colonization (from distant sources in the case of high Arctic islands) to stand alone as the main phenomenon shaping biodiversity and distribution patterns in many Arctic areas. However, some scepticism about power of colonization processes in determining biogeographical patterns has been also displayed, due to almost absent dispersal capabilities in soil invertebrates (Danks 1978, Strathdee & Bale 1995). Despite this scepticism, there is little evidence that the invertebrate fauna or flora persisted in Svalbard during the last glacial maximum (approx. 11 Ma. – 10 Ka. BP) (Brochmann *et al.* 2003). However, recent studies indicate Svalbard as a possible location for glacial refugia in one plant species (Westegaard *et al*. 2011). Long distance dispersal (LDD) of invertebrates was hypothesised for a number of taxa (Aphididae, Syrphidae, Tipulidae) by the observations of Charles Elton in 1925 (Elton1925). However, despite its importance, the long standing question on how dispersal and colonization shapes species distribution remains still unanswered for most (if not all) Arctic invertebrates (Coulson 2007).

Even though Arctic species respond differently to different environmental conditions, a clear Arctic biogeographical pattern is found, with a series of distinct groups (Hultén, 1937, Alsos *et al.* 2007). Nonetheless, factors controlling the distribution of species are often obscure and difficult to resolve (Reese *et al.* 2005, Aráujo & Guisan

2006). Knowledge of the recent history of the Arctic biota is essential in order to understand the present status of the Arctic ecosystem, and to project the nature of their responses to potentially rapid climate change, (ACIA 2004). Evidence of the impact of recent climate change on biological systems has been reported across different regions of the planet (Walther *et al.* 2002) and particularly in the polar regions (Kennedy 1995, McCarty 2001, Parmesan 2006). Hence there is an urgent need for comprehensive biodiversity and biogeographical studies including a deep understanding of the factors determining the distribution of species. For Arctic species in general, and for Arctic invertebrates in particular, gene flow to high Arctic islands from mainland populations already inhabiting warmer environments may expedite adaptation to warmer conditions forecasted by climate modellers, acting as a *gene-pool life-boat* for species currently dwelling Arctic habitats (Paper V). However, from where, and if at all, this *life-boat* is to come for most Arctic invertebrates has never been clarified. Accidental dispersal (related to lack of dispersal adaptations) of invertebrates have been repeatedly recorded (Glick 1939, Crawford 1995, Hawes et al. 2007), including high Arctic instances (Elton 1925, Danks 1978, Laarsonen 1985, Coulson *et al.* 2002b).

Colonization of isolated islands can happen at an exceptional speed, as it was shown through terrestrial surveys in the Icelandic island of Surtsey. Just two years after the initiation of the eruption that gave origin to the island, 14 species of invertebrates were collected, including wingless invertebrates such as gamasid mites (Lindroth 1965). Two years later this number had increased to 63 species (Lindroth 1967). Long

distance dispersal (LDD), defined as those events configuring the tail of a dispersal kernel. Such LDD events are not conceived as silent and almost undetectable any longer, but rather as underestimated phenomena due to inherent difficulties of direct measurement and observation (Bullock & Clarke 2000, Kuparinen 2006 and references therein). LDD has been also shown to shape the geographical distribution of many taxa (Brochman *et al*. 2003, Nathan 2006, Chapman *et al.* 2007). It has been pointed out that nonstandard means of dispersal (accidental dispersal), those different to the route the organism is adapted for, are often responsible for long distance dispersal (Higgins et al. 2003). Identification of standard means of dispersal to Arctic islands is also essential to further understand the mechanisms of biological invasions, identify invasive species and target conservation strategies (Suarez *et al.* 2001, Lindström *et al.* 2011). Although soil invertebrates often do not show any particular dispersal adaptation (e.g. they can walk, but are wingless), five mechanisms are defined as main potential dispersal vectors for passive LDD: 1) wind (Glick 1939, Gressit & Yosimoto 1974, Nkem *et al.* 2006, Hawes *et al.* 2007), 2) water currents (Nkem *et al.* 2006, Coulson 2002a, McGaugrhan *et al.*2010), 3) drift ice and wood (Darwin 1859, Elton 1925, Johansen & Hytteborn 2001), 4) phoresis (Lebedeva & Krivoloutsky 2003, Ledeveba & Lebedev 2008, Coulson *et al*. 2009) and 5) human-mediated dispersal (Elton 1925, Frenot *et al.* 2005). The relative contributions of each of these mechanisms to the overall dispersal of invertebrates within, and to, the Arctic however have never been quantified.

A comprehensive knowledge of the biodiversity patterns is essential to effectively monitor a population (Shaffer *et al.* 1998), assess climate driven species range shift (Walther *et al.* 2002, Thomas et al. 2004), conservation biology (Rushton 2004), or even test biogeographical, ecological and evolutionary hypotheses (Leathwick 1998). Patterns found at a range of spatial scales will have unique causes and biological consequences. Such patterns are key to predicting and understanding the underlying mechanisms under which the system develops (Levin 1992). In that frame, macroecology arises as a way to study relationships between organisms and their environments as well as explain statistical patterns of abundance, distribution and diversity (Blackburn & Gaston 2002). The present thesis aims to apply a macroecological approach, implementing field surveys (Paper I), community descriptions (Papers II, VI, VII, VIII, IX), molecular ecology (Paper III), and statistical biogeography (Paper IV) to provide insights into species distribution patterns at different spatial scales in the Arctic, to further understand the mechanisms shaping Arctic biogeography and thus ultimately determine historical, geographical and environmental factors, defining current invertebrate species distribution in the Arctic.

It has been hypothesized that no terrestrial invertebrate species could have survived in the high Arctic during the Last Glacial Maximum (LGM) (Pugh & McInnes 1998, Brochmann *et al.* 2003), and no cryptic refugia have been identified in high Arctic islands. Consequently, the following hypotheses are to be tested:

22

1) *Environmental factors, such as climatic regimes, restrain Arctic invertebrate species distribution at both the landscape and geographical scales.*

2) *Recent glacial history, glacial survival and colonization, have a made a detectible contribution to current distribution of invertebrate species in the Arctic.*

The answers to these questions will provide baseline knowledge from which predictions about future changes in biodiversity can be made.

3. Arctic glacial history

Most of the high Arctic remained permanently covered by ice during the Last Glacial Maximum (LGM), the Wiscosian/ Weichselian glacial episode, and for possible ice-free areas in the high Arctic, the environment is thought to have been harsh enough that no soil fauna could have survived *in situ* (Brochmann *et al.* 2003). It hence follows that most of the high Arctic, if not all, has been colonized not earlier than 10,000 B.P. when the ice began to retreat. The extent and timing of advance and retreat of the ice sheets during the LGM nonetheless varied between regions (Svendsen *et al.* 2004), and static maps of LGM ice sheet extension are often misleading when identifying possible glacial refugia. Furthermore, knowledge on LGM ice sheet extent and thickness are in general large scale reconstructions with often doubtful boundaries and low resolution power considering small islands of ice-free ground (see Astakhov 1998, Briner *et al*. 2009, Paus *et al.* 2006). Late Glacial nunataks, with pioneer dwarf-shrub vegetation have been described from south central Scandinavia 16 Ka B.P. (Paus *et al.* 2006). Areas in the Canadian Arctic (Andrews 1987) where outlet glaciers of the Laurentide ice sheet retreated approximately 12-10 Ka B.P. (Briner *et al.* 2009), and north east Greenland (Tremblay *et al.*1999) have been suggested to be ice free during the LGM. Other areas, such as Beringia and Eastern Siberia as far as Taymyr peninsula, appear to have been completely ice free for most, if not all, of the Pleistocene (2.5 Ma- 12 Ka. BP) (Elias *et al.,* 1997, Astakhov 1998, Mangerud *et al.* 2002, Elias & Croker 2008). In the Svalbard Archipelago, some ice free areas could have occurred in

Murchinsonfjorden (Kubischta *et al.* 2010) and Danskøya (Landvik *et al.* 2003) with several instances where the reconstruction cannot accurately define whether those areas were ice free or covered by a thin, cold based sheet (Hormes *et al.* 2011). Ice free extensions, with a possible role as glacial refugia, have been also suggested from Iceland (Rundgren *et al.* 1999).

Ice-free areas during the LGM can be also inferred through biological evidence. Large extensions of ice-free ground in the Beringia land bridge area have been demonstrated by a number of taxa persisting in situ throughout the Quaternary glaciations (Fedorov & Stenseth 2002, Abbott & Brochmann 2003, Cook *et al*. 2005, Weider & Hobæk 2000). This area possessed broad extensions of tundra vegetation and a dominating mesic climate during the LGM, with a dominant dry steppe- tundra ecosystem in western Beringia and the interior regions of eastern Beringia (Elias & Croker, 2008). In most of the eastern Palaearctic, large mammal fossil records, such as the charismatic mammoth, remain as an imprinted signature of non- glacial ecosystems (Iacumin *et al*. 2000). Moreover, large areas of north-western Greenland and the Canadian Arctic archipelago were assigned as putative glacial refugia as early as the studies of Eric Hultén (1937) based on plant community assemblages. Most of those areas have been subsequently supported as LGM glacial refugia by molecular methods (Fedorov & Stenseth 2002, Abbott & Brochmann 2003, Cook *et al*. 2005, Weider & Hobæk 2000, Skrede *et al.* 2006, Alsos *et al*. 2007).

4. Study area

The whole Arctic region (*sensu* Babenko & Fjellberg 2006) (Figure 1) was considered for an Holarctic Biogeographical analysis (Paper IV), while the north Atlantic/ Barents Sea regions were considered for a phylogeographical analysis using the Cytocrome Oxidase I (COI) gene in the springtail species *Megaphorura arctica*, (Paper III) including samples from two Icelandic, one Norwegian and one Greenlandic location. The Svalbard archipelago represents the most intensively sampled area.

Svalbard is the main study area for the biodiversity studies (Papers II, VI, VII, VIII, IX), for a review on overwintering strategies of Arctic invertebrates (Paper V) and for the study on snow depth and local distribution of the endemic aphid *Acyrthosiphon svalbardicum* (Paper I).

The Svalbard archipelago lies in the Arctic Ocean, between 74° and 81° North and 10° and 35° East, over 400 km west from Greenland and 600 km from North of Norway. Svalbard west coast is mainly influenced by the West- Spitsbergen current, a northern branch of the north Atlantic current, which flows parallel to the western coast of Svalbard, creating a milder climate to the eastern part of the Archipelago, mostly influenced by the Siberian branch of the Transpolar Drift (Figure 2) (Johansen & Hytteborn 2001). With 60% of the land area permanently covered by snow and ice (Hisdal 1998), ground frozen for approximately 10 months a year (Coulson *et al*.

1995) and an annual precipitation varying from over 350 mm (Ny-Ålesund) to 190 mm (Svalbard airport) or less, Svalbard presents a variety of habitats from wet and mesic tundra to true polar desert and from nutrient poor soils to highly nutrient rich ornithogenic soil under birdcliffs (Jónsdottir 2005)
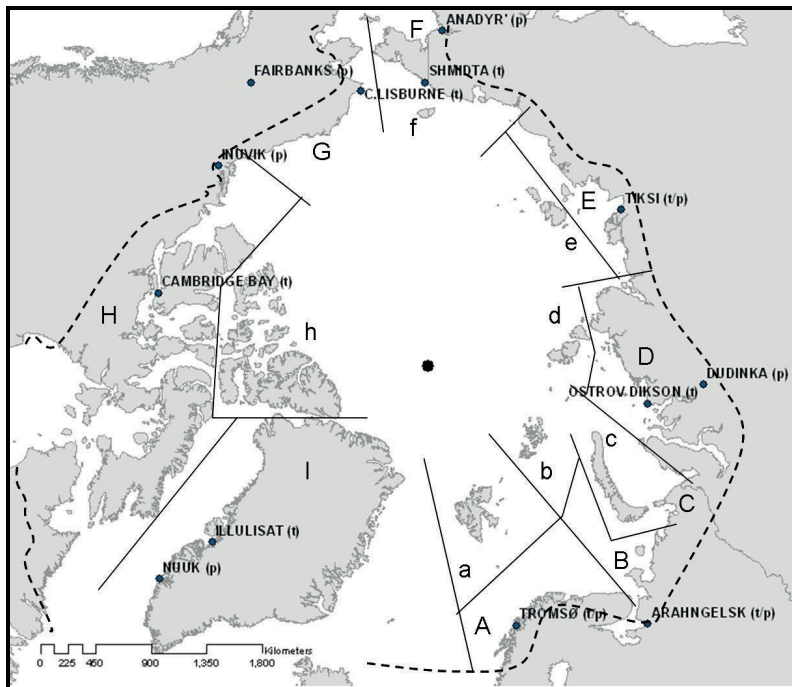

