

**Coming to terms with conservation  
under climate change:  
Using species distribution models and translocation  
trials for estimating the need and potential of  
assisted migration**

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# Table of Contents

Abstract.....	5
Abstrakt.....	6
1. Introduction.....	7
1.1 Climate, climate change, and species distributions.....	7
1.2. Conservation under climate change: considering assisted migration.....	9
1.3. From theory to practice – evaluating conservation need using the scientific method.....	11
1.4. Outline and aims of this thesis .....	12
2. Materials and methods .....	12
2.1. Deciphering the concept of moving species under climate change .....	12
2.1.1. Terminological analysis .....	12
2.1.2. Analysing definitions .....	14
2.2. Predicting range shifts under climate change to inform am decisions.....	14
2.3. Applying sdms while taking uncertainties into account.....	15
2.3.1. Species data .....	15
2.3.2. Climatic data.....	16
2.3.3. Modelling techniques .....	16
2.3.4. Underlying assumptions .....	17
2.3.5. Application of sdms and output analyses .....	17
2.4. Translocation experiment .....	18
2.4.1. Measuring plant fitness through proxies.....	18
3. Results and discussion.....	19
3.1. What is assisted migration?.....	19
3.1.1. What should we call it and how should we define it?.....	19
3.1.2. How is it different from other translocations?.....	20
3.2. Translation of predictions in range change for assisted migration assessment.....	20
3.2.1. Migration need and potential.....	20
3.3. Accounting for uncertainty and the unknown .....	21
3.3.1. What about local adaptation?.....	22
3.3.2. The case of siberian primrose.....	22
3.3.3. Dealing with erroneous assumptions.....	23
3.4. Gaining more knowledge on the importance of climate in climate change .....	23
3.5. Deciding on assisted migration .....	25
4. Conclusions .....	26
Acknowledgements.....	26
References.....	28

This thesis comprises the following publications and manuscripts, which are referred to in the text by their Roman numerals:

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Study design	<b>MHH</b> , EV, SL	<b>MHH</b> , SA, LS	<b>MHH</b> , RH, TR	<b>MHH</b> , JL, JH	<b>MHH</b> , MTH, SL
Data gathering and/or preparation	<b>MHH</b> , EV	—	<b>MHH</b> , SF	JL, <b>MHH</b>	<b>MHH</b> , IL, MTH, SL, LS
Analysis	<b>MHH</b> , EV, SL	SA, <b>MHH</b>	<b>MHH</b> , SA	JL, <b>MHH</b>	<b>MHH</b> , MTH, SL
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# Abstract

Global climate change will make the current habitat of many species unfavourable. It can also cause species' suitable areas to shift or disappear. Under rapid climate change many species will not be able to adapt or disperse fast enough. Therefore, human-mediated dispersal of species has been proposed as a conservation method for mitigating the negative effects of climate change on biodiversity.

In scientific discussions on the method, several different terms and definitions have been used. Such inconsistent use of terminology can lead to misunderstandings and to conflicting studies and evaluations of the method. In this thesis, assisted migration (AM) is suggested as the preferred term for the idea of translocating species threatened by climate change, and a concise definition that distinguishes it from other translocation practices is proposed.

Should AM be accepted as a conservation tool, there is a demand for a readily applicable, rapid, and effective way of evaluating the species-specific benefit of AM. This thesis presents a method for estimating the need and potential of AM from predictions of changes in the range of species. The method is applied to several plant species and this thesis thus provides one of the first data-based estimations of the need to apply AM as a conservation strategy under different scenarios of climate change. The results indicate that the need and potential of AM for these species increases substantially with the strength of climate change and the temporal extent of climate change projections.

Furthermore, this thesis suggests ways to deal with uncertainties in the process of obtaining range change predictions through species distribution models. Conventional assumptions concern-

ing local adaptation within species, according to which species are treated as a single entity, may lead to erroneous predictions when applying species distribution models. Here, the magnitude of error in conservation guidance that can be introduced through opposing assumptions concerning local adaptation is explored. It is found that the assumption of local adaptation and, therefore, separate modelling of populations can provide different and more precautionary outcomes compared to the assumption of no local adaptation and, hence, modelling the species as a whole.

To obtain insight into the presence of intraspecific local adaptation to climatic conditions, a translocation trial of two geographically separated populations of the same plant species was initiated. The preliminary results presented here indicate that one of the studied populations is less adapted to conditions in its home environment while the other population exhibits stronger local adaptation. Knowledge of this kind provided by experimental studies should be reflected in studies using species distribution modelling to reduce uncertainty in predictions and threat estimates based on the models.

This thesis concludes that predictive tools such as species distribution models hold great potential in providing rough estimates of future trajectories for conservation of biodiversity and could provide a useful scientific basis for policy decisions. However, more in-depth knowledge, which can be gained through experimental approaches, is needed to detail how individual species and populations may respond to altered conditions in their environment and which conservation method is the most relevant.

## Abstrakt

Den globala klimatförändringen kommer att förändra många arters habitat. Arternas nutida levnadsområden kan bli ofördelaktiga då lämpliga förhållanden förflyttas eller försvinner på grund av klimatförändringen. Många arter kommer inte att kunna flytta i takt med den snabba klimatförändringen. Därför har man föreslagit en ny artskydds metod för att minska klimatförändringens negativa effekter på biodiversiteten: att människan skulle hjälpa arter migrera till nya lämpliga områden.

I den vetenskapliga diskussionen angående metoden har flera olika termer och definitioner använts. En dylik inkonsekvent tillämpning av terminologi kan leda till missförstånd samt oförenliga undersökningar och utvärderingar av metoden. I denna avhandling föreslås assisterad migration (AM; eng. *assisted migration*) som den rekommenderade termen för att beskriva idén om att flytta arter vilka hotas av klimatförändringen. En koncis definition som åtskiljer metoden från närbesläktade begrepp presenteras.

Ifall AM skulle accepteras som en artskydds metod finns det ett behov av applicerbara och effektiva sätt av utvärdera fördelar av metoden för enskilda arter. Denna avhandling presenterar en metod för av utvärdera behovet och potentialen av AM utgående från förutsägningar angående förändringar i utbredningsområden. Metoden appliceras på flera växtarter och denna avhandling utgör därmed en av de första databaserade bedömningarna av behovet att applicera AM som en artskydds metod under olika scenarier av klimatförändring. För de undersökta arterna påvisar resultaten att behovet och potentialen av AM ökar märkbart med en förstärkning och förlängning av klimatförändringen.

Vidare föreslår denna avhandling olika sätt att behandla osäkerheter i processen för att erhålla

förutsägningar med hjälp av utbredningsmodeller. Konventionella antaganden angående anpassning inom arten, enligt vilken man behandlar arten som en enhetlig helhet, kan leda till felaktiga slutsatser eftersom populationer inom arten kan vara anpassade till lokala förhållanden. I avhandlingen utforskas omfattningen av felbedömningar inom artskydd som kan introduceras via motsatta antaganden angående lokal anpassning. Resultaten indikerar att fristående modeller av populationer enligt antagandet att populationer är anpassade till lokala förhållanden kan leda till annorlunda och mer akt samma bedömningar av framtida utbredningsområden jämfört med den konventionella metoden att behandla arten som en helhet.

För att belysa förekomsten av anpassning till klimatiska förhållanden inom en art anlades ett transplantationsförsök var två geografiskt separerade populationer av samma art odlades i olika klimatförhållanden. De preliminära resultaten som presenteras här påvisar att en av de undersökta populationerna är relativt svagt anpassad till sina hemförhållanden medan den andra populationen uppvisar starkare lokal anpassning. Dylik information, vilken kan uppnås via experiment, borde återspeglas i studier var utbredningsmodeller används för att förminska osäkerhet i förutsägelseorna och på dem baserade hotbedömningar.

I denna avhandling dras slutsatsen att metoder för att åstadkomma förutsägningar, så som utbredningsmodeller, har hög potential för att ge grova estimat angående möjliga framtida utkomster för biodiversitetsskydd och kan utgöra en användbar vetenskaplig bas för beslutsfattandet. Mer djupgående information, som kan uppnås via experimentella tillvägagångssätt, behövs ändå för att specificera hur individuella arter och populationer kan komma att reagera på miljöförändringar och vilken artskydds metod som då är mest relevant.

## 1. Introduction

About 30 years ago, in an essay on the greenhouse effect and nature reserves, Peters and Darling (1985) anticipated that changes in climate brought about by the burning of fossil fuels may lead to natural resource managers being forced to move species between nature reserves in order to provide them with a suitable climatic environment. Almost a century earlier, Arrhenius (1896) had developed a method to calculate how the level of carbon dioxide in the atmosphere could affect surface temperatures. Based on his findings, he postulated that releasing carbon dioxide through the use of fossil fuels would cause global warming. Since then, climatologists have confirmed and specified Arrhenius' calculations. Already, a global warming of 0.85°C since preindustrial times has been observed, and a rise of 0.3–4.8°C in average global temperatures is expected by the end of the 21<sup>st</sup> century, depending on how society alters its activities<sup>1</sup> (Stocker et al. 2013).