Figure 1 *Area nomenclature and limits as defined by Babenko and Fjellberg 2006, including the weather stations used in the Holarctic biogeographical study (Paper IV) (indicating form of data obtained as t: temperature and p: precipitation).Capital letters define continental areas whereas and lower case indicate Arctic islands (A: west Europe, B: east Europe, C: Ural, D: west and middle Siberia, E: east Siberia, F: north-east Asia, G: western America, H: eastern America, I: Greenland, a: Svalbard, b: Franz Josef Land, c: Novaya Zemlya, d: Severanya Zemlya, e: New Siberian islands, f: Wrangel Island, h: Queen Elisabeth islands and Ellesmere Island).*
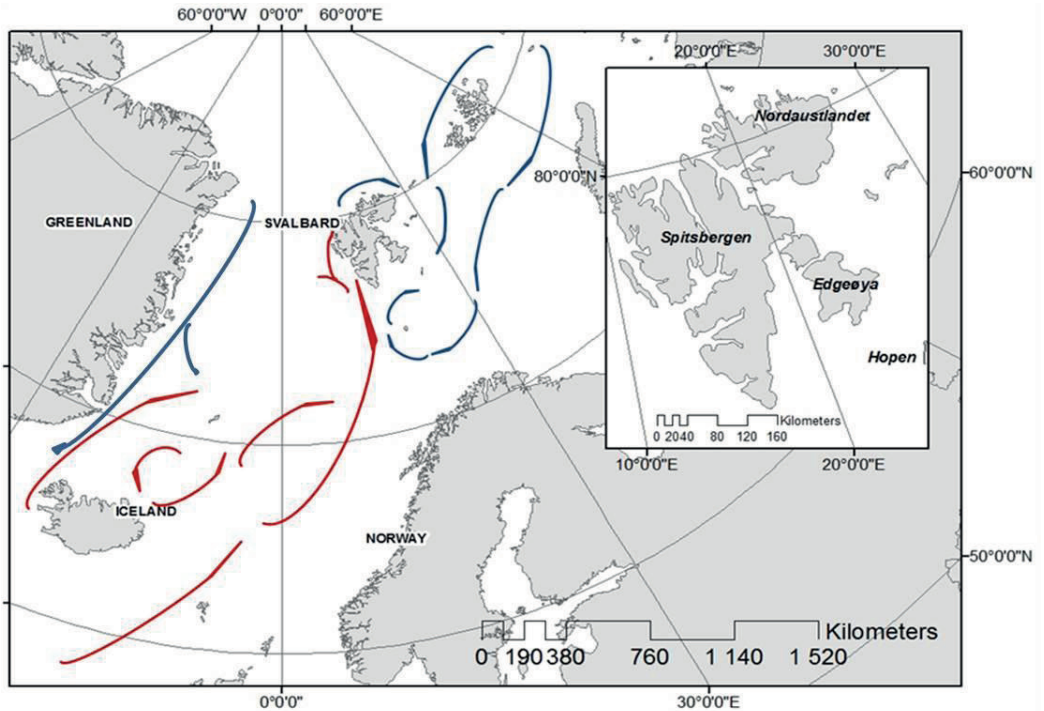
Figure 2 *Main North Atlantic study area, including ocean currents pattern in the North Atlantic and influence area of the Svalbard Archipelago (In red warm water, in blue cold polar currents). In the right box, main study islands of the Svalbard Archipelago. Source: Iceland Marine Research Institute, Rudels et al. 2005.*

The Arctic is far from being a homogeneous landscape with regard to temperature and precipitation regimes (Figure 3). The North Atlantic Current, and the associated air currents, transfer warm and humid air to the high Arctic, with the areas directly influenced being Iceland, Fennoscandia, Greenland, Svalbard (Piechura *et al*. 2001) and to a minor extent the Canadian archipelagos (Danks 1978). The Canadian Arctic

is mainly influenced by cold and dry Arctic air and to a minor extent by the cool and moist Pacific airstream and Atlantic air currents (Danks 1978).

Svalbard represents a unique study platform for post-glacial colonization patterns, not only due to its level of isolation from the closest land, but for the wide range of studies regarding climatology, geology, glacial history and ecosystems existing for this archipelago (for example Hjelle *et al*. 1993, Førland *et al*. 1997, Hodkinson *et al*. 1998, Coulson *et al.* 2000, Coulson 2007, Kubischta *et al.* 2010). Most invertebrate research carried out on Svalbard comes from the vicinity of the settlements of Longyearbyen (Isfjorden) and Ny-Ålesund (Kongsfjorden) on the west coast (Coulson 2007) (Figure 4), these are different to the eastern part of Svalbard due to climatology, putative dispersal routes (Alsos *et al.* 2007) and the extent of possible ice-free areas during the LGM (Landvik *et al.* 2003). The islands of Nordaustlandet, in the north east of Svalbard, and Edgeøya, in the east, were specially targeted during my research due to the lack of invertebrate studies in this region with a few scattered exceptions (Fjellberg 1997, Summerhayes & Elton 1928, De Smet *et al.*1994).
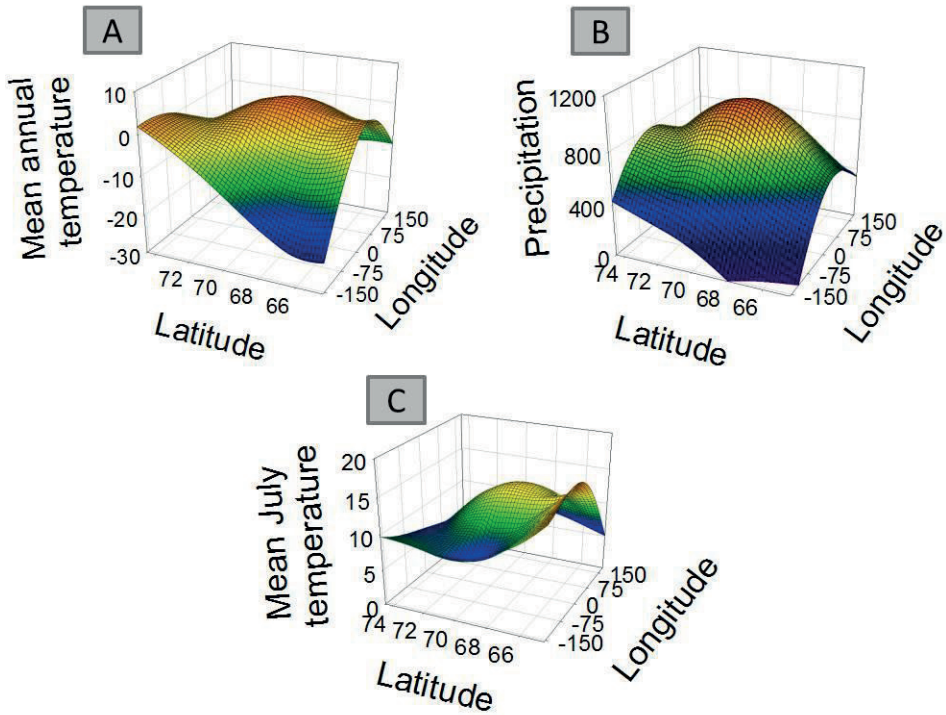
Figure 3 Mean annual temperature (A), annual precipitation (B) and mean temperature of the warmest month (C) patterns in the Arctic represented in a latitude-longitude coordinate system. The Figures show the temperature and precipitation distribution throughout the Arctic and where the coldest / warmest and wettest / driest areas are.
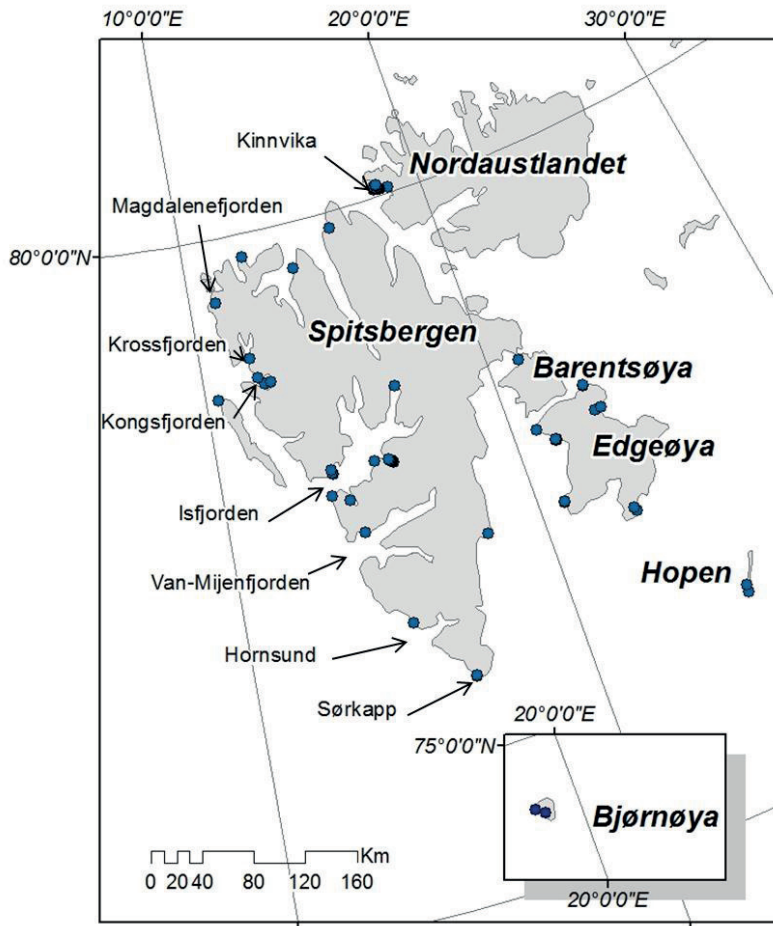
Figure 4 Svalbard sampling sites for the studies included in this thesis.

Locations sampled included a variety of habitats, nutrient- rich birdcliffs (Florabukta and Fjortendejulibukta), mesic tundra heath (Kapp Linne, Sørkapp), wet moss tundra (Russebukta) polar semi desert (Trygghamna and Diskobukta) and true polar desert (Nordaustlandet and Hambergbukta) (Figure 5 and 6).
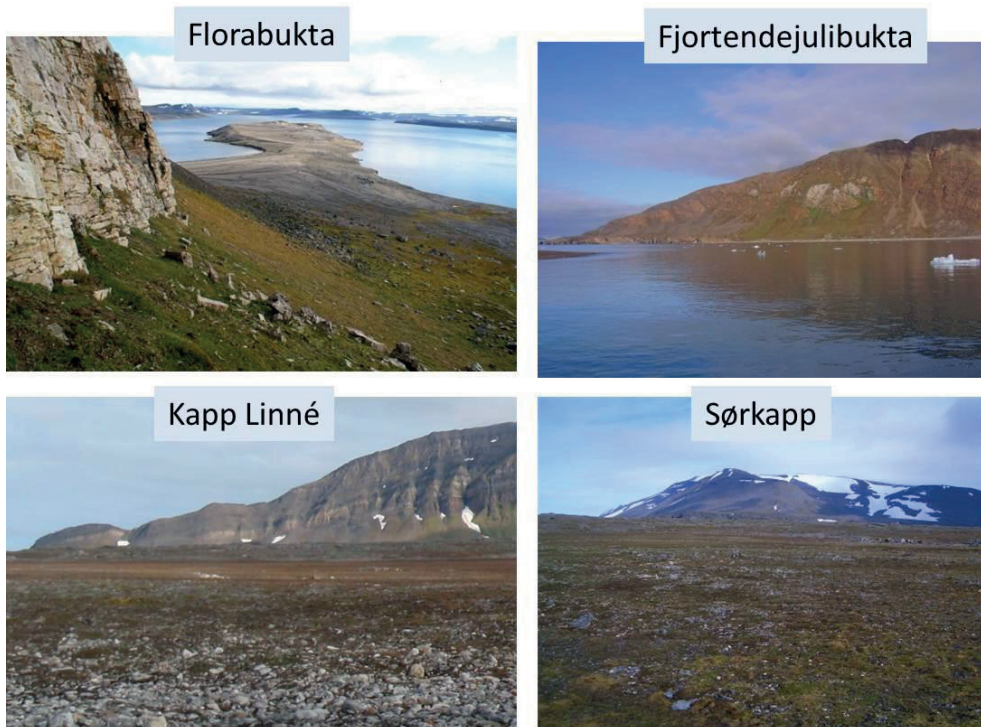

Figure 5 *Sampling sites at birdcliffs in Florabukta (Nordaustlandet),*

Fjortendejulibukta (Krossfjorden) and mesic tundra sites in Kapp Linné (Isfjorden)

and Sørkapp.

Figure 6 Sampling sites at polar semi desert in Diskobukta (Edgeøya) and Trygghamna (Isfjorden), wet moss tundra in Russebukta (Edgeøya) and polar desert in Nordaustlandet and Hambergbukta (East coast of Spitsbergen).

5. Methodology and results

5. 1. Environmental factors affecting species distribution at the landscape scale

Knowledge of the environmental factors controlling the biology and distribution of a specie is an essential key to further understand the abilities of the specie to track its environmental niche in changing times (Walther *et al.* 2002). Many studies are undertaken on restricted spatial scales. However, it is also important to appreciate that the probability of incorrectly estimate the effect of unusual events increases with the reduction in the scale of the study (Blackburn & Gaston 2002), and thus the ability to accurately describe factors controlling species biology. However surveys at the local scale are essential to accurately define species ranges changes at the short time scale related to environmental conditions, mostly when complex interactions between both abiotic and biotic variables have to be considered.

The endemic aphid *Acyrthosiphon svalbardicum* (Heikinheimo, 1968), host specific to *Dryas octopetala* L. (Rosaceae)*,* occurs along the southern coast of Kongsfjorden (Spitsbergen), where it is abundant on coastal ridges. The probability of aphid occurrence in a patch of *D. octopetala* has been described as decreasing towards the entrance of the fjord and with distance from the shore (Strathdee & Bale 1995). This

conclusion was drawn by studies regarding environmental factors affecting aphid distribution in Kongsfjorden area, carried out during the early 1990's (Strathdee *et al.* 1993, Strathdee & Bale 1995). They concluded that the aphid was restricted to those areas which clear up from snow earlier in the season, where the aphid would experience the minimum number of day degrees required to complete its obligate holocyclic life cycle (insect undergoes sexual reproduction during at least part of its life cycle). Field validation was nonetheless constrained to six *D. octopetala* patches in a 2.7 by 3.5 m. south facing plot at a single location in Ny-Ålesund (Strathdee & Bale 1995). Moreover, contradictory conclusions were drawn in a later study, when the aphid appeared as more abundant than expected under deeper snow profiles (Dollery *et al.* 2006).

The distribution of *A. svalbardicum* distribution in Kongsfjorden was presented in paper I as a case study on factors which can affect local distribution of species. The case was initially chosen as an example where a single environmental factor (the timing of snow melt) strongly determines the distribution range of the species. The aims were to test whether changes in species range had been recorded since the distribution map by Strathdee & Bale in 1995 and whether this distribution could be directly related to snow depth as a proxy for timing of snow melt. The distribution range of *A. svalbardicum* along the southern shore of Kongsfjorden (Svalbard) (Figure 7) was revisited in 2009 and 2010 and snow depth was mapped at peak snow depth (April), and plant phenology, aphid presence, and aphid phenology was recorded in August.
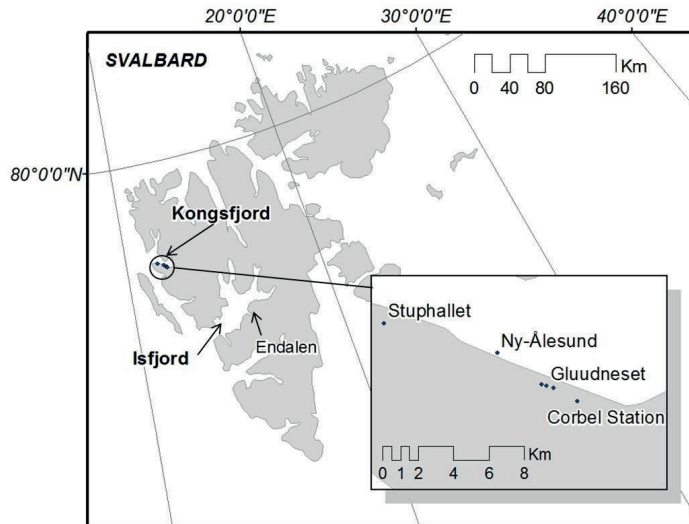
Figure 7 *Study locations in Kongsfjorden (Svalbard archipelago).*

Results showed a much more complex picture than that initially described by Strathdee & Bale (1995). In addition to a relationship with snow depth, a strong relationship was also found between both aphid distribution and host plant phenology. However a linear relation between snow depth and plant phenology did not allow inferring causality of independent factors. Strathdee & Bale (1995) could have overlooked the potential relation of plant phenology on aphid distribution for the same reason. Even though a clear relationship was found between snow depth and the species distribution this factor could not explain patch occupancy of the host plant by the aphid throughout its full range, neither can a combination of snow depth and host plant phenology.

The aphid can produce an extra generation of sexual morphs when the thermal conditions are appropriate, a condition that has been pointed as a possible pre-adaptation of this species for warmer conditions (Strathdee 1993, Hullé *et al*. 2008). However, Hullé *et al*. (2008) pointed out that during the period 1992-2006 the summer thermal budget for the species has increased by 180 degree-days, sufficient to produce the increase in egg production (Strathdee *et al*. 1995). Field validation nonetheless did not confirm the hypothesis, as the extra generation was not found in a series of expected years (Hullé *et al*. 2008). On the other hand, the increase in the summer thermal budget could, to a certain extent, explain why the species was found in more patches under deep snow profiles than expected. Yet once again this would not explain the absence of the species in suitable patches. Inter-annual variations in snow depth, ice thickness, length of summer, plant phenology and predation pressure, together with the limited dispersal ability of the aphid might be to a certain extent driving the dynamics of a metapopulation, in which not always all suitable patches are colonized, and colonization of suboptimal habitat can occur (Hanski 1998).

The following conclusions could be drawn from this study:

1) Factors limiting species distribution are difficult to resolve yet important to understand, especially if projections of responses to climate change are to be accurately modelled.

2) Snow depth can be used in the high Arctic as a proxy for timing of snow melt since the snow depth data collected in 2009 for showing a strong significant linear relation with timing of snow clearance.

3) There is a significant relationship between snow depth and both site occupancy and aphid phenology.

4) There is a significant relationship between plant phenology and both site occupancy and aphid phenology.

5) These relationships cannot accurately describe the distribution at landscape scale as they do not explain lack of occurrence in patches under shallow snow depths with advanced plant phenology.

6) The dispersal abilities of the species have been significantly underestimated since the distribution range of the species has shown an expansion of 4.7 km to the fjord mouth since 1995.

7) These results form a baseline study for future research on changes in species local distribution.

5.2. Invertebrate diversity in the Svalbard Archipelago

In order to understand future changes in biodiversity and biogeographical patterns, comprehensive descriptions of current communities arise as essential background knowledge. In the case of the Svalbard archipelago, over 1,000 species of invertebrate have been recorded, including some 500 species of insects, spiders and mites (Coulson 2007), although there are very few records of the invertebrate fauna from the east coast including the islands of Nordaustlandet and Edgeøya. This is an important omission. Studies from south, south east and eastern islands of Svalbard (Sørkapp, Storfjord, Edgeøya, Barentsøya, Kong Karls Land, Kvitøya, Hopen) are also almost completely absent (Coulson 2007, Babenko & Fjellberg 2006) except brief descriptions (Fjellberg, 1984) and vague citations (Fjellberg, 1994). After a thorough bibliographic research in invertebrate fauna of the Norwegian Arctic (Fjellberg 1984; Fjellberg 1994; Fjellberg 1997; Coulson 2000 and references therein; Babenko & Fjellberg 2006; Coulson & Refseth 2004, Coulson 2007 and references therein) no published records of the invertebrate fauna of Edgeøya were found, besides scattered studies in Rotifera and Tardigrada (De Smet *et al.* 1994) leaving an area of more than 5,000 km^2 almost completely undescribed; data from some microarthropod groups such as Mesostigmatic mites seem to be completely absent. In one of the few publications describing the insects of Nordaustlandet, Fjellberg (1994) describes 34 species of Collembola, three of which were new records to Svalbard and are species still not observed on the west coast, indicating the possible existence of a

different community in the east coast from those at the west coast, possibly due to different climatology and influence from air and ocean currents (Figure 2). These different influences from air and ocean currents between east and west Svalbard could also imply different immigration histories for east populations in comparison with western ones. Several areas of the Svalbard archipelago were visited for biodiversity surveys (Papers II, VI, VII, VIII, IX), with special emphasis on the eastern areas of the archipelago (Figure 4).

Edgeøya

Two sampling campaigns, in 2009 and 2010, were carried out to survey the invertebrate fauna of Edgeøya (Paper II) (Due to delay in the taxonomical evaluation of samples from the campaign in 2010, only the specimens identified from 2009 campaign are discussed on the manuscript- Paper II). From 2009 campaign, they were identified a total of 38 species of collembolan (two of them new records for Svalbard) 11 species of enchytraeid worms (three of them new records for Svalbard) and five species of spiders, 19 species of oribatid mites, nine mesostigmatic mites (one new to Svalbard).

Nordaustlandet

A total of 24 species of Collembola were identified in the study from Nordaustlandet (Paper IX), including three records new to the area. Five species of gamasid mites

were found in the samples, all new records to Nordaustlandet. Nine species of spiders were found, increasing the number of spiders identified from Nordaustlandet up to 12 out of the total of 19 spider species identified from Svalbard. None of the invertebrate species found in this survey were new records for Svalbard.

In the light of the results of these biodiversity surveys, a few observations are noteworthy:

1) In total nine invertebrate species were newly recorded from Svalbard (Table 1), seven of them in the eastern island of Edgeøya and which have never identified before from western locations in spite of the extensive literature from western regions of Svalbard (Coulson 2000, Coulson & Refseth 2004, Coulson 2007 and references therein).

2) The nine new species records which arise from a limited sampling effort indicate, as suggested, that the Svalbard invertebrate checklist is far from complete.

3) Six out of nine new records come from the eastern island of Edgeøya and have not been recorded from western locations in Svalbard, suggesting the existence of specific eastern invertebrate assemblages.

4) Four out of the six new species described from Edgeøya have East Palaearctic distribution. This could be an indication of the dispersal route to Svalbard from eastern Palaearctic areas following the transpolar drift.

Table 1 *Species records new to Svalbard in the frame of this thesis*

Acarina	**Location**
Mesostigmata	
Zercon andrei Sellnick 1958	Bjørnøya
Zerconopsis muestairi (Schweizer, 1949)	Bjørnøya
Saprosecans baloghi Karg, 1964	Edgeøya
Collembola	
Folsomia bisetosella Fjellberg, 2005	Adventdalen/ Edgeøya
Folsomia ciliata Babenko & Bulavintsev, 1993	Edgeøya
Pseudanurophorus psammophilus (Potapov & Stebaeva, 2002)	Edgeøya
Enchytraeidae	
Cernosvitoviella cf. Pusilla Nurminen, 1973	Edgeøya
Marionina sp.nov.	Edgeøya
Mesenchytraeus melanocephalus Christensen & Dózsa-Farkas, 1999	Edgeøya

5.3. Phylogeographical analysis

Phylogeography considers time and space jointly when mapping a particular gene genealogy, unravelling the historical components of the spatial distribution of gene lineages, and hence representing an ideal tool by which to test biogeographical hypotheses (Avise 2000, Beheregaray 2008). It is a growing field which has widely and valuably contributed to diverse research areas such as speciation (Avise 2000, Hewitt 2001), biogeography (Hewitt 1996, Abbott and Brochmann 2003, Nolan *et al*. 2006, Caruso *et al*. 2009, Sanmartín 2008, McGaughran *et al*. 2011), or even conservation biology since the technique can reveal fine spatial patterns such as phylogeographical breaks over short distances (Hewitt 2001, Petit 2004, Garrick *et al*. 2004, Garrick *et al*. 2007). This approach has been demonstrated to a particularly useful tool to assess colonization processes (Juan *et al*. 2000, Weider 2003, Alsos *et al.* 2007), origin and distribution of biodiversity (Weider & Hobæk 2000, Beheragaray 2008). It has also proven its use in identifying glacial refugia (Tremblay & Shoen 1999, Fedorov & Stenseth 2002, Rowe *et al*. 2004, Skrede *et al.* 2006, Stevens *et al*. 2006), including cryptic refugia, where organisms could have been present during intensive glacial episodes although probably scattered and in low densities (Provan & Bennet 2008).

Both historical and recent colonization events may play a role in shaping species distribution. Svalbard has been suggested as possible glacial refugia for the Arctic plant species *Arenaria humifusa* (Westegaard *et al*. 2011), and recent

phylogeographical studies in continental Antarctica, indicated the relevance of cryptic refugia in shaping species phylogeographical patterns, challenging common understanding of glacial survival and Antarctic glacial history (Convey *et al.* 2008, McGaughran *et al.* 2011, Mortimer *et al.* 2010). Ocean currents have been also shown to play an important role shaping collembolan biogeographical patterns in Antarctica (McGaughran *et al.* 2010). On the Northern Hemisphere, the North Atlantic has been historically considered as an important dispersal barrier between Palaearctic and Nearctic areas (Hultén 1937). However, genetic spatial distribution across North Atlantic, Barents Sea and Arctic regions has never been described for terrestrial invertebrates.

Megaphorura arctica (Tullberg, 1876) (Hexapoda: Collembola), represents a unique Arctic model invertebrate species given the number studies to date (e.g. Hayward *et al.* 2000, Coulson *et al.* 2002a, Holmstrup *et al.* 2002, Worland & Block 2003, Purac *et al.* 2008), as well as being often cited in reviews on overwintering strategies for its well-known protective dehydration mechanism (Paper V) (Clark & Worland 2008, Bale & Hayward 2010). 199 mitochondrial DNA sequences encoding for Cytochrome Oxidase I gene (COI), were obtained from *M. arctica* individuals belonging to 19 different Arctic and North Atlantic populations. A series of bioinformatics tools were applied to those sequences to determine haplotype spatial distribution patterns across north Atlantic areas as described in paper III.

Mitochondrial DNA represents an excellent tool for invertebrate phylogeographical studies due to high evolutionary rate (Brown *et al*. 1979), ease of use since it is haploid (Zhang & Hewitt 1996), low recombination levels and being close to evolutionary neutral (Rokas 2003; but see Nardi *et al*. 2001 for a heteroplasmy case, existence of different mitochondrial haplotypes within the same cell, in the collembolan species *Tetradontophora bielaniensis*). In the case of Collembolan there are also a high number of suitable primers (Simon *et al*. 1994). Nevertheless, mitochondrial DNA should be used carefully when inferring population size, ecological patterns, the ability of the species to respond to environmental changes (Bazin *et al*. 2006), or as unique marker when applying molecular clock approaches (Zhang & Hewitt 1996).