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<sup>1</sup>The IPCC (Intergovernmental Panel on Climate Change) uses scenarios of different strengths in climate change to describe possible futures. In its fourth assessment report (IPCC 2007) these are defined through four different narrative storylines that describe the relationships between emission driving forces, their development, and human activities (Nakicenovic et al. 2000). Each storyline represents a different demographic, social, economic, technological, and environmental development. Although none of them will necessarily occur exactly as described they are useful when analyzing future emission outcome and impacts, and for describing uncertainties related to them. For example, the A1B scenario describes a world with rapid economic growth using both fossil and non-fossil energy. With the fifth assessment report in 2014 (IPCC 2014), the storylines were substituted with Representative Concentration Pathways (RCPs) describing four different trajectories of greenhouse gas concentrations (contrary to emissions). The RCPs differ from the storylines mainly by defining time periods during the 21<sup>st</sup> century, when a peak and subsequent decline in emissions will happen, for calculating greenhouse gas concentrations. For example, RCP 4.5 is defined based on a peak in emissions around 2040 after which a substantial decline in emissions is assumed.

Climate is a dominant force in shaping the general geographical distribution of species on our planet (Holdridge 1947, Walter 1979). Species and the ecosystems they compose represent Earth's biodiversity, which underpins all human life and activity and on which our societies depend. Indeed, climate change and diminished biodiversity<sup>2</sup> have been put forward as the only two forces that, on their own, have the potential to drive the Earth System into a new state if their specific boundaries are overstepped (Steffen et al. 2015). This new state would be inhospitable to humans and force radical changes to our daily lives and to the way our societies function. If we avoid transgressing these boundaries, the probability of a shift in state is radically reduced. Staying within a safe operating space can be achieved through reducing greenhouse gas emissions, using natural resources sustainably, and conserving biodiversity.

### 1.1. Climate, climate change, and species distributions

The basis for understanding species distributions can be found in niche theory. While the early niche concepts (e.g., Grinnell 1917) linked the niche to a particular location in space, the later Hutchinsonian niche (Hutchinson 1957) is defined as an attribute of species or populations: as a consequence of natural selection and evolution, a species has certain requirements, which govern where it can and cannot occur. Hutchinson further divided the niche into the *fundamental* and *realized* niche, where the fundamental niche is the n-dimensional hypervolume within which the population growth rate of a species is indefinitely positive. The realized niche, on the other hand, constitutes what remains of the hypervolume after competitive exclusion.

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<sup>2</sup>Steffen et al. (2015) use the term *biosphere integrity* within which they refer to two key roles of the biosphere in the Earth System: the genetically unique material, which provides the potential for life to co-evolve with the abiotic system and offers resilience, and the functioning that the biosphere provides within the Earth System.

However, also other factors than abiotic and competitive ones, such as dispersal limitations, symbiotic relationships, and the often neglected subterranean diversity (Jing et al. 2015) can affect where certain species occur, and are nowadays usually acknowledged in definitions of the realized niche. The environmental space, nevertheless, creates the primary restriction of species occurrences (the ‘hypervolume’) and it can be measured and analysed more easily than biotic factors (Franklin 2010). In governing the environmental space, climate is a dominant factor, and climatic parameters have been found to correlate well with species distributions (e.g. Luoto et al. 2007, Bucklin et al. 2015). Although this does not allow inference regarding causal effects (Austin 2002), climatic conditions are often used as proxies for describing occurrences of species.

As changes in the environmental conditions cause species’ current ranges to shift, expand, diminish, or disappear, this forces species to either adapt (change their niche), move (change the area where the niche is utilized), regress (reduce the area where the niche is utilized), or go extinct. From palaeoecological records, we know that, during previous changes in climate, some species have declined or gone extinct and some have adapted to the new conditions. However, it seems as though a large part of species have reacted through shifting their geographical ranges to follow suitable conditions (Donoghue 2008, Brook and Barnosky 2011).

A similar reaction under contemporary climate change could be assumed. Nevertheless, the past is not necessarily a good predictor of the future in this case, since some key factors are different. Mainly, climate change is currently occurring at a much faster pace<sup>3</sup> than before, exacerbating temporal constraints in the migration of species. Additionally, the habitat matrix for most species is fragmented, due to human utilisation of natural resources. Although some species are currently

reacting by shifting their ranges (Lenoir and Svenning 2015), the fast pace of change and presence of anthropogenic dispersal barriers reduce the likelihood of species reaching emerging suitable habitat in time (Schloss et al. 2012; Corlett and Wescott 2013). Hence, an increasing number of species are likely to become threatened by climate change, decline, and possibly go extinct (Dawson et al. 2011, Urban 2015).

How changes in the environment will affect a specific species depends both on its intrinsic sensitivity<sup>4</sup> (e.g., physiological tolerance; Case et al. 2015) and its exposure to change<sup>5</sup> (e.g., the velocity of climate change; Loarie et al. 2009). There are many pathways through which a change in climate can result in species declines or extinctions. The new conditions may simply exceed the physiological limits of a species, e.g., if it becomes too hot or too dry for a species to exist. More often, however, the pathways are more complex, and the effects are mediated through interactions with other co-dependant species or pathogens (e.g., McLaughlin et al. 2002, Pounds et al. 2006). As species will respond individualistically to climate change, this may lead to changes in beneficial interactions between species (Hughes 2012). Dependent species may move apart from each other and species that do not co-exist today may come to interact in the same area or time<sup>6</sup>. Cascading effects on commu-

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<sup>3</sup>Loarie et al. (2009) have estimated temperature change to proceed at a global mean pace of 0.42 km yr<sup>-1</sup>.

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<sup>4</sup>Certain characteristics may predispose species to threats brought about by climate change, such as poor dispersal ability, low genetic diversity, and habitat specialisation, can be recognized (Foden et al. 2008; Pearson et al. 2014; Pacifici et al. 2015).

<sup>5</sup>Climate will not change uniformly over the globe or seasons. For example, measured and modelled changes indicate that in Europe yearly average temperatures have risen and will rise more than the global average; this is especially true for northern Europe, where most of the warming additionally is expected to occur in winter time (Christensen et al. 2013).

<sup>6</sup>Instances of climate-change-induced changes in species interactions have been observed among invertebrates, e.g., the butterfly *Euphydryas editha bayensis* whose larval host plant ceased to emerge at the right time (McLaughlin et al. 2002).



nities may follow, e.g., through effects on resource use and interspecific competition. In the most extreme cases this may lead to co-extinctions of species.

Deciphering the exact cause and chain of events of climate change-induced effects can thus be challenging, especially as many other human activities, such as forest logging and pollution, are simultaneously taking their toll on biodiversity. Additionally, extinctions or declines may be happening unnoticed since a large part of existing biodiversity remains undiscovered (e.g., Fontaine et al. 2012). To further complicate the issue, different populations of species may not share the same affinity to climatic conditions over the entire range of the whole species, but rather be locally adapted to conditions in their area of occurrence (Atkins and Travis 2010) causing differential reactions of populations of the same species<sup>7</sup>.

What we do know with relative certainty, is that extinctions are currently taking place at a rate several times faster than before the Anthropocene<sup>8</sup>. According to De Vos et al. (2015) extinction rates are currently 1,000 times higher than the natural extinction rate<sup>9</sup>, and may become 10,000 times higher in the future. Many species are expected to decline or go extinct (Moritz and Agudo 2013). Some currently existing climatic conditions are expected to disappear altogether, and new combinations of climatic conditions, which no extant species has ever experienced, will likely appear (Williams et al. 2007). As species shift

their ranges and community compositions are altered due to changes in the abiotic environment, this may even lead to the appearance of novel ecosystems (Hobbs et al. 2006).

To safeguard biodiversity during such changes, the conservation of species with the help of protected areas, migration corridors, and translocations is important, in addition to reducing the underlying threats.

## 1.2. Conservation under climate change: considering assisted migration

As climate change increases the number of species in need of conservation, it poses challenges to the conservation community and forces a re-evaluation of established procedures in biodiversity management (Hunter et al. 2010). The conventional conservation methods have focused on nature outside of the human sphere, such as wilderness or wildlife, which we attempt to preserve, or restore if disturbed. However, current changes together with the increasing understanding of dynamic processes in nature force us to accept human influence and the lack of pristine wilderness (Marris 2008). As a consequence of climate change, the suitable areas for many species may soon be spatially incompatible with the reserves established to protect the species (Araújo et al. 2011; although see Thomas and Gillingham 2015).

In the 1990s, discussion on how to manage biodiversity under a changing climate started taking place in the scientific literature (Heller and Zavaleta 2009). Suggested methods for conservation under climate change included increasing connectivity and protected areas, intensifying *in situ* management, e.g., by mitigating other threats, and intensifying *ex situ* protection<sup>10</sup>. Although men-

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<sup>7</sup>In this thesis, I use the term *species* as a general term for referring to interrelated groups of living organisms. Occasionally, I discuss *populations*, to refer to specific groups of the species that, within the group, may share more similar traits than what they do with representatives of other populations of the same species.

<sup>8</sup>The Anthropocene is a suggested, although not official, name for the geological period in Earth's history when humans have had a major influence on the geobiosphere (see, e.g., Monastersky 2015).