From the 19 populations, 25 haplotypes were found: six exclusive to Iceland, one exclusive to Greenland, one to Norway, 16 exclusive to Svalbard and one shared between several Svalbard areas and the populations in north Iceland. The most common haplotype in Svalbard (A) is also shared with the north Iceland population (Figure 8). Five structural groups can be defined from mtDNA data both by spatial analysis of molecular variance (SAMOVA) (Dunpaloup *et al.* 2002) and nested clade phylogeographical analysis (Templeton 2004) (Group 1 includes most of Svalbard populations and north Iceland, Group 2 including Greenland, Group 3 mainland Norway, Group 4 south Iceland, and Group 5 Vårsolbukta population on the west coast of Svalbard) (Figure 8), with putative dispersal barriers mainly arranged along

the longitudinal axis of the north Atlantic Ocean, with transversal barriers over Icelandic and Norwegian land. (Figure 9).
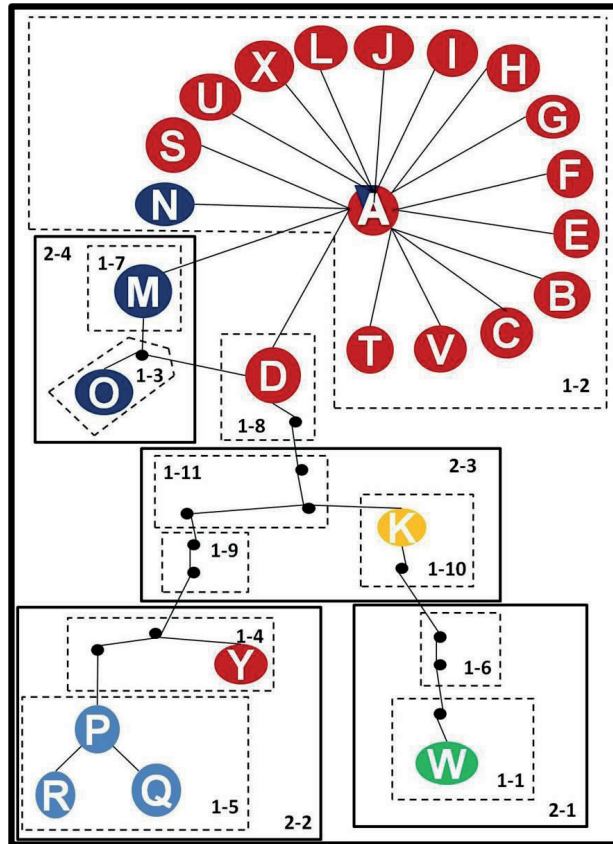

Figure 8 Nested Clade Phylogeographical Analysis representing 3 nested clade levels (1- dotted line; 2- normal solid line; 3- bold solid line). It includes colour codes for the geographical distribution of the haplotypes: in red, Svalbard; in dark blue, North Iceland; in light blue, South Iceland; in yellow, Greenland; and in green, mainland Norway. In black are represented missing haplotypes.

No population structure within Svalbard was detected. However two links between Svalbard and Iceland were observed. The data suggests Iceland to be the most likely source for populations colonizing the Svalbard archipelago. The existence of one common, ancient, haplotype in Svalbard together with a high number of closely related haplotypes suggests recent colonization with subsequent expansion, while the existence of a relationship between south Iceland and Svalbard through the Vårsolbukta population suggests separate colonization events. Examination of the data with SAMOVA, revealed dispersal barriers between all the Svalbard, Greenland, Norway, and north of Iceland, but not between Svalbard and Iceland, supporting the hypothesis of Iceland as source for Svalbard populations. Hierarchical clustering based on genetic differentiation estimates (Fst) shows a close relationship between groups 1 (Svalbard and Iceland) and 2 (Greenland), 4 (Iceland north) and 5 (Vårsolbukta), leaving mainland Norway as the most distant group (Figure 10).
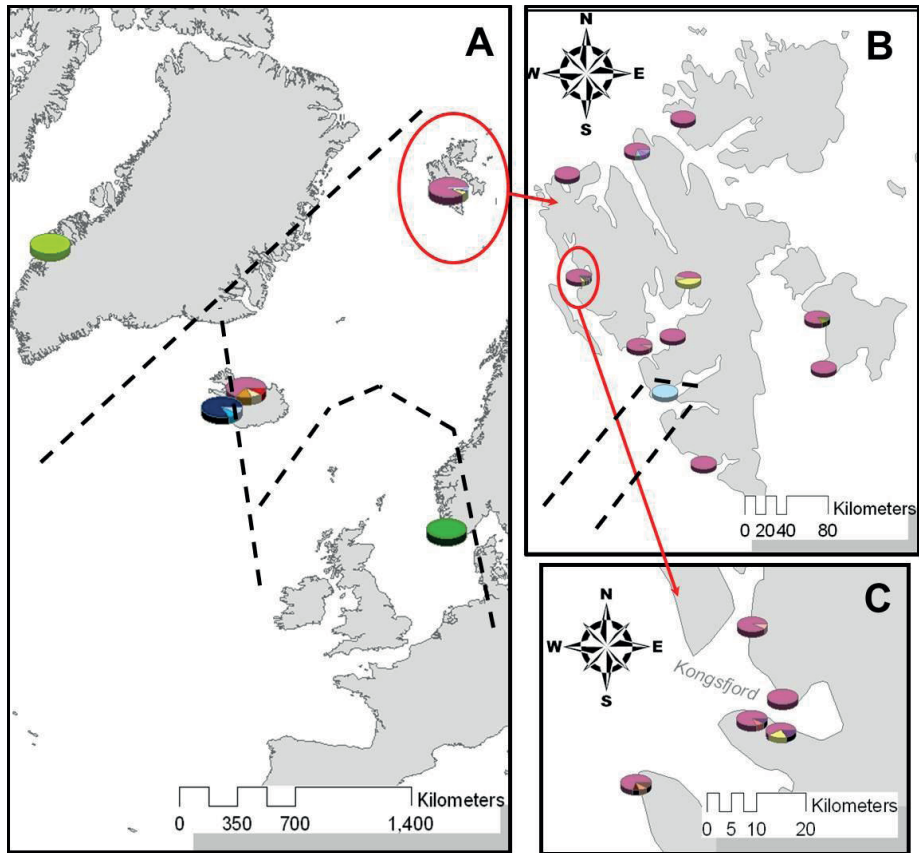
Figure 9 *Geographical distributions of haplotypes (colour pies), in the Atlantic area,*

Svalbard and Kongsfjorden area in Spitsbergen. Dotted line represents putative

dispersal barriers estimated by Spatial Molecular Analysis of Variance implemented
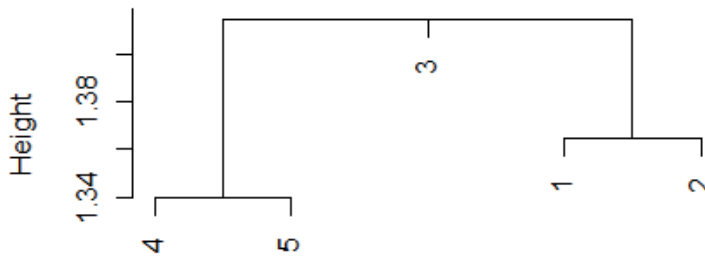
in SAMOVA 1.0

48

Figure 10 *Dendrogram based on genetic distances (Fst) between the 5 groups*

defined by SAMOVA (1: Svalbard and Iceland north; 2: Greenland; 3: mainland

Norway; 4: Iceland South; 5: Vårsolbukta –Svalbard–). The dendrogram shows a

closer relation between Vårsulbukta population and South Iceland, and a closer

relation between the Svalbard/Iceland North complex (1) with Greenland (2) than

with mainland Norway (3).

In spite of lacking some data from the remaining areas on the distribution range in northern Norway, Novaya Zemlya and Dolgii Island (due to lack of collections of the species), ocean current circulation is suggested as the main factor shaping the species distribution, which is further supported by the following evidence:

1) Putative dispersal barriers occur across the north-south axis of the North Atlantic Ocean; east-west dispersal barriers are just found over land.

2) The North Atlantic Current flows in the direction Iceland to Svalbard, facilitating sea transport between Iceland and Svalbard, while circular currents

(gyres) in the Icelandic sea between Iceland and Jan Mayen (Iceland Marine Research Institute) would prevent or difficult particles to be transported transversally in the direction Greenland- Norway.

3) Ocean currents have been previously suggested as an important factor shaping genetic population structure for Antarctic collembolan species (McGrauhan *et al.* 2010).

4) This species has been shown to survive up to 14 days on sea water (Coulson *et al.* 2002a), making long distance dispersal of the species by ocean currents possible.

5.5. Biogeographical analysis

It has never been clarified whether any pattern defines the distribution of most species of Arctic invertebrates, although it is appreciated that not all species live everywhere. Darwin (1859) already postulated that areas with similar climatic conditions can vary greatly in species composition. Environment and physiological limitations, together with dispersal abilities are frequently indicated as main factors determining species ranges in different groups (Woodward & Kelly 2002), but more recently it has been suggested that historical influences can contribute to contemporary patterns of biodiversity to a similar or greater extent than contemporary climatic regimes (Stevens 2006).

Over the last decade, macroecolological approaches, including large-scale biogeographical analysis, have become a very valuable tool to evaluate biodiversity status (Blackburn & Gaston 2002, Woodward & Kelly, 2002, Stevens 2006, Clarke *et al*. 2007, Kent 2007, Calosi *et al*. 2010, Chown & Gaston 2010). In paper IV this approach is implemented for Arctic collembolan distributions, based on newly developed distance- based test statistics to test for the existence of clusters of species according to their geographic ranges (Henning & Hausdorf 2004). Should the biogeography of Arctic Collembola be determined by current climatic regimes, distribution patterns would follow climatic features rather than defined geographical or historical factors. The distribution ranges of 358 Arctic species of Collembola (from a total of 390 species described from Arctic areas), were collated into one

comprehensive dataset for the entire Arctic area (see supplementary material from Paper I V). This data compilation was possible thanks to recent efforts made to standardize the existing knowledge into a homogeneous dataset (Babenko & Fjellberg 2006, Coulson 2007, Babenko 2010). The dataset was analysed in combination with 10 years (1996- 2005) temperature and precipitation data from 15 Arctic areas as indicative of contemporary climatic regimes, to test for the role of current climatic factors in the distribution of Collembola species.

The biogeographical pattern found, detailed in paper IV, showed nine distinct clusters (Figure 11). The geographical distribution of these clusters shows a strong similarity with patterns found in cDNA haplotype distribution described for the Holarctic region for the plant species *Saxifraga oppositifolia* (Abbott *et al.* 2000). Common elements are found within Siberian areas, Beringia, Atlantic areas and Canadian Arctic, just wide-ranged species are shared among all them, and just one cluster is found throughout the Arctic, the latter comprising few, and exclusively cosmopolitan and holarctic species. Endemic collembolan species occur in north and mid-Siberia (D), Beringia (F and G), the Canadian Arctic (H) and Greenland (I), all of which have been previously indicated as including possible refugia during LGM by a number of authors and for a series of taxa (Hultén 1937, Fedorov & Stenseth 2002, Abbott and Brochmann 2003, Weider and Hobæk 2003, Tremblay and Shoen 1999).

The geographical distribution of the species belonging to each cluster (Figure 12) does not follow current climatic envelopes (Figure 3). The distribution pattern

nonetheless is related to historical geographical events such as LGM ice extent and glacial refugia (see section 5), and posterior colonization patterns including northbound colonization routes from southern areas and colonization from glacial refugia in Beringia and East and mid-Siberia. Northbound colonization patterns as the Arctic deglaciated would explain why most species colonizing Atlantic areas have European-western Palaearctic distributions, species colonizing eastern Siberia have mostly Asiatic distributions and species found in the Canadian Arctic are mainly Nearctic. In the case of high Arctic Canada and many Siberian Arctic islands, only wide-ranging species colonize them rather than species commonly found on the closer mainland. This fact together with the low number of species colonizing high Arctic islands could indicate recent colonization of these areas.
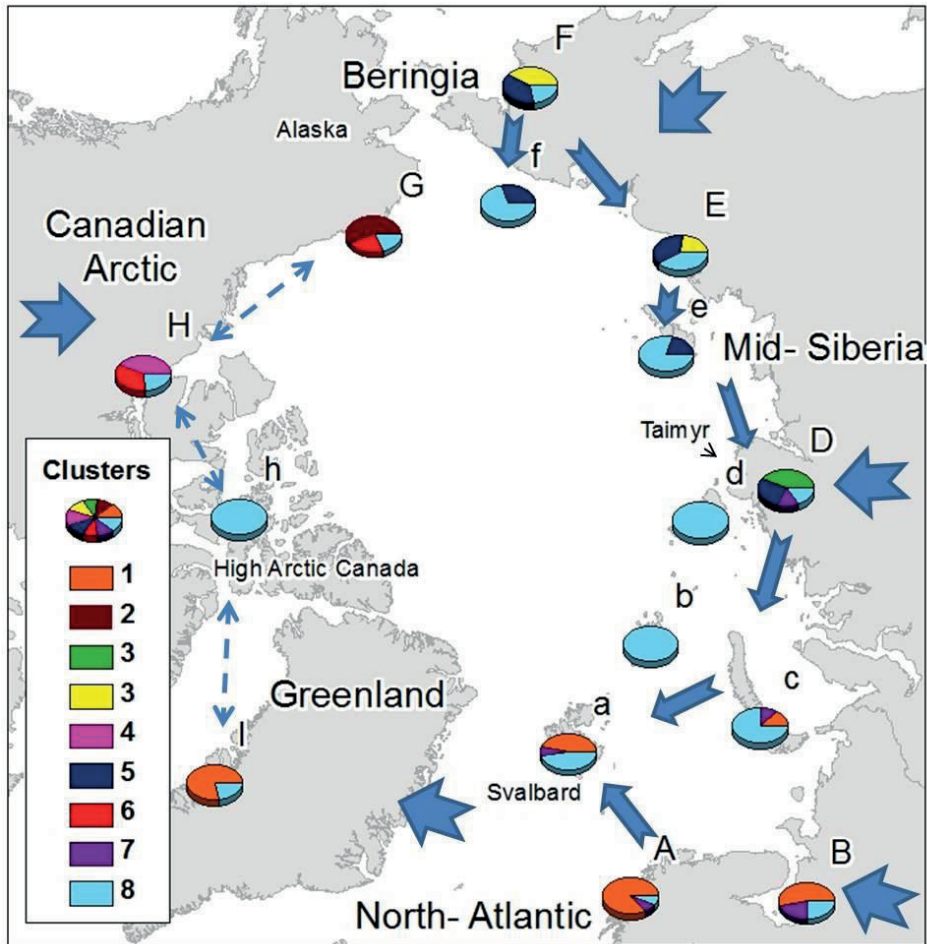
Figure 11 *Gaussian mixture clustering geographically represented as number of species allocated to each cluster at each Arctic area. Arrows represent suggested dispersal routes to (thick arrows) and within (thin arrows) Arctic areas. Dashed arrows indicate areas of unresolved main dispersal routes.*
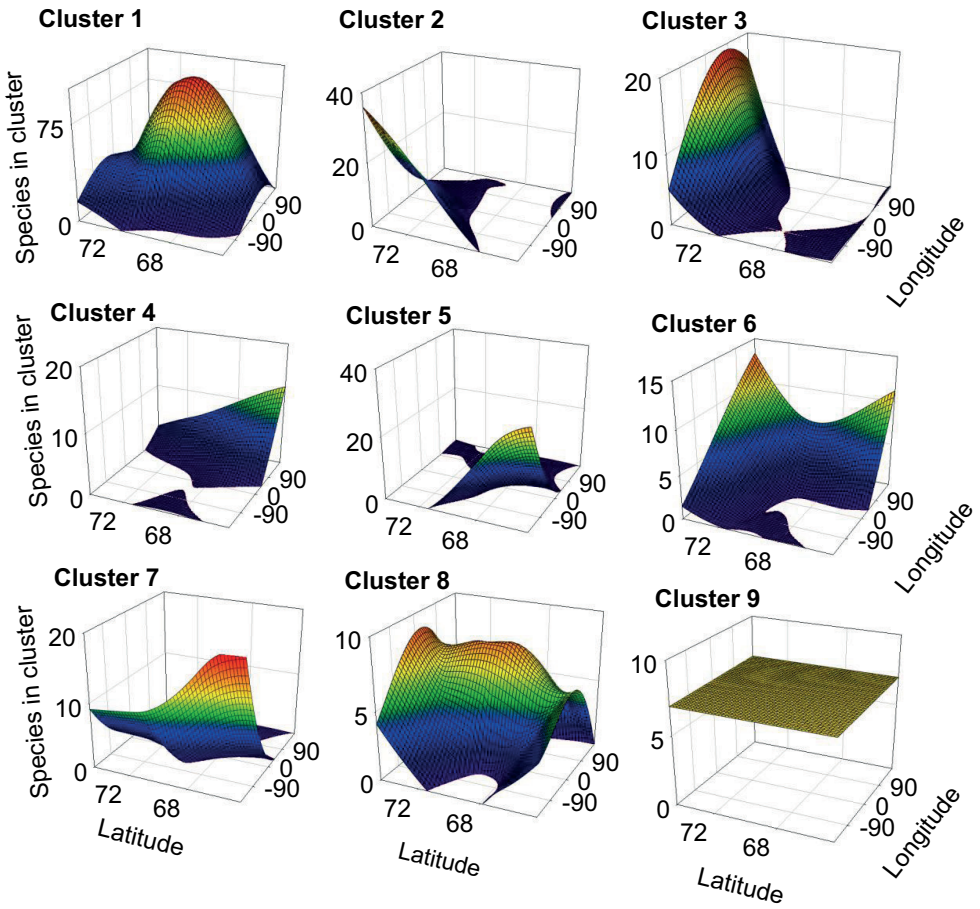
Figure 12 *The main distributions of the species in a longitude and latitude axis system for each species cluster. The 3D plots represent a projection of the number of species from each cluster found in the Arctic at each longitude/latitude coordinate.(For full reference see Paper IV).*

Biogeographical cluster distribution does not follow current climatic regimes patterns as shown in paper IV. There is only one defined biogeographical cluster which distribution shows a linear response to both temperature (Figure 13), and precipitation (Figure 14) (Cluster 1). This cluster however is composed of western Palaearctic species and is distributed across north Atlantic areas (western Palaearctic, Svalbard Archipelago and Greenland). Adjacent areas are more likely to be influenced by similar climatic regimes, and these areas are under the influence of the North Atlantic Oscillation (Dickson et al. 2000). Therefore, there is a possibility that these environmental parameters are in effect autocorrelated with the distribution clusters.
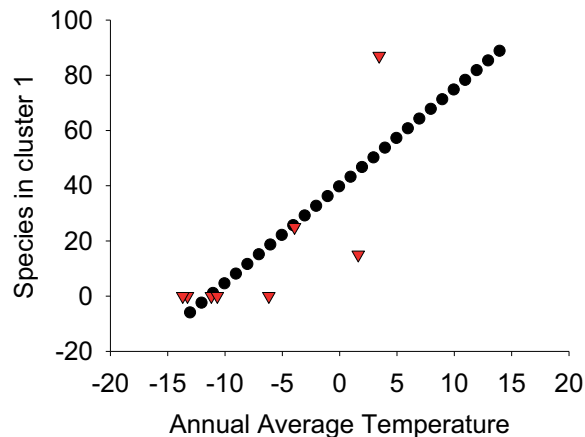

Figure 13 *Number of species found in cluster 1 in relation to mean annual temperature. In red: real data, with annual temperature averaged from daily temperature recorded at different Arctic weather stations from 1996- 2005 (Paper IV). In black: model data calculated using polynomial regression (r^2= 0.59, F= 11.40, p<0.05).*

When the calculations are performed based on average temperature of the warmest month (July), rather than yearly average temperature, only cluster 6 (distribution along eastern Palaearctic and Asian part of Beringia) correlates with a second order polynomial (Figure 15).
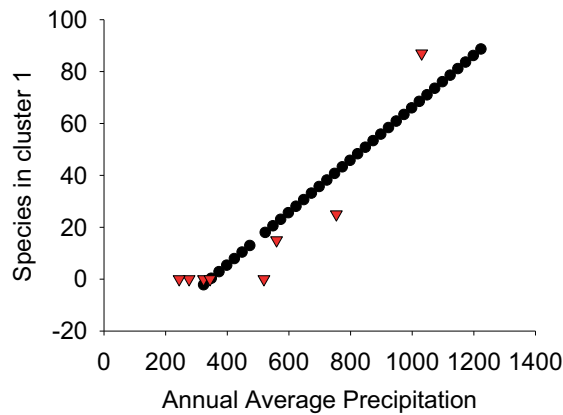

Figure 14 *Number of species found in cluster 1 in relation to annual precipitation. In red: real data, with annual precipitation data gathered by the World Meteorological Organization at different Arctic weather stations (Paper IV). In black: model data calculated using polynomial regression ($r^2 = 0.83$, F= 29.25, p<0.05).*
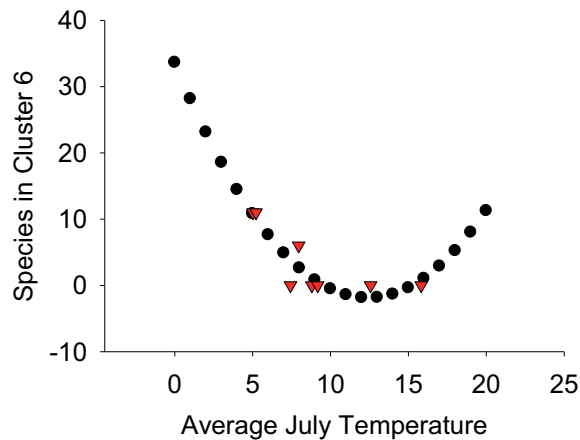
Figure 15 *Number of species found in cluster 6 in relation to average temperature in the warmest month (July). In red: real data, with July temperature averaged from daily temperature recorded at different Arctic weather stations in July from 1996-2005 (Paper IV). In black: model data calculated using polynomial regression (r^2= 0.82, F= 11.40, p<0.05).*

The biogeographical pattern underlying collembolan species distribution in the high Arctic is thereby defined, with the following key points:

1) The biogeographical pattern based on species distribution described is consistent with those described by molecular methods including microsatellites and AFLP (Skrede *et al*. 2006, Alsos et a. 2007) cDNA RFLP (Abbott & Brochmann 2003).

2) No evidence of glacial survival in high Arctic islands can be found.

3) Glacial refugia can be inferred through specific elements in Beringia and East Palaearctic.

4) Although presence of endemism in Greenland and Canadian high Arctic Archipelago could indicate the refugia described for Arctic plants, no evidence of such refugia are found.

6. Discussion

In the present thesis I have shown that the biogeographical patterns described illustrate the limitations of environmental factors *per se* to determine species distribution ranges. Dispersal, including long distance dispersal, is suggested as an essential element shaping microarthropod species distribution across all geographical scales. In this thesis Arctic invertebrate biogeographical patterns are observed at four levels:

1) *Landscape*:- Observable patterns in soil invertebrate distribution have previously been described (Danks 1978, Coulson *et al*. 2003b, Hodkinson *et al.* 2004, Hågvar *et al.* 2009). Microscale distribution patterns in the soil mesofauna are commonly known to occur due to slight variations in soil microenvironments and the aggregation tendency of a number of soil fauna groups (Danks 1978, Coulson *et al.* 2003b), or due to colonization processes in newly exposed ground on glacier forelands (Coulson *et al*. 2003a, Hodkinson *et al*. 2004, Hågvar *et al.* 2009). However, the exact factors controlling the distribution are often difficult to resolve. Even within a single species, it has been shown how even when a straight forward relationship can be inferred through a unique environmental factor (or a combination of environmental variables) and the species distribution, it is a complex task to be able to predict species occurrence at landscape scale (Paper I).

2) *Regional:-* In the Svalbard archipelago, the presence of species in the eastern regions not recorded from the better known west coast suggests the existence of different communities in comparison with western locations in the archipelago. Nonetheless, lack of information on some groups makes it difficult to establish clear differences (Papers II, VI, VII, VIII, IX) or infer causes for the observed patterns.

3) *Geographical:-* At a molecular level, a north-east link between Icelandic and Svalbard populations is found, while dispersal barriers appear mainly aligned along the north-south axis of the North Atlantic Ocean (Paper III).

4) *Holarctic:-* At a Holarctic level, nine different biotic clusters are observed (Paper IV), each cluster confining different type of species (mostly Palaearctic species in cluster 1, 3, 4, 6 and 8, mostly Nearctic in cluster 2, and cosmopolitan or Holarctic in cluster 9, while Beringian species are found in clusters 2,3 and 4).

Lack of biogeographical structure is often associated with long-distance dispersal (Shönswetter *et al.* 2008), occurring as a result of the homogenization of species distribution across all suitable habitats. On the other hand, if an ancestral biota was fragmented by vicariance events (Hausdorf & Hennig 2003), or environmental pressures such as current climatic regimes, are strongly influential in determining the current distribution of species, biotic elements or species clusters should emerge. Arctic species show specific physiological adaptations to take advantage for the short Arctic summer season, and to survive harsh winter conditions (Paper V). It would be

reasonable to expect the distribution of species in high latitudes to be dependent on physiological adaptations and thus strongly limited by the environment. However, for none of the studied scales can current environmental conditions provide an adequate explanation of the observed biogeographical patterns. Indeed, it has been asserted that in the absence of a time reference, traditional ecogeographic perspectives tend to over-emphasize the role of contemporary ecological pressures in shaping spatial distribution of organismal traits (Avise 2000). Hence there is a need to contextualise the biogeographical patterns within a historical frame and to account for dispersal phenomena. An example of how dispersal and metapopulation dynamics play an essential role in determining the species distribution is given with the case study of *A. svalbardicum* (Paper I). On that study it is shown how projections, based on combinations of the best suitable environmental predictors of the species distribution, cannot predict the local species distribution range with precision. Studies in the polar desert areas of Nordaustlandet (Paper IX) have shown how invertebrate communities occur in the most extreme polar desert environments, often lacking higher plants and where just scarce lichens and cyanobacteria colonies are present. Furthermore, many species have been shown not to be limited to certain environmental factors but rather show high flexibility in the environmental conditions they tolerate (Paper IV). Altogether, these facts constrain the power of environmental factors to accurately predict distribution ranges.