<sup>9</sup>The natural, or background, extinction rate can be defined as "the geologically recent rate of extinction before human actions inflated them" (De Vos et al. 2015).

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<sup>10</sup>*In situ* conservation means protecting a species in its natural environment, e.g., by setting up protected areas or by prohibiting hunting or gathering of the species in concern. *Ex situ*, on the other hand implies protecting the species off-site, e.g., in a zoo or botanic garden, often with the ultimate aim of reintroducing the species to its natural environment.

tioned already in 1985 (Peters and Darling 1985), human-aided translocation of species beyond their historical distribution still remained a curiosity and was not often mentioned in the 20<sup>th</sup> century<sup>11</sup>.

As the reality of climate change started to become evident and scientist predicted (Thomas et al. 2004) and observed (Parmesan and Yohe 2003, Parmesan 2006) the effects of ongoing climate change in nature, an intensive scientific discussion surrounding what was called assisted colonisation, assisted migration, or managed relocation sparked in the late 2000s (Hewitt et al. 2011; hereafter referred to as assisted migration or AM, see **Chapter I**). A citizen initiative encouraging people to move the threatened conifer *Torreya taxifolia* further north in the USA (Barlow and Martin 2004) may have added fuel to the debate.

For example, McLachlan and colleagues (2007) outlined a framework for discussing different points of view in AM. The first decision-making framework explicating the circumstances under which AM could be conducted was published the following year (Hoegh-Guldberg et al. 2008). Mueller and Hellmann (2008) argued that invasions are less likely when plants are moved within continents. The possible need to adjust regulations was discussed (e.g., Chapron and Samelius 2008), and butterflies were reported having been moved further north in the UK as part of a scientific study (Willis et al. 2009).

Another decision-making framework, which took societal and political aspects into consideration, was presented by a newly formed working group on the issue (Richardson et al. 2009), which simultaneously introduced a new term for the concept: managed relocation (hence the name Managed Relocation Working Group<sup>12</sup>). A series

of commentaries discussing the pros and cons of AM were published mainly in the journal Trends in Ecology and Evolution (Fazey and Fisher 2009, Ricciardi and Simberloff 2009a; 2009b, Sax et al. 2009, Schlaepfer et al. 2009, Schwartz et al. 2009, Vitt et al. 2009). The risk for translocated species becoming invasive was one of the strongest arguments against AM. It was counter-argued by juxtaposing the risks of invasion with that of extinctions, a doubt that endangered species would pose a great risk, and the fact that evidence of re-located species causing extinction of other species is scanty, especially within the same continent (Gurevitch and Padilla 2004; Mueller and Hellmann 2008).

In the 2010s, the discussion slowly started to move more towards actually considering AM as a conservation tool. Minter and Collins (2010) outlined ecological ethics for AM, while Thomas (2011) called for an end to trying to recreate past ecological communities and argued that translocations of species to new environments may, in many cases, be the only viable option if we want to preserve Earth's biodiversity. The Managed Relocation Working Group sketched a research agenda by defining challenges within different disciplines, such as ethics, law and ecology, that need to be addressed when it comes to AM (Schwartz et al. 2012).<sup>13</sup>

Lately, the heated debate has cooled down and it seems almost as though AM has found its place among more traditional conservation tools, being mentioned as a possible method in the discussion of many papers (e.g., Li et al. 2014), although reports on its implementation remain scarce to date. By now, several frameworks based on different conceptualisations have been presented for determining whether and when a species needs AM, as well as for planning the process (e.g., McDonald-Madden et al. 2011, Shoo et al. 2013, Perez

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<sup>11</sup>Although, in 1994 Taylor and Hamilton were the first to coin a specific term for the approach (assisted colonisation; Taylor and Hamilton 1994) and in 1995 the IUCN termed the method *benign introduction* or *conservation introduction* in their guidelines for re-introductions (IUCN 1995).

<sup>12</sup>The Managed Relocation Working Group was formed in 2008 and consists of ecologist, legal scholars, ethicists, and economist who collaborate on the topic of managed relo-

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cation (see: [http://www3.nd.edu/~hellmann/MRWorkingGroup/Managed\\_relocation.html](http://www3.nd.edu/~hellmann/MRWorkingGroup/Managed_relocation.html)).

<sup>13</sup>For a complete list of the 868 publications mentioning the concept by term up until 2012 see Table S1 of **Chapter I**.

et al. 2012, Rout et al. 2013, Schwartz and Martin 2013). Furthermore, moving species because of climate change appears not to be just one concept, but many different actions, which can be placed on a continuum from moving a threatened species a very short distance to creating whole new ecosystems to accommodate change (Seddon 2010). However, it remains unestablished how existing information could be used to identify candidate species for AM, as many of the presented decision-making frameworks require information that is not readily obtainable (Ahteensuu et al. 2015).

### 1.3. From theory to practice – evaluating conservation need using the scientific method

The future outlook of what climate change will entail both for biodiversity and its conservation contains many uncertainties (Kujala et al. 2013). These can be categorized as those stemming from (1) epistemic uncertainty, i.e., lack of knowledge either because the information has not been obtained or because randomness and variation make obtaining such information difficult or impossible; (2) linguistic uncertainty, e.g., that a concept is vaguely or ambiguously defined, or that a term can belong to alternative concepts (Regan et al. 2002); and (3) human decision uncertainty. The latter uncertainty arises from different values and world views of people, which affect conservation through, e.g., the kind of regulations people construct, what is emphasized in research funding, what decisions are made concerning climate change at large and conservation methods specifically, or even how different people can interpret the same data differently. According to Kujala et al. (2013), epistemic uncertainties relating to AM have been recognised, but few authors have raised the issue of vague and ambiguous concepts and terminology with the attempt to reduce linguistic uncertainty.

To anticipate the effects of climate change on biodiversity and to decide which conservation actions are best suited for a species, basic information on species' climatic requirements is para-

mount. Through obtaining such information, some epistemic uncertainty can be reduced. We need predictions of the ramifications that anthropogenic effects can have on biodiversity to enable resource allocation, political decisions, and management of biodiversity.

Predictions in ecology can be divided into explanatory and anticipatory ones (Mouquet et al. 2015). The former attempt to establish explanations that are based on data and repeated experiments, where a hypothesis is deduced from theory. From the hypothesis, a prediction is made and tested (Peters 1991). An example of a testable, explanatory prediction in a climate change and biodiversity setting would be a greenhouse experiment where temperatures are varied for a plant species. The prediction is that *warmer and colder temperature than what the plant is accustomed to will cause reduced fitness of the plant*. This prediction is derived from the hypothesis that *species are adapted to conditions in their natural distribution area*, which in turn is based on niche theory. If data from the experiment are in line with the prediction, the hypothesis is supported and the theory is reinforced (however, never verified; Popper 1935). A contradictory result should lead the researcher to modify or discard the theory, which can even lead to a paradigm shift, where the theory is exchanged altogether.

Anticipatory predictions differ from explanatory ones since they do not aim at testing theory and hypotheses (Mouquet et al. 2015). Instead, they rely on the notion that the underlying theory is valid. Following the earlier example, an anticipatory study would assume that the species is adapted to the conditions in which it currently occurs. To make predictions, the researcher could use species distribution models (SDMs), which correlate occurrences of the species with temperature data in its occurrence area to build a model of this relationship. This model can then be projected onto different possible future conditions and the results can inform us about various future spatial trajectories for the plant species if temperatures rise and if the niche theory holds.

Predictions of range change obtained through anticipatory modelling, such as SDMs, have been promoted as a tool for planning conservation under climate change (Schwartz 2012; Guisan et al. 2013). By using such models, species can be assessed much more effectively in terms of time and number of species than by gathering species-specific knowledge through experiments and observations. There is also potential in using the models for anticipating the suitability of AM for specific species (Chauvenet et al. 2012). Nonetheless, there are problems and uncertainties involved in the use of such models (Heikkinen et al. 2009). Some of them stem from the data and tools that we use. Other uncertainty is introduced from assumptions that are based on underlying theory. Depending on whether the assumption is applied as such or redefined on the basis of case-specific knowledge, the results obtained may differ. The practical plans for conservation, including decisions on whether to use AM or not, may therefore be different.

#### 1.4. Outline and aims of this thesis

The main aim of my thesis is to provide methods and practices for guiding assessments concerning AM. The thesis is therefore mostly concerned with anticipatory predictions (**Chapters II, III, and IV**), although also explanatory ones (**Chapter V**), as I attempt to specify the underlying assumptions regarding local adaptation for a specific species.

However, to begin with, I tackle the prevailing linguistic uncertainty by proposing a term and definition for the concept (**Chapter I**). On the basis of this, I define the subsequent study questions, which concern how one can identify species or populations for which AM may be a feasible conservation approach. I conceptualize the characteristics of predictions in range change for AM candidate species and propose objective and comparable metrics for this procedure (**Chapter II**). I then apply the method to a dozen species to assess AM pressure using SDMs under various scenarios

of climate change (**Chapter III**). To examine uncertainties brought to the modelling process from underlying ecological theories, I examine the difference in conservation guidance that two opposing assumptions on local adaptation can bring in through anticipatory modelling (**Chapter IV**), and conduct an experiment to test which assumption is more valid for a specific species (**Chapter V**).