Research on landscape distribution patterns of *A. svalbardicum* (Paper I), provide an insight as to why the distribution of the species cannot be fully defined based on

environmental predictors. Those factors failed to model the actual species distribution due to autocorrelation between the measured variables, a common phenomenon in ecological studies (Legendre 1993). At landscape level, community differences between areas, based on species presence, in Svalbard archipelago (Papers II, VI, VII, VIII, IX) are difficult to resolve as in most cases these differences are based on rare species, and cosmopolitan, and possibly good dispersers and wide ranged species, tend to rapidly spread among neighbouring areas eliminating community differences over a short scale. At the molecular level (Paper III) linkage between populations is defined but these results cannot be translated into migration rate as several loci, or high number of variable sites, are required for such detail (Beerli 2006). These molecular data could be translated into time since colonization, however such calculations assume constant mutation rate across populations within the studied timeline, an assumption which, should it not be true, could lead to error orders of magnitude bigger that the time scale considered (Ayala 1999, Pulquério & Nichols 2006). Biogeographical analysis based on collembolan Holarctic distribution data (Paper IV) presented a clear image of how biogeographical patterns can be established simply based on species/absence data when the appropriate analytical tools are applied to a robust data set. This study did nonetheless fail to find any pattern within the Svalbard archipelago, exposing limitations on the geographical range this type of study is applicable.

No indications of invertebrate glacial survival in the high Arctic are found. Neither is support for the more distinct glacial refugia in the Canadian high Arctic Archipelago

reported by several authors (Fedorov & Stenseth 2002, Abbott & Brochmann 2003, Wider & Hobæk 2003) despite weak evidence through the presence of endemic species in Greenland and Canadian high Arctic archipelago (Paper IV). Lack of such evidence could be due to a lack of differentiation, in relation to species distribution, between east and west Greenland, as the species distributions in databases assume Greenland as a single biogeographical unit. This is also a drawback with data for the high Arctic Canadian archipelago. Studies both in Svalbard and mainland Norway however show how Collembola can act as pioneer organisms colonizing glacier forelands (Coulson *et al*. 2003a, Hågvar *et al.* 2009). Hence both *in situ* glacial survival and colonization from long distance locations do not seem unlikely. On that line, and in addition to previous evidence of LGM refugia in several Arctic areas, evidence of *in situ* survival in Beringia and in areas eastern of the Ural Mountains of Arctic Collembola have been defined through the biogeographical analysis (Paper IV) (Figure 16) while phylogeographical analysis points to Iceland as a proximate source of the populations of the collembolan species *Megaphorura arctica* (Paper III).
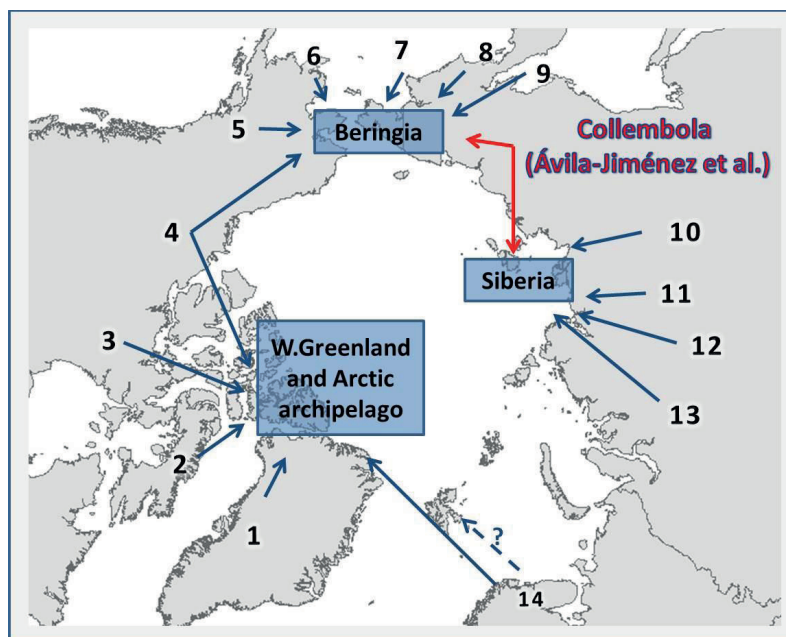
Figure 16 *Examples of species surviving in Arctic areas during LGM, indicating the*

approximate location of the glacial refugia. They are indicated published evidence of

glacial survival in the three main described refugia. West Greenland/Arctic

Archipelago refugium: (1: Dryas integrifolia (Abbott & Brochmann 2003); 2:

Saxifraga oppositifolia (Abbott & Brochmann 2003); 3: Collared lemming (Fedorov

& Stenseth 2002); 4: Daphnia pulex complex (Wider & Hobæk 2003)), Beringia

refugium (Collembola (II); 4: Daphnia pulex complex (Wider & Hobæk 2003); 5:

Saxifraga oppositifolia (Abbott & Brochmann 2003); 6: Lepus othus (Waltari & Cook

2005); 7: Lepus arcticus (Waltari & Cook 2005); 8: Collared lemming (Fedorov &

Stenseth 2002); 9: Dryas integrifolia (Abbott & Brochmann 2003)) and East Ural

refugium (Collembola (II); 10: Lepus timidus (Waltari & Cook 2005); 11: Carex spp.

(Abbott & Brochmann 2003); 12: Mammoth (Iacumin et al. 2000); 13:Dryas

octopetala (Skrede et al. 2006); 14: Arenaria humifusa (Westegaard et al. 2011)).

7.   Status of the Arctic and implications

Arctic terrestrial fauna presents a series of overwintering adaptations, outlined on Paper V. Species particularly adapted to cold habitat are sensitive to suffer an impact from four principal factors: (1) warmer winter temperatures, with an increased frequency of extreme events such as freeze–thaw cycles and surface icing; (2) changes in snow fall and snow lie; (3) pollutant load; and (4) dispersal of invertebrates. The latter has been repeatedly emphasized within this thesis, and evidence has been presented on how recent glacial history, glacial survival and colonization, have a noticeable contribution to current species distribution in the Arctic. The influence of historical events on the biogeography of Arctic invertebrates can be stronger than that exerted by current environmental factors. Nonetheless, effects that environmental factors have on species distribution and diversity should not be underrated.

In an era of rapid and widespread environmental change, the need for targeted conservation strategies and carefully considered use of natural resources has never been more pressing (Greenslade 2008). To best conserve or preserve global biodiversity it is important to understand how biogeographical distribution patterns are shaped, in order to set a baseline from which predictions about future changes in biodiversity can be made (Ackerly *et al*. 2010). The present thesis and publications associated to it have focused in giving regional descriptions (Papers II, VI, VII, VIII, IX), but more importantly recent biogeographical (Paper IV) and phylogeographical

(Paper III) studies suggest a history of Arctic colonization, putting for the first time the biogeographical pattern into a historical framework.

Changes in the large scale distribution pattern of soil invertebrates could have a significant effect on ecosystem function, development and ecosystem services, and fine- tuned species- poor Arctic soils are particularly vulnerable to change (Barret *et al.* 2008, Hartley 2008). For the Holarctic area, long distance dispersal from LGM refugia arises as a main factor defining current species distribution. Today, 10,000 years after the LGM and since the opening of suitable (perhaps optimal) niches in the Svalbard archipelago, not all species able to survive there have yet reached the region. Ocean currents have been discussed several times as a particularly efficient dispersal vector for Arctic collembolans. Dispersal and colonization patterns presented in this thesis, and based both in species diversity and molecular data, do not clearly relate to migration patterns of birds. However, studies in phoretic invertebrates in birds (Levedeba & Krivolutsky 2003, Levedeba & Levedev 2008) and recent studies on invertebrate communities in Arctic bird nests (Pilskog, 2011), showed a large variation in invertebrate assemblages (both in birds and in nests) in relation with the bird species considered. These differences might hinder the possibilities of detecting a general biogeographical pattern in a multispecies analysis.

Mortality related to desiccation (Hodkinson *et al.* 1998) is often discussed as limiting the ability of soil invertebrates to disperse long distances airborne (Hawes *et al.* 2007). Nevertheless, it is repeatedly acknowledged as a dispersal vector (Glick 1939,

Gressit & Yosimoto 1974, Coulson *et al*. 2002b, Nkem *et al*. 2006, Hawes *et al*. 2007) and aerial dispersal of invertebrates attached to soil particles and plant, moss or lichen fragments should be accounted as a possibility. Overwintering strategies (Paper V) could be also argued as possible enhancer of airborne dispersal of cold (and often desiccation) hardened organisms in winter conditions.

The estimated temperature changes for Arctic areas range from an increase of 4.3 to 11.4°C in winter and 1.2 to 5.3°C in summer (Christensen *et al*. 2007). At the same time, precipitation is expected to increase by 10 – 30 %, with the greatest increase in winter. This will result in a thicker snow layer in winter. However, since temperature is also increasing, the period when the soil is covered by snow is expected to decrease on average, due to an earlier spring melt and greater evaporation (Christensen *et al*. 2007). There is also an indication of increased frequency of positive air temperature events during the winter.

Species such as the endemic aphid *A svalbardicum* are expected to take advantage of the longest summer, although increased mortality has been shown in soil invertebrates due to increase in winter ice thickness (Coulson *et al*. 2000), a phenomenon expected to increase in frequency (Christensen *et al*. 2007). Connectivity of species such as *M. arctica* with southern populations as Iceland has been shown by molecular methods (IV), however, phylogeographical analysis based on a single loci does not allow for accurate calculation of migration rates between populations (Hamilton *et al*. 2005),

and hence such connectivity could be frequent or just reflect a historical phenomenon.

Biogeographical analysis of the Arctic nonetheless, does not reveal current climatic regimes as the main factor determining the current distribution of Arctic Collembola (V), and even though it is likely some species may see their survival compromised by raising temperatures (Hodkinson *et al*. 1998), mostly due to desiccation in the case of soft bodied invertebrates, lethal thermal ranges are unlikely to be reached in the near future (Hodkinson et a. 1996).

The existence of a Holarctic element in collembolan biogeography composed mainly by cosmopolitan species indicates the ability of certain species to rapidly disperse to and colonize any suitable niche. A warming Arctic hence is not safe from fast invasions from southern species, not even if human mediated dispersal, responsible for the majority of biological invasions in Antarctica (Frenot *et al*. 2005) is prevented. The list of invertebrate species in the Arctic is rapidly increasing with the growing unified effort of ecologists and taxonomist to define biodiversity levels and determine and classify the high number of organisms yet to be discovered in many remote and barely described Arctic areas. How many of these species are recent colonisers or simply previously overlooked, time and further research could tell.

8. References

Abbott, R. J. and C. Brochmann (2003). History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology*, 12(2), 299-313.

Abbott, R. J., Smith, L. C., Milne, R.I., Crawford, R. M. M., Wolff, K. and Balfour, J. (2000). Molecular Analysis of Plant Migration and Refugia in the Arctic. *Science,* 289 (5483), 1343-1346.

ACIA Scientific Report .2005. www.acia.uaf.edu/pages/scientific.html

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., and Kraft, N. J. B. (2010). The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, 16(3), 476-487.

Alsos, I. G., Eidesen, P. B., Ehrich, D., Skrede, I., Westergaard, K., Jacobsen, G. H., Landvik, J. Y., Taberlet, P. and Brochmann, C. (2007). Frequent long- distance plant colonization in the changing arctic. *Science,* 316, 1601-1608.

Andrews, J.T. (1987). The late Wisconsin glaciation and deglaciation of the Laurentide ice sheet. North America and Adjacent Oceans during the Last Deglaciation, 13–37. The Geological Society of America, Boulder, Colorado.

Araújo, M. B. and Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography,* 33(10), 1677-1688.

Astakhov, V. (1998). The last ice sheet of the Kara Sea: Terrestrial constraints on its age. *Quaternary International,* 45-46, 19-28.

Avise, J. C. (2000). Phylogeography: The history and formation of species. Harvard University Press.

Ayala, F. J. (1999). Molecular clock mirages. *BioEssays,* 21(1), 71-75.

Babenko, A., and Fjellberg, A. (2006) Collembola septentrionale. A catalogue of springtails of the Arctic regions. KMK Scientific Press Ltd, Moscow.

Babenko, A. (2010). The springtail (Hexapoda, Collembola) fauna of Wrangel Island. *Entomological Review*, 90(5), 571-584.

Bale, J. S. and Hayward, S. A. L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology,* 213(6), 980-994.

Barrett, J. E., Virginia, R. A., Wall, D. H., Adams, B. J. (2008). Decline in a dominant invertebrate species contributes to altered carbon cycling in a low-diversity soil ecosystem. *Global Change Biology,* 14(8), 1734-1744.

Bazin, E., Glémin, S., and Galtier, N. (2006). Population Size Does Not Influence Mitochondrial Genetic Diversity in Animals. *Science,* 312(5773), 570-572.

Beerli, P. (2006). Comparison of Bayesian and maximum-likelihood inference of population genetic parameters. *Bioinformatics,* 22(3), 341-345.

Beheregaray, L. B. (2008). Twenty years of phylogeography: the state of the field and the challenges for the Southern Hemisphere. *Molecular Ecology*, 17(17), 3754-3774.

Blackburn, T. M. and Gaston K. J. (2002). Macroecology: concepts and consequences. 43rd annual symposium of the British Ecological Society, University of Birmingham, Blackwell.