In summary, this thesis aims to answer the following questions:

1. How should assisted migration be defined?
2. How can species eligible for assisted migration be identified from predictions in range change?
3. How much uncertainty can be introduced through lack of knowledge concerning intraspecific local adaptation, and how can more knowledge be gained?

## 2. Materials and methods

The materials and main methods used in **Chapters I, III, IV, and V** are presented in Table 1. **Chapter II** is a conceptual study, wherefore no material was used. The application of the methods is described in more detail below.

### 2.1. Deciphering the concept of moving species under climate change

In **Chapter I**, we simultaneously scrutinized two aspects of the idea concerning conservation translocations of species under climate change: the term used to designate it and the definition of the term.

#### 2.1.1. Terminological analysis

For the terminological analysis in **Chapter I**, we recorded all terms referring to moving species under climate change that we found in literature published by the end of the year 2012. The idea was usually referred to using a ‘complex term’, which consists of two or more words (e.g., *managed relocation* or *facilitated dispersal*). One of the words (usually a noun; e.g., *relocation* or *dispersal*) can

**Table 1.** Description of the material and methods used in this thesis. SDM= Species Distribution Model; MaxEnt= Maximum Entropy; GLM= Generalized Linear Model; GBM= Generalized Boosted Model; LMM= Linear Mixed-effect model; GLMM= Generalized Linear Mixed-effect Model. <sup>1</sup>= Global Biodiversity Information Facility (GBIF 2013); <sup>2</sup>= Kastikka Finnish plant distribution database (Lampinen et al. 2012); <sup>3</sup>=Hertta, Finnish Environment Institute, unpublished database.

	I	III	IV	V
Main material	Literature.	Occurrence and climate data.	Occurrence and climate data.	Living plants propagated from wild- collected seed.
Study species	–	<i>Bromus benekenii</i> , <i>Carex ornithopoda</i> , <i>Carex pulicaris</i> , <i>Galium saxatile</i> , <i>Geranium lucidum</i> , <i>Hottonia palustris</i> , <i>Hypericum montanum</i> , <i>Melica uniflora</i> , <i>Polygala vulgaris</i> , <i>Primula farinosa</i> , <i>Radiola linoides</i> , <i>Sisymbrium supinum</i> , <i>Viola reichenbachiana</i> .	Karner Blue butterfly ( <i>Lycaeides melissa samuelis</i> ) and Siberian primrose ( <i>Primula nutans</i> ssp. <i>finmarchica</i> ).	Siberian primrose ( <i>Primula nutans</i> ssp. <i>finmarchica</i> ).
Material source	Google Scholar, ISI Web of Science, Scopus Elsevier, Hein Online and EBSCO (Academic Search Online), two review articles (Hewitt et al. 2011 and Loss et al. 2011).	GBIF <sup>1</sup> , Kastikka <sup>2</sup> , Hertta <sup>3</sup> , Hultén and Fries (1986).	GBIF <sup>1</sup> , Kastikka <sup>2</sup> , Hertta <sup>3</sup> , herbarium records, Hultén and Fries (1986), and site records from various sources (see Acknowledgements in Chapter IV).	Five sites in Haukipudas and Ii in Finland and six sites in Sør-Varanger in Norway.
Study area	Global.	Eurasia delimited by 10.4 and 70.1 decimal-degrees East longitude and 34.1 and 72.1 decimal-degrees North latitude.	North America and Northern Europe: 1,000 km buffer around the occurrence points for each species.	Six botanic gardens in Estonia (Tartu: N58.38, E26.72), Finland (Helsinki: N60.20, E24.95; Rauma: N61.13, E21.50; Joensuu: N62.60, E29.72; Oulu: N65.06, E25.47), and Norway (Svanvik: N69.45, E30.04).
Climate or weather data source	–	Climate data: current climatic conditions averaged for the period 1961-1990 (New et al. 2002); GISS-E2-R/ RCP 2.6 NASA Goddard Institute for Space Studies; MIROC5/RCP 4.5 and MIROC-ESM/ RCP 8.5 University of Tokyo, National Institute for Environmental Studies and Japan Agency for Marine-Earth Science and Technology.	Climate data: current climatic conditions: average climate for 1950-2000 represented by nineteen bioclimatic variables were obtained from the WorldClim dataset (Hijmans et al. 2005); Future climate: UKMO-HadGEM1/ A1B Research program on Climate Change, Agriculture and Food Security (Ramirez and Jarvis 2008).	Weather data: Finnish Meteorological Institute, the Estonian Weather Service, and the Norwegian Meteorological Institute.
Main study method	Content analysis.	SDM.	SDM.	Translocation experiment.
Statistical methods used	–	SDMs (MaxEnt, GBM, GLM), GLMM.	SDMs (MaxEnt), Principal component analysis, Niche similarity test.	LMM, GLMM.

be understood as the main term that is qualified by restrictive modifying terms (adjectives or adjectival phrases; e.g., *managed* or *facilitated*). For instance, in the complex term *managed relocation*, the modifying term *managed* aims to single it out from other instances of *relocation*. We analysed the meanings of the main and modifying terms separately, to avoid subjective cross-effect and to find the most suitable main and modifying term.

### 2.1.2. Analysing definitions

In the analysis of definitions in **Chapter I** we included only peer-reviewed articles that in their title, abstract, or keywords mention a term for the measure. We used content analysis, a method that can be employed to identify patterns across qualitative data (Miles and Hubermann 1994).

Our analysis units were single words or parts of sentences used in the definitions. We classified them into 70 groups according to similarity in meaning, and placed them in eight main categories representing different themes or parts of the definition: The main categories were: *action* (what is done; e.g., *movement*); *specification of action* (in what manner is it done; e.g., *human-aided*); *what* (what is transferred; e.g., *species*); *specification of what* (e.g., *threatened*); *where from* (e.g., *degraded habitats*); *where to* (recipient area; e.g., *further north*); *specification of where to* (e.g., *suitable*); and *motivation* (e.g., *climate change*). We reconstructed a descriptive definition of the idea by examining the groups under each theme, and selecting the expressions that best helped describe the idea sufficiently while only including the necessary aspects of the concept.

## 2.2. Predicting range shifts under climate change to inform AM decisions

Predicted changes in suitable areas can be categorized as loss and gain of area of potential occupancy (Thomas et al. 2011), and the combination of loss and gain would be essential information relating to AM. SDMs have been used to anticipate

the effects of climate change on species and their distributions (e.g., Thomas et al. 2004). Predictions can also be obtained with the help of mechanistic models based on, e.g., species' physiological thresholds obtained through explanatory experiments (Morin and Thuiller 2009), or through expert elicitation (Martin et al. 2012). In **Chapter II**, we outline how to translate any such predictions into quantitative measures of AM need and potential.

We first define *migration need* as the relative need to compensate for the loss of range caused by climate change. We quantify migration need ( $M_{Need,t}$ ) at a given time  $t$  as the proportion of a species' current distribution area that will be lost due to climate change:

$$\text{Eq. 1} \quad M_{Need,t} = \frac{A_{Original} - A_{Remnant,t}}{A_{Original}}$$

$A_{Original}$  is the size of the distribution at the time selected as the initial point of the assessment ( $t = 0$ ), and  $A_{Remnant,t}$  is the part of  $A_{Original}$  that remains climatically suitable at a time  $t$  in the future.  $M_{Need,t} = 0$  means that the entire current distribution area is covered by projected future suitable area, i.e.,  $A_{Original} = A_{Remnant,t}$ , and that there is no need for migration because of climate change. The higher the value of  $M_{Need,t}$ , the more of the current distribution area is no longer suitable, and at  $M_{Need,t} = 1$  none of the species' current area remains suitable.

The second component, migration potential ( $M_{Potential,t}$ ), can be represented as the prospect of migration at time  $t$  when new area has become suitable with change in climate. We model  $M_{Potential,t}$  as the proportion of new suitable area from the total suitable area at a certain point in time:

$$\text{Eq. 2} \quad M_{Potential,t} = \frac{A_{New,t}}{A_{New,t} + A_{Remnant,t}}$$

$A_{New,t}$  is the area that was previously unoccupied but is or has, according to the predictions, become suitable due to climate change. The prospective future range at a certain point in time is  $A_{New,t} + A_{Remnant,t}$ . A small value of  $M_{Potential,t}$  indicates that there is little possibility for range expansion un-

der climate change compared to what the species has left ( $A_{\text{Remnant},t}$ ). The species will therefore benefit only marginally from reaching the new area, as most of the suitable climate covers parts of its original distribution. Conversely, a high  $M_{\text{Potential},t}$  value indicates that the species could increase its range considerably compared to what is left of  $A_{\text{Original}}$  if it were able to disperse. For species that have limited ability to disperse fast enough on their own, the need for and potential of migration correspond to the need for and potential of assisted migration.