Briner, J. P., Davis, P. T. and Miller, G. H. (2009) Latest Pleistocene and Holocene glaciation of Baffin Island, Arctic Canada: key patterns and chronologies. *Quaternary Science Reviews*, 28 (21-22), 2075-2087.

Brochmann, C., Gabrielsen, T. M., Nordal, I., Landvik, J. Y. and Elven, R. (2003). Glacial survival or tabula rasa? The history of the North Atlantic biota revisited. *Taxon,* 52, 417- 450

Brown, W. M., George, M. , and Wilson, A. C. (1979). Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences*, 76(4), 1967-1971.

Bullock, J. M., and Clarke, R. T. (2000). Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia,* 124, 506- 521.

Calosi, P., Bilton, D. T. , Spicer, J. I., Voltier, S. C., and Atfield, A. (2010). What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, 79(1), 194-204.

Caruso, T., Hogg, I. D., Carapelli, A., Frati, F., and Bargagli, R. (2009). Large-scale spatial patterns in the distribution of Collembola (Hexapoda) species in Antarctic terrestrial ecosystems. *Journal of Biogeography,* 36(5), 879-886.

Chapman, D. S., Dytham, C., and Oxford, G. S. (2007). Modelling population redistribution in a leaf beetle: an evaluation of alternative dispersal functions. *Journal of Animal Ecology,* 76, 36- 44.

Chown, S. L. and Gaston, K. J. (2010). Body size variation in insects: a macroecological perspective. *Biological Reviews,* 85(1), 139-169.

Christensen J.H., Hewitson B., Busuioc A., Chen A., Gao X., Held I., Jones R., Kolli R. K., Kwon W.–T., Laprise R., Magaña V., Mearns L., Menédez C. G., Räisänen J., Rinke A., Sarr A., and Whetton P. (2007). Regional Climate Projections. In: S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.): *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Pp. 847-940. Cambridge University Press, Cambridge, United Kingdom and New York, N.Y.

Clark, M. and Worland, M. (2008). How insects survive the cold: molecular mechanisms—a review. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology,* 178(8), 917-933.

Clark, M., Thorne, M., Pura, J., Grubor-Lajsic, G., Kube, M., Reinhardt, R., and Worland, M. R. (2007). Surviving extreme polar winters by desiccation: clues from Arctic springtail (Onychiurus arcticus) EST libraries. *BMC Genomics*, 8(1): 475.

Convey, P., Gibson, J. A. E., Hillenbrand, C. D., Hodgson, D. A., Pugh, P. J. A., Smellie, J. L. and Stevens, M. I. (2008). Antarctic terrestrial life-challenging the history of the frozen continent?" *Biological Reviews.* 83, 103-117.

Cook, J. A., Hoberg, E. P. , Koehler, A., Henttonen, H., Wickström, L., Haukisalmi, V., Galbreath, K., Chernyavski, F., Dokuchaev, N,

Lahzuhtkin, A., MacDonald, S. O., Hope, A.,Waltari, E., Runck, A., Veitch, A., Popko, R. Jenkins, E. Kutz, S. and Eckerlin, R. (2005). Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study,* 30, 33-44.

Coulson, S. J. (2000). A review of the terrestrial and freshwater invertebrate fauna of the high Arctic archipelago of Svalbard. *Norwegian Journal of Entomology,* 47, 41- 63.

Coulson, S. J. (2007). Terrestrial and freshwater invertebrate fauna of the high Arctic archipelago of Svalbard. *Zootaxa,* 1448, 41- 58.

Coulson S.J. (2009) Association of the soil mite Diapterobates notatus (Acari, Oribatidae) with Cynomya mortuorum (Linnaeus, 1761) (Calliphoridae, Calliphorinae): implications for the dispersal of oribatid mites. *International Journal of Acarology*, 35, 175-177

Coulson, S.J., and Refseth, D. (2004). The terrestrial and freshwater invertebrate fauna of Svalbard (and Jan Mayen). In: Prestrud P, Strøm H, Goldman HA (Eds). *A catalogue of the terrestrial and marine animals of Svalbard*. Skrifter 201. Norwegian Polar Institute, Tromsø.

Coulson, S. J., and Birkemoe, T. (2000). Long- term cold tolerance in Arctic invertebrates: recovery after 4 years at below -20 deg.C. *Canadian Journal of Zoology,* 78, 2055- 2058.

Coulson S.J., Hodkinson I.D., Strathdee A.T., Block W., Webb N.R., Bale J.S. and Worland M.R. (1995). Thermal environments of Arctic soil organisms during winter. *Arctic and Alpine Research,* 27, 365-371.

Coulson, S. J., Leinaas, H. P., Ims, R. A., and Søvik, G. (2000). Experimental manipulation of the winter surface ice layer: the effects on a High Arctic soil microarthropod community. *Ecography* 23, 299- 306.

Coulson, S. J., Hodkinson, I. D., Webb, N. R., and Harrison, J. A. (2002a). Survival of terrestrial soil- dwelling arthropods on and in seawater: implications for trans- oceanic dispersal. *Functional Ecology,* 16, 353- 356.

Coulson, S. J., Hodkinson, I. D., Webb, N. R., Mikkola, K., Harrison, J. A. and Pedgley, D. E. (2002b). Aerial colonization of high Arctic islands by invertebrates: the diamondback moth Plutella xytostella (Lepidoptera: Yponomeutidae) as a potential indicator species. *Diversity and Distribution,* 8, 327- 334.

Coulson, S. J., Hodkinson, I. D., and Webb, N. R. (2003a). Aerial dispersal of invertebrates over a high-Arctic glacier foreland: Midtre Lovenbreen, Svalbard. *Polar Biology,* 26(8), 530-537.

Coulson, S.J., Hodkinson, I.D. and Webb, N.R. (2003b) Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of the vegetation mosaic. *Ecography,* 26; 801-809.

Crawford R. L., Sugg P. M., and Edwards J. S. (1995). Spider arrival and primary establishment on terrain depopulated by volcanic eruption at Mount St. Helens, Washington. *The American Midland Naturalist,* 133, 60–75.

Danks, H.V. (1979). Canada and its insect fauna. Memoirs of the Entomological Society of Canada.

Darwin, C. (1859). On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. London.

De Smet, W.H., Van Rompu, E.A. and Beyens, L. (1994). Contribution to the rotifers and aquatic Tardigrada of Edgeøya (Svalbard). *Fauna Norvegica Serie A,* 9, 19-30.

Dickson, R. R., Osborn, T. J., Hurrell, J. W., Meincke, J., Blindheim, J., Adlandsvik, B., Vinje, T., Alekseev, G., and Maslowski, W. (2000). The Arctic Ocean response to the North Atlantic Oscillation. *Journal of Climate,* 13 (15), 2671-2696.

Dollery, R., Hodkinson, I. D. and Jónsdóttir,I. S.(2006). Impact of warming and timing of snow melt on soil microarthropod assemblages associated with Dryas- dominated plant communities on Svalbard. *Ecography*, 29, 111- 119.

Elias, S. A. and Crocker, B. (2008). The Bering Land Bridge: a moisture barrier to the dispersal of steppe-tundra biota? Quaternary Science Reviews, 27(27-28), 2473-2483.

Elias, S. A., Short, S. K. and Birks, H. H. (1997) Late Wisconsin environments of the Bering Land Bridge. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 136, 293-308.

Elton, C. S. (1925). The dispersal of insects to Spitsbergen. *Transactions of the Entomological Society of London,* 73, 289- 299.

Fedorov, V. B. and Stenseth, N. C. (2002). Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (Dicrostonyx groenlandicus). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1505), 2071-2077.

Fjellberg, A. (1984). Collembola from Jan Mayen, Bjørnøya and Hopen, with addition to the species list from Spitsbergen. *Fauna Norvegica,* 31, 69- 76.

Fjellberg, A. (1994). The collembola of the Norwegian Arctic islands . Oslo, Norsk Polarinstitutt.

Fjellberg, A. (1997). Collembola from Nordaustlandet, Svalbard. *Fauna Norvegica Serie B,* 44, 71- 75.

Førland, E. J., Hanssen-Bauer, I. and Nordli Ø. (1997). Climate statistics and long term series of temperature and precipitation at Svalbard and Jan Mayen. Det norske meteorologiske institutt.

Frenot, Y., Chown, s. L., Whinam, J., Selkirk, P. M., Convey, P., Skotnicki, M., and Bergstrom, D. M. (2005). Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews,* 80, 45- 72

Garrick, R. C., Sands, C. J., Rowell, D. M., Tait, N. N., Greenslade, P. and Sunnucks, P. (2004). Phylogeography recapitulates topography: very fine-scale local endemism of the saproxylic 'giant' springtail at Tallaganda in the Great Dividing Range of south- east Australia. *Molecular Ecology*, 13, 3329-3344.

Garrick, R. C., Sands, C. J., Rowell D. M., Hillis, D. M. and Sunnucks, P. (2007). Catchments catch all: long-term population history of a giant springtail from

the southeast Australian highlands- a multigene approach. *Molecular Ecology,* 16(9), 1865-1882**.**

Glick. P.A. (1939). The Distribution of insects, spiders, and mites in the air**.**

Greenslade, P. (2008). Has survey effort of Australia's islands reflected conservation and biogeographical significance? An assessment using Collembola. *European Journal of Soil Biology,* 44(5-6), 458-462.

Gressit, J. L. and Yosimoto, C. M. (1974). Insects Studies in Northern Alaska. *Pacific Insects,* 16 (1), 11–30.

Hågvar, S. (2010). Primary Succession of Springtails (Collembola) in a Norwegian Glacier Foreland. *Arctic, Antarctic, and Alpine Research,* 42(4), 422-429.

Hamilton, G., Currat, M., Ray, N., Heckel, G., Beaumont, M., and Excoffier, L. (2005). Bayesian Estimation of Recent Migration Rates After a Spatial Expansion. *Genetics*, 170(1), 409-417.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41-49.

Hartley, I. P., Hopkins, D. W., Garnett, M. H., Sommerkorn, M., and Wookey, P. (2008).Soil microbial respiration in arctic soil does not acclimate to temperature. *Ecology Letters*, 11(10), 1092-1100.

Hausdorf, B. and Hennig, C. (2003). Biotic Element Analysis in Biogeography. *Systematic Biology*, 52(5), 717-723.

Hawes, T. C., Worland, M. R., Convey, P., and Bale, J. S. (2007). Aerial dispersal of springtails on the Antarctic Peninsula: implications for local distribution and demography. *Antarctic Science*, 19(1), 3- 10.

Hayward, S. A. L., Worland, M. R., Bale, J. S., and Convey, P. (2000). Temperature and the hygropreference of the Arctic collembolan Onychiurus arcticus and mite Lauroppia translamellata. *Physiological Entomology,* 25, 266- 272.

Hennig, C. and Hausdorf, B. (2004). Distance-based parametric bootstrap tests for clustering of species ranges. *Computational Statistics and Data Analysis,* 45(4), 875-895.

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society,* 58, 247- 276.

Hewitt, G. M. (2001). Speciation, hybrid zones and phylogeography — or seeing genes in space and time. *Molecular Ecology,* 10(3), 537-549.

Higgins, S. I., Nathan, R., and Cain, M. L. (2003). Are long- distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology,* 84(8), 1945- 1956.

Hisdal, V. (1998). Svalbard Nature and History. Norsk Polarinstitutt Polarhåndbok no.12, Oslo.

Hjellle, A. (1993). Geology of Svalbard. Norsk polarinstitutt. Oslo.

Hodkinson, I. D., Coulson, S. J., Webb, N. R., and Block, W. (1996). Can high Arctic soil microarthropods survive elevated summer temperatures? *Functional Ecology,* 10, 314- 321.

Hodkinson, I. D., Webb, N. R., Bale, J. S., Block, W., Coulson, S. J. and Strathdee, A. T. (1998). Global change and Arctic ecosystems: conclusions

and predictions from experiments with terrestrial invertebrates on Spitsbergen. *Arctic and Alpine Research,* 30(3), 306- 313.

Hodkinson, I. D., Coulson, S. J., and Webb, N. R. (2004). Invertebrate community assembly along proglacial chronosequences in the high Arctic. *Journal of Animal Ecology,* 73, 556- 568.

Holmstrup, M., Bayley, M., and Ramløv, H. (2002). Supercool or dehidrate? An experimental analysis of overwintering strategies in small permeable arctic invertebrates. *Proceedings of the National Academy of Science*, 99(8), 5716- 5720.

Hormes, A., AkÇAr, N., and Peter, W. (2011). Cosmogenic radionuclide dating indicates ice-sheet configuration during MIS 2 on Nordaustlandet, Svalbard. *Boreas.* DOI: 10.1111/j.1502-3885.2011.00215.x

Hullé, M., Bonhomme, J., Maurice, D., and Simon, J.C. (2008). Is the life cycle of high arctic aphids adapted to climate change? *Polar Biology,* 31(9), 1037- 1042.

Hultén, E. (1937). Outline of the history of arctic and boreal biota during the quaternary period: their evolution during and after the glacial period as indicated by the equiformal progressive areas of present plant species. Stockholm, Thule. Dissertation, Lund University.

Iacumin, P., Nikolaev, V., and Ramigi, M. (2000). C and N stable isotope measurements on Eurasian fossil mammals, 40 000 to 10 000 years BP: Herbivore physiologies and palaeoenvironmental reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 163(1-2), 33-47.