We combine  $M_{\text{Need},t}$  and  $M_{\text{Potential},t}$  into a single metric, which we call  $I_{\text{AM},t}$  (AM index).  $I_{\text{AM},t}$  is composed of the geometric mean of its components:

$$\text{Eq. 3} \quad I_{\text{AM},t} = \sqrt{M_{\text{Need},t} \cdot M_{\text{Potential},t}}$$

High values of  $I_{\text{AM},t}$  indicate that a species has both the need of AM and the potential to benefit from it. Hence, AM may be an appropriate approach in the conservation of this species.  $M_{\text{Need},t}$ ,  $M_{\text{Potential},t}$  and  $I_{\text{AM},t}$  are all unitless metrics between zero and one, which facilitates their interpretation and comparison between species.

To help decide when the index is relatively large or small, i.e., how appropriate AM would be as a conservation method for a specific species, we calculated the values of  $I_{\text{AM}}$  that, at a specific point in time, correspond to the Red List-inspired threat categories (IUCN 2001) presented by Thomas et al. (2011). When  $I_{\text{AM},t}$  is calculated based on predictions a decade into the future, a species with  $0.1 < I_{\text{AM},1} < 0.2$  is a possible candidate for AM, a species with  $0.2 < I_{\text{AM},1} < 0.27$  is a probable candidate for AM and a species with  $I_{\text{AM},1} > 0.27$  is a strong candidate for AM. For a prediction 100 years into the future (10 decades) the corresponding thresholds for  $I_{\text{AM},10}$  are 0.31, 0.58, and 0.74.

**Chapter III**, we apply this approach to 13 poorly dispersing plant species for which we predicted range change with the help of SDMs, and evaluate their need and potential of AM under different climate change scenarios and future time periods.

## 2.3. Applying SDMs while taking uncertainties into account

SDMs are statistical tools constructed by training a model with environmental (or other) variables from known presences (and absences) of a species to produce a model that describes the conditions under which a species occurs (Franklin 2010). The model can then be applied in various contexts, e.g., to understand the relationship between a species and its environment, to test ecological or biogeographical hypotheses about species distributions, to predict the suitability of an unsurveyed environment, or to hind cast and forecast into other times.

Problems and uncertainties involved with SDMs stem from different sources and it is important to be aware of them and interpret the results in the light of the weaknesses and assumptions of the model (Hampe 2004; Araújo and Peterson 2012). These challenges can be divided in four categories (following Fernández and Hamilton 2015) that concern (1) species data, (2) environmental data, (3) modelling techniques, and (4) assumptions based on underlying hypotheses.

Despite these recognized problems, the relative applicability of SDMs render them an attractive tool for providing time and cost effective assessments on range changes under environmental change. In **Chapter III**, we apply the framework presented in **Chapter II** to real-life species while taking model uncertainty into account using consensus modelling (Araújo and New 2007) to reduce uncertainties stemming from different choices of environmental data (here only climatic data) and modelling techniques. In **Chapter IV** we take a more general look at the magnitude of error that underlying assumptions concerning local adaptation can bring into conservation decisions through the modelling process.

### 2.3.1. Species data

Species occurrence data should preferably be obtained through ample systematic inventories of the species in question, where both the presence

and absence is recorded with scientific rigour. It is, however, time-consuming and expensive to collect such data. Lately, presence data based mainly on natural-history collections have increasingly become available (Maldonado et al. 2015) and also utilized to a great extent (GBIF 2015). Such data, however, may contain errors and biases as the data are typically aggregated into coarse grain leading to overestimated occupancy area (Franklin 2010) and may contain sampling bias since all areas would not have been surveyed as intensively (Aikio et al. 2010). Nevertheless, there are many advantages with species occurrence databases, such as the large geographic span, wide temporal span, and good availability.

In **Chapters III** and **IV**, we based our information on species occurrences on such presence data, mainly obtained through the Global Biodiversity Information Facility (GBIF 2013). In **Chapter III**, we studied 13 vascular plant species (Table 1), selected on the basis of poor dispersal ability, threat status, and data availability. Our study species in **Chapter IV** were the Karner Blue butterfly (*Lycaeides melissa samuelis* Nabokov) in North America and the Siberian primrose (*Primula nutans* Georgi ssp. *finmarchica* (Jacq.) Löve & Löve) in northern Europe. Both taxa are threatened and occur in geographically separated populations, probably experiencing little gene flow among them (Gompert et al. 2006, Kreivi et al. 2006).

Occurrence data for all species were obtained from GBIF (2013) but augmented with information from national databases, site survey records, herbaria, and range maps (Table 1). Each grid cell was designated as *present* for a species if at least one occurrence point fell into that cell; otherwise, the cell was designated as *absent*.

### 2.3.2. Climatic data

Choosing variables to use in an SDM is an important part in the modelling process. The variables should represent the environmental conditions that affect the distribution of the focal species. Most SDM studies on a global or large scale use climatic parameters as predictors although several other

environmental factors, such as habitat availability, soil conditions, and biotic interactions can affect where a species occurs. Climatic data and future projections of climate are readily available, and climate has been shown to correlate well with species occurrences (e.g., Bucklin et al. 2015).

In **Chapters III** and **IV**, we focused on identifying broadly-suitable climatic conditions to evaluate how area suitable for the species or populations will shift under different scenarios of climate change. Therefore, we only used climatic variables to model species distributions.

Climate can be described through various variables reflecting temperature, precipitation, their interactions, and seasonality. Choosing the best descriptors is a further challenge in building SDMs (Synes and Osborne 2011, Barbet-Massin and Jetz 2014), since it is not necessarily known which aspects of climate represent the primary climatic niche that controls and affects species distributions (Franklin 2010).

The problem can be approached through, among other things, using (1) statistically important variables that do not correlate (Austin and van Niel 2011, Synes and Osborne 2011); (2) all potentially important variables although they may be correlated (Braunisch et al. 2013); or (3) variables assumed to generally govern the distribution of species (Sykes et al. 1996; Bakkenes 2002). In **Chapter III**, we constructed three variable sets selected on the basis of each approach. In **Chapter IV**, we were not specifically interested in accounting for uncertainty stemming from choice of variables and, thus, we used only one of the above-mentioned approaches (1) and constructed one variable set per species using uncorrelated variables.

### 2.3.3. Modelling techniques

The choice of modelling technique can also affect SDM outputs. There is a suit of techniques available, and in **Chapter III**, we used three modelling methods representing different approaches (Elith & Graham 2009, Heikkinen et al. 2009). Two of them were presence-absence techniques: a generalized linear model (GLM) and a general-



ized boosted model (GBM). The third technique in **Chapter III**, and the only one in **Chapter IV**, was MaxEnt, which uses presence-only data and describes the study area by creating so-called background points (Phillips et al. 2006).

### 2.3.4. Underlying assumptions

A common assumption in SDMs is *niche conservatism* (Wiens and Graham 2005), i.e., that individuals of the same species have retained the same niche over space and time. In practice this implies that all individuals of the species are assumed to share the same affinity towards certain environmental conditions. However, if populations are locally adapted to the specific conditions that prevail where the population occurs the populations may have to be modelled separately. Often, however, we lack information concerning intraspecific local adaptation.

To test the effect that using opposing assumptions could have in SDMs, we modelled species and populations separately in **Chapter IV**. We used principal components analysis (PCA) to identify potential climatically distinct populations of Karner Blue butterfly and Siberian primrose. We used this information, together with knowledge of the taxonomy and the spatial genetic structure of the species (Gompert et al. 2006, Kreivi et al. 2011), to define the ‘populations’ for this study. Karner Blue butterfly occurrence points were divided into Western and Eastern populations and Siberian primrose into Southern and Northern populations. We constructed separate SDMs for the two populations of each species as well as for each species as a whole.

### 2.3.5. Application of SDMs and output analyses

To reduce uncertainty resulting from various choices made in the modelling process, ensemble or consensus modelling can be applied (Franklin 2010). Different parts of the model (e.g., algorithms, parameters, species data, environmental data, and projection time) can be varied to produce several projections that can then be combined to distinguish where most models agree.

We applied consensus modelling in **Chapter III** through varying the climatic variable set and modelling technique, producing nine models per species (three variable sets times three modelling techniques). The nine separate SDMs were fitted into data representing three different climate scenarios (mild, moderate, and strong) averaged over four future time periods. The projection outputs were used to develop a consensus output for each scenario and time period and to calculate  $M_{Need,t}$ ,  $M_{Potential,t}$  and  $I_{AM,t}$  (presented in **Chapter II**). The consensus outputs were used for identifying candidates for AM through converting the AM index into categories describing benefit of AM for the species (section 2.2).

To evaluate the degree to which a random choice of an individual SDM (with a certain combination of climate variable set and modelling technique) could affect AM need and potential, we tested the effect of variable set and modelling technique on the value of the metrics (**Chapter III**).

In **Chapter IV**, we used one algorithm, one set of climatic parameters, and one climatic projection to predict future suitable areas for Karner Blue butterfly and Siberian primrose. This enabled us to concentrate on the differences that the species approach and the population approach produced. We projected the models over seven future time periods under a scenario reflecting current CO<sub>2</sub> growth rates.

To evaluate the effects on conservation decisions from modelling the species as a whole or modelling the populations separately (**Chapter IV**), we used the predicted suitable area to devise broad conservation plans based on each approach. Since we do not know if the populations of these species are locally adapted, we compared the negative and positive effects of the conservation strategy if the assumption it is based on (local climatic adaptation of populations versus the assumption of species not being differentiated into populations) turns out to be right or wrong.

## 2.4. Translocation experiment

Experiments, such as laboratory, greenhouse, common-garden, or translocation trials (Kawecki & Ebert 2004, De Frenne et al. 2013) can provide information on the degree of intraspecific local adaptation. In such experiments, the conditions of the individuals under study are altered, either artificially by creating conditions (e.g., in a greenhouse) or by placing the individuals in existing conditions representing different treatments (e.g., at geographically different locations; Frei et al. 2014). To test the degree of species and population adaptation to climatic conditions for one of the species studied in **Chapter IV**, Siberian primrose, we set up a reciprocal translocation experiment (**Chapter V**).

The subspecies *P. nutans* ssp. *finmarchica* occurs in Fennoscandia and is divided into two varieties according to morphological and ecological characteristics (Mäkinen and Mäkinen 1964): *P. nutans* ssp. *finmarchica* var. *finmarchica* inhabits the shores of the Arctic Sea (corresponds to the Northern population in **Chapter IV**) while *P. nutans* ssp. *finmarchica* var. *jokelae* (corresponds to the Southern population in **Chapter IV**) occurs by the Bothnian Bay in Finland and Sweden and by the White Sea in Russia (Fig. 1 in **Chapter V**).

Siberian primrose has probably spread to the White Sea region along the retreating sea ice edge after the latest glacial period, and later colonised the Bothnian Bay and Arctic Sea regions from there (Mäkinen and Mäkinen 1964). Due to the relatively long spatial and temporal distance between the varieties, it is plausible to assume limited gene flow between the areas. Indeed, these three main populations of the Siberian primrose (by the Arctic Sea, White Sea, and Bothnian Bay) have been shown to be genetically distinct (Kreivi et al. 2006; 2011), and they may have adapted to the local environmental conditions.

Seeds from wild populations of both varieties were collected in 2012 (Table 1). A common-garden trial was set up in 2013 in six botanic gardens in Estonia, Finland and Norway (Fig. 1 in **Chapter**

**V**), which represent climatic treatments. Local adaptation of the two populations is tested in a reciprocal part of the experiment (Kawecki and Ebert 2004) by comparing the success of plants of different origin in Oulu (representing the home environment for the southern variety) and Svanvik (home environment for Northern variety). The effect of a more southern climate is tested by measuring the success of the plants of both varieties grown in Rauma, Joensuu, Helsinki, and Tartu.

### 2.4.1. Measuring plant fitness through proxies

The fitness of genotypes can be described as the relative success with which they transmit their genes to the next generation (Silvertown and Charlesworth 2001). Fitness defined as such can, however, be hard to measure directly. Instead, components of fitness can be defined on the basis of characteristics that would be expected to correlate with succeeding in transmitting genes to the next population. Survival can thereby be a measure of fitness: a dead individual cannot transmit genes. Also, we know that the physical size of an individual tends to correlate with its fitness (Silvertown and Charlesworth 2001), and therefore the size of a plant can be used as another proxy for fitness. A high reproductive output increases the chance of transmitting genes to the next generation. Therefore, plants that produce more flowers and more viable seeds than their conspecifics can be expected to have a higher fitness than those producing fewer.

In **Chapter V**, we measured survival, size, and flowering to describe the success or fitness of individuals of Siberian primrose at different locations, and used these as alternative response variables in our models. Survival was measured as a simple binomial *alive* or *dead* in autumn 2014. Flowering was measured as number of flowers per individual two weeks after the first flower appeared at the experimental location. For the purposes of analysis, this was transformed into a binomial variable describing whether the individual flowered or not (*yes/no*). Size was approximated through measur-

ing area from photographs taken perpendicularly from above.

As the *a priori* explanatory variable, we used the experimental garden. However, since the weather conditions during the study period may have varied and thus not necessarily reflected the average climate of each site, we used two different combinations of weather data (see Table 1 for source) as alternative explanatory variables: mean temperature during summer 2014, and the first principal component of several weather parameters describing the study period. In **Chapter IV**, we had examined important climatic variables for both study species, to identify climatic features that may differ in the occurrence area of the populations and, therefore, if manipulated in experimental settings, have the potential to yield fitness differences between populations, if they are locally adapted. Weather parameters representing the climatic features important for the Siberian primrose were included in the PCA in **Chapter V**.

### 3. Results and discussion

#### 3.1. What is assisted migration?

Through our literature search conducted with the aim of finding terms and definitions used for the idea of moving species under climate change (**Chapter I**), we were simultaneously able to quantify the discussion on the topic in scientific literature. We found that the idea was mentioned in the scientific literature over 850 times from 1994 to 2012 (Fig. 2 in **Chapter I**). Clearly, the topic had inspired much discussion, as publications mentioning it increased over the years, especially during the last few years of our study period. However, it is uncertain whether all authors were actually discussing the same thing.

The plethora of terms and the many different definitions used for the concept mean that a specific author may have understood the concept as *X* and used the term *A* to describe it. Another author might have defined it differently, as *Y*, but used the

same term *A*. A third author, also describing the concept as *Y*, might prefer the term *B*. In the first case, the authors are using the same term to discuss two different things. In the second case, although the authors mean the same thing they use different terms to denote it. Both cases are bound to lead to misconceptions and thereby increased linguistic uncertainty.

Although moving of organisms because of climate change may include many different actions, such as conserving poorly dispersing habitat specialists to choosing suitable seeds for forestry, our aim was to present the most suitable term denoting the idea of *aiding the dispersal of species threatened by climate change* presented by Peters and Darling (1985), and to formulate a standard definition for it (**Chapter I**). The definition should concisely communicate the idea of the concept and consists of all necessary and sufficient conditions distinguishing it from other related ideas. The use of such a definition, coupled with a consistent use of a term, ensures that discussions, studies, and applications of the concept relate to the same thing.

##### 3.1.1. What should we call it and how should we define it?

In **Chapter I**, we found 40 different terms and 75 definitions for the concept. The most commonly used terms were *assisted migration*, *assisted colonisation*, and *managed relocation* (Fig. 3 in **Chapter I**). For reasons elaborated upon in **Chapter I**, we propose *assisted migration* as the preferable term for the focal conservation approach and recommend the following definition:

*“Assisted migration means safeguarding biological diversity through the translocation of representatives of a species or population harmed by climate change to an area outside the indigenous range of that unit where it would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time”.*

We propose that only actions that meet this definition should be called *assisted migration*. Some important features of the definition include:

1) AM not only relates to the species as a human-defined entity, but can also concern translocations of populations within the range of the species to which the populations belong.

2) AM excludes translocations for economic reasons (e.g., forestry<sup>14</sup>) by restricting this measure to species and populations threatened by climate change with the aim of safeguarding biodiversity.

3) AM excludes conservation translocations motivated by other threats than climate change, and

4) AM excludes conservation translocations targeted to areas outside the predicted suitable area under climate change.

In fact, Siipi and Ahteensuu (in press) have argued, that the fourth aspect of the definition can bear an important ethical difference in the discussion on AM since the predicted area can be viewed as part of the species' future natural range<sup>15</sup>.

### 3.1.2. How is it different from other translocations?

The definition of assisted migration presented in **Chapter I** distinguishes this method from other translocation actions in various ways, but it can, nevertheless, potentially be confused with some other translocation measures, such as conservation introduction (Fig. 5 in **Chapter I**). However, conservation introduction as defined by the IUCN (2012) can imply any conservation-motivated translocation of a species outside of its range. As an example, in the debate surrounding AM, moving polar bears to the Antarctic has been mentioned as an example of the extravagance of the

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<sup>14</sup>In **Chapter I**, we propose the use of *predictive provenancing* when discussing adaptation of forestry to climate change by choosing suitable seed sources for future managed forests.

<sup>15</sup> It has been proposed that a species loses some of its value by being translocated outside of its range (Sandler 2010). However, Siipi and Ahteensuu (in press) counter-argue that if we view the predicted range as part of the natural range, where the species would be migrating were it not for lack of time or dispersal barriers, this loss of value does not happen as readily.

method (Marris 2008; Albrecht et al. 2013). However, such a translocation would not fall within the concept of AM as outlined in **Chapter I**, since the Antarctic is not part of the future range “*where [the polar bear] would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time*”. If such a translocation were indeed conducted, it should be classified as a conservation introduction, not as AM.

## 3.2. Translation of predictions in range change for assisted migration assessment

We arrived at a definition for AM (**Chapter I**) in which the recipient area is specifically mentioned as being one that is predicted to become suitable. Hence, anticipatory predictions, such as SDMs, become potential tools for identifying species that could benefit from AM. Several suggestions for how to quantify predictions of range change to assess threat from climate change have been presented (Thomas et al. 2004, Shoo et al. 2005, Thomas et al. 2011, and Maggini et al. 2014)<sup>16</sup>. Nevertheless, how predicted range changes should be understood when it comes to AM has not been defined.