Iceland Marine Research Institute. www.hafro.is

Johansen, S. and Hytteborn, H. (2001). A contribution to the discussion of biota dispersal with drift ice and driftwood in the North Atlantic. *Journal of Biogeography,* 28(1), 105-115.

Jónsdóttir, I. S. (2005). Terrestrial ecosystems on Svalbard: Hetereogeneity, complexity and fragility from an Arctic island perspective. *Biology and Environment* ,105B(3), 155- 165.

Juan, C., Emerson, B. C., Oromí, P. and Hewitt, G. M. (2000). Colonization and diversification: towards a phylogeographic systhesis for the Canary Islands. *Tree,* 15(3), 104- 106.

Kennedy, A. D. (1995). Antarctic Terrestrial Ecosystem Response to Global Environmental Change. *Annual Review of Ecology and Systematics,* 26, 683- 704

Kent, M. (2007). Biogeography and landscape ecology. *Progress in Physical Geography,* 31(3), 345-355.

Kubischta, F., K. L. Knudsen, Kaakinen, A. and Saloonen, V. P. (2010). Late Quaternary foraminifera record in Murchisonfjorden, Nordaustlandet, Svalbard. *Polar Research,* 29(3), 283-297.

Kuparinen, A. (2006). Mechanistic models for wind dispersal. *Trends in Plant Science*,11(6), 296- 301.

Laarsonen E. (1985). Butterflies from Spitsbergen. *Baptria* 10, 69-72.

Landvik, J. Y., Brook, E. J., Gualtieri, L., Raisbeck, G., Salvigsen, O. and Yiou, F. (2003). Northwest Svalbard during the last glaciation: Ice-free areas existed. *Geology,* 31(10), 905-908.

Leathwick J. R. (1998). Are New Zealand's Nothofagus Species in Equilibrium with Their Environment? *Journal of Vegetation Science,* 9(5), 719-732.

Lebedeva, N. V., and Krivolutsky, D. A. (2003). Birds spread soil microarthropods to Arctic islands. *Doklady Biological Sciences*, 391, 329- 332.

Lebedeva, N. V., and Lebedev, V.D. (2008). Transport of Oribatid mites to the polar areas by birds. Integrative Acarology. Proceedings of the 6th European Congress. 359- 367.

Legendre, P. (1993). Spatial Autocorrelation: Trouble or New Paradigm? *Ecology,* 74(6), 1659-1673.

Levin, A. S. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology*, 73(6), 1943- 1967.

Lindroth, C. H., Anderson, H., and Bödvarsson, H. (1965). Report on the Surtsey Investigation in 1965. Terrestrial Invertebrates, Department of Enfomology, Lund, Sweden.

Lindroth, C. H., Anderson, H., Bödvarson, H., and Ritcher. (1967). Preliminary Report on the Surtsey Investigation in 1967. Department of Entomology, Lund. Sweden.

Lindström, T., Håkansson, N., and Wennergren, U. (2011). The shape of the spatial kernel and its implications for biological invasions in patchy

environments. *Proceedings of the Royal Society B: Biological Sciences*, 278(1711), 1564-1571.

Linnaeus, C. (1781). Excerpts from Dissertation II, on the increase of the habitable earth.

Mangerud, J., Astakhov, V. and Svendsen, J. I. (2002). The extent of the Barents-Kara ice sheet during the Last Glacial Maximum. *Quaternary Science Reviews,* 21(1-3), 111-119.

McCarty, J. P. (2001). Ecological consequences of recent climate change. *Conservation Biology,* 15(2), 320- 331.

McGaughran, A., M. I. Stevens and Holland, B. R. (2010). Biogeography of circum-Antarctic springtails. *Molecular Phylogenetics and Evolution,* 57(1), 48-58.

McGaughran, A., Stevens, M. I., Hogg, I.D., and Carapelli, A. (2011). Extreme Glacial Legacies: A Synthesis of the Antarctic Springtail Phylogeographic Record. *Insects,* 2(2), 62-82.

Mortimer, E., van Vuuren, B. J., Lee, J. A., Marshall, D. J., Convey, P. and Chwon, S. L. (2010). Mite dispersal among the Southern Ocean Islands and Antarctica before the last glacial maximum. *Proceedings of the Royal Society B: Biological Sciences*. DOI: 10.1098/rspb.2010.1779

Nardi, F., Carapelli, A. , Fanciulli, P., Dallai, R. and Frati, F. (2001). The Complete Mitochondrial DNA Sequence of the Basal Hexapod Tetrodontophora bielanensis: Evidence for Heteroplasmy and tRNA Translocations. *Molecular Biology and Evolution*, 18(7), 1293-1304.

Nathan, R. (2006). Long- distance dispersal of plants. *Science,* 313, 786- 788.

Nkem, J. N., Wall, D. H., Virginia, R. A., Barret, J. E., Broos, E. J., Porazinska, D. L., and Adams, B. J. (2006). Wind dispersal of soil invertebrates in the McMurdo Dry Valleys, Antarctica. *Polar Biology,* 29, 346- 352.

Nolan, L., Hogg, I. D., Stevens, M. I., and Haase, M. (2006). Fine scale distribution of mtDNA haplotypes for the springtail Gomphiocephalus hodgsoni (Collembola) corresponds to an ancient shoreline in Taylor Valley, continental Antarctica. *Polar Biology*, 29, 813- 819.

Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics,* 37(1), 637- 669.

Paus, A., Velle, G., Larsen, J., Nesje, A., and Lie, Ø. (2006). Lateglacial nunataks in central Scandinavia: Biostratigraphical evidence for ice thickness from Lake Flåfattjønn, Tynset, Norway. *Quaternary Science Reviews*, 25(11-12), 1228-1246.

Petit, R. J. (2004). Biological invasions at the gene level. *Diversity and Distributions,* 10(3), 159-165.

Piechura, J., Beszczynska- Möller, A., and Osinski, R. (2001). Volume, heat and salt transport by the West Spitsbergen Current. *Polar Research,* 20(2), 233- 240.

Pilskog H. E. (2011). The invertebrate fauna of Svalbard bird nests; ecology and as facilitating colonisation of an Arctic archipelago. M.Sc. Thesis.

Provan, J., and Bennett., K. D. (2008). Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology and Evolution*, 23(10), 564-571.

Pugh, P. J. A., McInnes, S. J. (1998). The origin of Arctic terrestrial and freshwater tardigrades. *Polar Biology,* 19, 177- 182.

Pulquério, M. J. F. and Nichols, R. A. (2006). Dates from the molecular clock: how wrong can we be? *Trends in Ecology and Evolution,* 22(4), 180- 184.

Purac, J., Burns, G., Thorne, M. A. S., Grubor-Lajsic, G., Worland M. R., and Clark, M. S. (2008). Cold hardening processes in the Antarctic springtail, Cryptopygus antarcticus: Clues from a microarray. *Journal of Insect Physiology*, 54, 1356- 1362.

Reese, G. C., Wilson, K. R., Hoeting, J., A. and Flather, C. H. (2005). Factors affecting species distribution predictions:a simulation model esperiment. *Ecological Applications,* 15(2), 554-564.

Rokas, A., Ladoukakis, E. and Zouros, E. (2003). Animal mitochondrial DNA recombination revisited. *Trends in Ecology and Evolution,* 18(8), 411-417.

Rowe, K. C., Heske, E. J., Brown, P. W., and Paige, K. N. (2004). Surviving the ice: Northern refugia and postglacial colonization. *Proceedings of the National Academy of Sciences,* 101(28), 10355- 10359.

Rudels, B., Björk, G., Nilsson, J., Lake, I., and Nohr, C. (2005). The interaction between waters from the Arctic Ocean and the Nordic Seas north of Fram Strait and along the East Greenland Current: results from the Arctic Ocean-02 Oden expedition. *Journal of Marine Systems*, 55(1-2), 1-30.

Rundgren, M. and Ingólfsson, Ó. (1999). Plant survival in Iceland during periods of glaciation? *Journal of Biogeography*, 26(2), 387-396.

Rushton, S. P., Ormerod, S. J.,and Kerby, G. (2004). New Paradigms for Modelling Species Distributions? *Journal of Applied Ecology,* 41(2), 193-200.

Sanmartín, I., van der Mark, P., and Ronquist, F. (2008). Inferring dispersal: a Bayesian approach to phylogeny- based island biogeography, with special reference to the Canary Islands. *Journal of Biogeography*, 35, 428- 449.

Schneeweiss, G. M. and Schönswetter, P. (2011). A re-appraisal of nunatak survival in arctic-alpine phylogeography. *Molecular Ecology,* 20(2), 190-192.

Shaffer, H. B., Fisher, R. N., and Davidson, C. (1998). The role of natural history collections in documenting species declines. *Trends in Ecology and Evolution,* 13(1), 27-30.

Schönswetter, P., Elven, R., and Brochmann, C. (2008). Trans-Atlantic dispersal and large-scale lack of genetic structure in the circumpolar, arctic-alpine sedge Carex bigelowii s. l. (Cyperaceae). *American Journal of Botany*, 95(8), 1006-1014.

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, and Flook P. (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87, 651-701.

Skrede, I., Eidensen, P., Piñeiro Portela, R., and Brochman, C. (2006). Refugia, differentiation and postglacial migration in arctic- alpine Eurasia, exemplified

by the mountain avens (Dryas octopetala L.). *Molecular Ecology,* 15, 1827-1840.

Stevens, R. D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proceedings of the Royal Society B: Biological Sciences*, 273(1599), 2283-2289.

Stevens, M. I., Greenslade, P., Hogg, I. D. and Sunnucks, P. (2006). Southern Hemisphere Springtails: Could any have survived glaciation of Antarctica? *Molecular Biology and Evolution,* 23(5), 874- 882.

Strathdee, A. T. and Bale, J. S. (1995). Factors limiting the distribution of Acyrthosiphon svalbardicum (Hemiptera: Aphididae) on Spitsbergen. *Polar Biology,* 15, 375- 380.

Strathdee, A. T., J. S. Bale, Block, W. C., Coulson, S. J., Hodkinson, I. D. and Webb, N. R. (1993). Effects of Temperature Elevation on a Field Population of *Acyrthosiphon Svalbardicum* (Hemiptera, Aphididae) on Spitsbergen. *Oecologia,* 96(4), 457-465.

Strathdee, A. T., Bale, J. S., Strathdee, F. C., Block, W. C., Coulson, S. J., Webb, N. R., and Hodkinson, I. D. (1995). Climatic severity and the response to temperature elevation of Arctic aphids. *Global Change Biology*, 1, 23- 28.

Suarez, A. V., Holway, D. A. and Case, T. J. (2001). Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. *Proceedings of the National Academy of Sciences,* 98(3), 1095-1100.

Summerhayes V.S. and Elton C.S. (1928). Further contributions to the ecology of Spitsbergen. *Journal of Ecology,* 16, 193–268.

Svendsen, J. I., Alexanderson, H. , Astakhov, Valery, I., Demidov, I., Dowdeswell, J. A.,Funder, S., Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H. W., Ingólfsson, Ó., Jakobsson, M., Kjær, K. H., Larsen, E., Lokrantz, H., Lunkka, J. P., Lyså, A., Mangerud, J., Matiouchkov, A., Murray, A., Möller, P., Niessen, F., Nikolskaya, O., Polyak, L., Saarnisto, M., Siegert, C., Siegert, M. J., Spielhagen, R. F., and Stein, R. (2004). Late Quaternary ice sheet history of northern Eurasia. *Quaternary Science Reviews*, 23(11-13): 1229-1271.

Templeton, A. R. (2004). Statistical phylogeography: methods of evaluating and minimizing inference errors. *Molecular Ecology,* 13(4), 789-809.

Thomas, C. D., Franco, A. M. A., and Hill, J. K. (2006). Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, 21(8), 415-416.

Tremblay, N. O. and Schoen, D.J. (1999). Molecular phylogeography of Dryas integrifolia: glacial refugia and postglacial recolonization. *Molecular Ecology,* 8(7), 1187-1198.

Walther, G.-R., E. Post, Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. and Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389-395.

Weider, L. J. and Hobaek, A. (2000). Phylogeography and arctic biodiversity: a review. *Annales Zoologici Fennici,* 37(4), 217-231.

Westergaard, K. B., Alsos, I. G., Popp, M., Edgelskjøn, T., Flatberg, K. I., and Brochmann, C. (2011). Glacial survival may matter after all: nunatak signatures in the rare European populations of two west-arctic species. *Molecular Ecology,* 20(2), 376-393.

Woodward F. I., and Kelly, C. K. (2002). Why are species not more widely distributed? Macroecology: concepts and consequences. 43rd Annual Symposium of the British Ecological Society, University of Birmingham, Cambridge University Press, Cambridge

Worland, M. R., and Block, W. (2003). Desiccation stress at sub- zero temperatures in polar terrestrial arthropods. *Journal of Insect Physiology,* 49, 193- 203.

Zhang, D.-X. and Hewitt, G. M. (1996). Nuclear integrations: challenges for mitochondrial DNA markers. *Trends in Ecology and Evolution,* 11(6), 247-251.

The Road goes ever on and on

Down from the door where it began.

Now far ahead the Road has gone,

And I must follow, if I can,

Pursuing it with eager feet,

Until it joins some larger way

Where many paths and errands meet.

And whither then? I cannot say.

-Bilbo Baggins-