### 3.2.1. Migration need and potential

The definition of AM further gives some indication of what kind of range change situations AM may be relevant for. In **Chapter II**, we argue that, for AM to be relevant, predictions in range change need to exhibit (1) a need for migration, i.e., the species is expected to experience a sizable loss of suitable area; and (2) a potential for migration, i.e., the species is expected to experience a sizable gain of new suitable area (Fig. 1 in **Chapter II**). Basically, through AM we try to compensate for lost distribution area by taking the species to the new area that it is unable to reach without assistance.

In terms of changes in range size and location, point (1) and (2) above can be understood as

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<sup>16</sup>However, see, e.g., Akçakaya et al. 2006 for a critique against this approach.

a loss of current occurrence area and a gain of new in relation to the area that remains suitable. Such changes can, at least in theory, be quantified using predictions in range change. In addition, for AM to be relevant the species would have a restricted ability to disperse to the new areas, i.e., it cannot be expected to make use of the gained areas without assistance.

In **Chapter III** we applied the approach presented in **Chapter II** for actual species. **Chapter III** is thus, to my knowledge, the first spatially explicit assessment of AM for several species. Our results show that the number of species that could benefit from AM increases further into the future and with stronger climate change. The difference in the proportion of species that were classified as AM candidates (Fig. 3 in **Chapter III**) by the end of the century under different climate change scenarios was striking. We found, that 7% of species were identified as AM candidates under a mild climate change scenario, while the corresponding percentage under a strong climate change scenario was over 90%. The differences between time periods and climate change scenarios are stark and illustrate the great challenges we may be up against within just a few decades, if climate change proceeds according to the most radical estimates and if we were to decide to use AM as a conservation strategy.

### 3.3. Accounting for uncertainty and the unknown

The anticipatory models used for predictions contain uncertainties, which are mostly epistemic to their nature. For example, the occurrence data may contain biases or the statistical method used may be flawed. In the prediction-process, the modeller may include irrelevant variables or exclude environmental information due to a lack of understanding of its relevance or because the data are not available. These uncertainties can trickle down to various estimates that are computed based on the predictions, such as the quantification of migration need and potential.

In **Chapter III**, we used consensus modelling to reduce uncertainty in our assessment. Although this does not make the models perfect it gives some more confidence in the estimates. It also allowed us to explore the full range of possibilities of AM need and potential under different scenarios of climate change and time periods, as we calculated the metrics on the basis of several projections.

We only took climatic predictors into account although other abiotic as well as biotic factors probably affect the occurrences of the species. It is possible that climate-based estimates yield conservative, i.e., less extreme threat assessments, since including additional constraints would probably lead to greater losses and smaller gains of area. On the other hand, Schwartz (2012) argues that SDMs in general tend to overestimate extinction probabilities, i.e., they predict relatively more area becoming unsuitable compared to emerging area. Therefore, caution in the interpretation and application of evaluation metrics that are based on SDMs, such as the AM index (**Chapters II** and **III**), is advisable.

We assumed that the species would not be able to disperse on their own (**Chapter III**). This is certainly a somewhat rough generalisation, although we chose the study species based on presumed poor dispersal capacity. In cases where information on species dispersal abilities is available, this could be included through a categorical species-specific assessment or by calibrating more complex models (e.g., using the *RangeShifter* platform; Bocedi et al. 2014). To enable such leaps in application of emerging methodology and allow evaluation of the degree to which species will be able to reach new areas on their own, we urgently need information on dispersal abilities of species. In addition to measuring actual dispersal distance per generation, generalisations and real-life estimates can also be gained through analysing observed range shifts under current climate change in fragmented habitats (Lenoir and Svenning 2015).

In **Chapter III** and **IV**, our starting point was that the occurrences of the species reflect their niche, i.e., that they are in ecological equilibrium

with the environment and therefore occur everywhere where their niches allow them to. Yet, we know that all species are not in environmental equilibrium because competition with other species excludes them from suitable area or because they have not yet had the opportunity to colonise all suitable areas (Svenning and Skov 2004). Furthermore, population dynamic factors can affect where a species occurs. Populations can exist in areas where they have a negative growth rate, i.e., individuals occur in suboptimal conditions that do not allow self-sustaining populations but depend on the influx of individuals from habitats of better quality (source-sink theory; Pulliam 1988). Metapopulation dynamics cause populations to be present and absent at different locations over time (Hanski 1998), and therefore all suitable patches are not at all times occupied by a species. In some cases the environment may have degraded or been lost, but individuals of the species still remain (extinction debt; Tilman et al. 1994, Helm et al. 2006). These dynamics may give a false impression of what conditions are suitable for a species.

Several other factors that are often not included in range change predictions, such as species-specific abundance, traits, population dynamics, and projected habitat change would also affect the anticipated effect of climate change on species (Akçakaya et al. 2006; Pearson et al. 2014). Nevertheless, the challenge remains: frequently we do not have such information on species, which renders broad-scale evaluations based on occurrences correlated with environmental data the most readily available approach.

### 3.3.1. What about local adaptation?

In ecology, including conservation biology and SDM studies, the species as a homogenous entity is often considered the main focal unit. Yet, the concept of species is a scientific construct that enables us to organize knowledge and draw conclusions and generalisations concerning groups of organisms<sup>17</sup>. Several studies have shown that some

<sup>17</sup>See, e.g., Hey (2001) and Lidén and Oxelman (1989) for discussions on the species concept.

populations of species are adapted to local conditions (Davis and Shaw 2001, Bolnick et al. 2003, Banta et al. 2012). This can be especially pronounced if populations are physically separated and cannot exchange genetic material effectively. Moreover, if environments in the distant parts of the species' distribution area are different, the populations may have adapted to the local conditions despite apparent gene flow.

In **Chapter III**, we assumed that all populations of each species have the same climatic niche, defined on the basis of climatic conditions in which the species as a whole occurs. If we had had reason to group the species in smaller entities, and had modelled the populations separately, we might have obtained very different AM index estimates, as both the projected suitable locations and extent of area predicted as suitable may have been affected. Indeed, the results of **Chapter IV** indicate that modelling populations separately can result in different areas (both location- and quantity-wise) being identified as suitable, as compared to modelling all populations of the species as a whole (see Fig. 3 and 4 in **Chapter IV**).

Therefore, using the species as a basic homogenous unit may not always be the most relevant way of grouping individuals in conservation biology (Frankham et al. 2012) or SDM studies (**Chapter IV**). Choosing the wrong grouping would influence threat estimates, such as the AM index, and lead to inappropriate conservation decisions. To reveal intraspecific differences, however, we would need to rely on explanatory predictions, such as experiments, which can inform us about whether the inclusion of local adaptation is necessary for making reliable predictions of species' responses to climate change.

### 3.3.2. The case of Siberian primrose

The initial results of the translocation experiment with populations of Siberian primrose (**Chapter V**) led us to deduce that the Southern population is not as strongly adapted to climatic conditions within its current distribution area as the Northern

population is<sup>18</sup>. Although the Southern population does best in northern conditions, it seems to thrive also in locations hundreds of kilometres further south. In contrast, the fitness of the Northern population declines steeply towards more southern locations, which indicates that climate change might have a direct negative effect on this population.

Based on these preliminary results, I here draw the conclusion, that shifts in suitable area for the Southern population should be evaluated using a model based on occurrence data of the whole species (such as the whole-species model calibrated in **Chapter IV**). For the Northern population, on the other hand, intraspecific niche conservatism should not be assumed, since the population seems to be adapted to the conditions in which it currently occurs. Therefore, for this population, an evaluation in range shift should be based on a model using occurrence data for the Northern population only (such as the population-model calibrated in **Chapter IV**). However, it should be noted, that the observations in **Chapter V** only represent the first two years of the experiment, and several years of monitoring are still needed to acquire a more robust picture of possible adaptation to local climatic conditions by the two varieties. Based on information gained through long-term experiments more exact mechanistic models could be calibrated in the future to substitute the more imprecise correlative SDMs.

### 3.3.3. Dealing with erroneous assumptions

To enable decisions while experimental knowledge is accumulated, we recommend using a precautionary framework for deciding what assumptions to give weight to. Through such an approach possible risks of choosing the wrong assumption can be accounted for (Fig. 6 in **Chapter IV**). We propose first looking for signs pointing to local adaptation within the species in question, e.g.,

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<sup>18</sup>However, our experimental gradient only covered sites further south of where the Northern population occurs. It may be that this population is plastic towards other conditions not included in the study treatments.

whether there are geographically disjunct populations. There is also a growing number of readily available methods for identifying genetically distinct populations, such as high-throughput sequencing of genetic markers (Gotelli and Stanton-Geddes 2015). Such methods could increase our ability to identify populations that may need to be treated as separate ‘species’ in SDMs.

If there is reason to assume intraspecific adaptation, we propose comparing the consequences of conservation strategies based on SDMs calibrated through opposing assumptions (Fig. 6 and 7 in **Chapter IV**). We can either assume local adaptation where there is none (i.e., make a type I error) or assume no local adaptation when populations actually are differentiated (i.e., make a type II error). Although either assumption may be wrong, the conservation strategies based on different models can be more or less detrimental if they turn out to be wrong. Therefore, a conservation manager needs to be aware of the risks, and try to minimize them, e.g., through combining aspects of conservation strategies based on both assumptions. In **Chapter IV** we further reason, that the assumption of local adaptation and resulting conservation strategies may be more precautionary and that making a type I error would therefore be less detrimental than making a type II error.

### 3.4. Gaining more knowledge on the importance of climate in climate change

In **Chapter III**, we found that the climatic variable set used in the SDMs had a larger influence on the value of the AM index metrics than the modelling techniques had. The variables selected on a statistical basis produced the highest AM index estimates, whereas the variables chosen for their general ecological relevance for plant species resulted in the lowest values. This also stresses the need to pay additional attention to choice of variables when applying SDM. Likewise, it further accentuates the pervasive role of epistemic uncertainties: if it is unknown which climatic variables are rele-

vant for a certain species, there is little applicable use of the notion that using different variable sets produce different estimates.

More information on species' requirements needs to be accumulated through explanatory approaches which can provide insight into important environmental variables for predictions (Diamond et al. 2012), and therefore improve the accuracy of various threat estimates, such as the AM index. Experimental methods (e.g., **Chapter V**) can specify the underlying predictive assumptions used, whereby anticipatory predictions relying on the assumptions can provide a less uncertain overview of what different scenarios of the future may entail.

Nevertheless, experiments are by no means a quick or easy solution. In **Chapter IV**, we had identified climatic features that may be important for deciphering local adaptation in experimental studies of Siberian primrose. Weather parameters representing these and other climatic features were, however, not able to explain our observations in **Chapter V**. Instead, the initial results from the translocation trials indicate that the site (i.e., the botanic garden) is a better explanatory variable for Siberian primrose survival than the prevailing weather conditions during the study period. It is possible that the experimental gardens contain additional variation that has very little to do with climate or weather, such as differences in weeding<sup>19</sup> and watering regimes. For flowering and size, the other explanatory variables (original size, planting time, and variety) explained our observations equally well as a model where weather conditions was included. It is possible, that the weather conditions at the closest weather station may also not reflect the micro-climatic conditions at the experi-

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<sup>19</sup>There seems to be a substantial difference in weed pressure between the experimental locations (**Chapter V**) with more weeds in the gardens further to the south (pers. obs.). As the study species is adapted to relatively low-stature vegetation on early-successional sea shores, the presence of weeds may have a significant effect, which is why we attempted to remove this factor by encouraging the local staff to weed the plots.

mental sites. More site-specific measurements and controlled laboratory or greenhouse trials could be useful to shed light on this aspect. Our observations may also be caused by this species not being strictly adapted to climatic conditions in its area of occurrence. Instead, light conditions or species interactions could be more important for Siberian primrose and would therefore need to be incorporated into both experiments and anticipatory models to enable conservation assessments.

It is important to remember that although experiments can give us important information about the *direct* effects of climate on species, climate change would in many cases affect species *indirectly* through contingencies such as sea level rise or the dynamics of other species. For example, climate change affects coral reefs through higher sea water temperatures, expelling the corals' symbiotic algae. This causes so called coral bleaching, i.e., the corals themselves die<sup>20</sup>. Altered climatic conditions may also lead to the species becoming more prone to pathogens, as may have been the case in the first extinction that has been linked to climate change, that of the Montverde golden toad (*Bufo perigrines*) in Costa Rica in 1989 (Pounds et al. 2006).

Although time-consuming, laborious, and not necessarily a problem-free remedy, empirical trials are important, as they can provide insight on the fundamental niche of a species and on the adaptive variation among populations. Sax et al. (2013) propose employing extensive existing but underutilized experiments: the horticultural occurrences and information connected to them in botanic gardens. Existing collections in botanic gardens can be used for studying species responses to climate (e.g., Hällfors et al. 2011), and hold potential for studying questions relating to AM (**Chapter V**; Hällfors et al. 2012). Additionally, such studies can give an approximation of the 'tolerance niche' of a species, i.e., the conditions under which it can exist without necessarily establishing

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<sup>20</sup>High water temperatures have already caused both local and regional extinction of some coral species (Glynn 2012).



self-sustaining populations (Sax et al. 2013). This concept is relevant in the discussion on AM, since areas within the tolerance niche provide suitable recipient locations while climate is changing, allowing long-lived species especially to establish and get a head start (Sax et al. 2013).

According to Gewin (2013) there have also been suggestions on establishing a systematic ‘chaperoned assisted migration’ network. Range predictions would be used to inform collection policy for botanic gardens, which would enable testing species’ reactions to climate and keeping species within suitable conditions as climate changes. However, to make full use of this potentially valuable data, it is important that the collections of botanic gardens are curated appropriately (Hällfors et al. 2010) and that due attention is paid to making them stable experimental grounds, so that noise in data stemming from factors other than the ones investigated can be avoided.

Nevertheless, no matter how well calibrated SDMs became with increased data, they will probably remain a better measure of climate change *exposure* than of the *sensitivity* of species to climate change (Moritz and Agudo 2013). This distinction is important and increases the significance of combining SDM-like approaches with more qualitative species trait assessments (e.g., Pearson et al. 2014). Therefore, studies on species autecology, including observational studies, continue to play an important role in providing background information on species. We also need a better understanding on the ability of species to persist through changes *in situ* through evolutionary adaptation (Hellmann and Pfrender 2011).

### 3.5. Deciding on assisted migration

Although approaches such as SDMs may contain much uncertainty (**Chapters IV and V**), merely calling for more studies and not utilizing existing, although uncertain, results as they become available can result in inaction, which in itself is also a value-laden choice of action (Ahteensuu and

Lehvävirta 2014). Thus, we need to stay aware of the uncertainties and risks connected to different methods while simultaneously making decisions based on the best available information.

The approach presented in **Chapters II and III** arguably provides only a rough estimate of AM need and potential. However, by highlighting those species whose predicted range change indicate a potential benefit from AM, the approach has the prospect of providing a first approximation and identifying the species most in need of further scrutiny. Most importantly, the approach can provide a comparable and objective measure for the AM need and potential of individual species.

In the future, estimations of a larger number of species could be conducted, while simultaneously investigating traits and other important characteristics that may reduce or increase the threat (e.g., Pearson et al. 2014). If used as part of a broader decision-making framework (e.g., Richardson et al. 2009), information from range change predictions can be combined with other evaluations, such as risk of invasion and societal acceptability, applying to less weight on only a single estimate.

Even though AM will certainly not be a panacea or quick-fix for all climate-change-threatened species, and traditional conservation measures like protected areas will probably still remain our most effective conservation tool (Hunter et al. 2010), we may need to reconsider our underlying value judgments and allow a more dynamic view of nature. Decisions on AM will inevitably be characterized by much human decision uncertainty both in terms of the degree of future climate change and the potential application of AM. Different values and interests concerning issues such as naturalness (Siipi 2008; Siipi and Ahteensuu 2014) will probably affect the perceived attractiveness of potential cases of AM (Javeline et al. 2015). Allowing lead-time for discussion and development of emerging issues such as AM allows society to prepare and adapt regulations and norms (Oye et al. 2014). Here, a clear articulation of the concept (**Chapter I**) is of paramount importance as it allows a critical evaluation of the applicability of the meth-

od and consequent development, if the method is deemed feasible.

The discussion on concepts and definitions should, however, continue as it is apparent that further nuances in translocation concepts need to be identified and described. Moving species under climate change may, for instance, involve translocating species to fulfil an ecological role in another system that has lost a functionally similar species because of climate change. This broader concept involving both assisted migration and the example described above could be called, e.g., managed relocation (pers. comm. J. Hellmann [member of Managed Relocation Working Group], May 2015).

#### 4. Conclusions

Because loss of biodiversity has already transgressed the boundary of high risk, we need to make decisions in the immediate term and base them on the knowledge we have at hand at the moment. The likely consequences of various decisions can be elucidated through scientific methods.

Anticipatory predictions can be used for highlighting potential shifts in species ranges and can aid in grasping the broad picture of climate change effects on species and their conservation under different climate change scenarios. The results of this thesis show that there may be a significant difference in the number of species benefitting from AM under various scenarios of climate change.

However, we need to continuously feed in to our theories with updated hypotheses on the basis of accumulating ecological knowledge and thereby reduce epistemic uncertainty. Predictive experiments can help specify the assumptions of models that aim to predict future ranges of species. By clearly articulating concepts and defining them for applied purposes, we can also reduce linguistic uncertainty.

It is, nevertheless, also up to others than ecologist or the scientific community at large to use the available scientific information when deciding what path to follow, and herein lies a large part of

the human decision uncertainty. In fact, all choices we make, whether to continue on the current course of development or to change attitudes and take actions to mitigate climate change, are choices humanity needs to take, preferably with the knowledge accumulated by science as a basis for this decision.

The conceptual underpinnings of this study provide a baseline that allows practitioners and researcher to evaluate the relevance of assisted migration for specific species and continue to develop studies, strategies, and regulations for this conservation method.

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