

# **Assessing and comparing climatic control on distribution and reproduction of alpine and lowland species in the sub-alpine habitat of western Norway.**

***Eric Meineri***

**Dissertation for the degree of philosophiae doctor (PhD)**

**University of Bergen, Norway**

**2011**

UNIVERSITETET I BERGEN





**Assessing and comparing climatic control on distribution  
and reproduction of alpine and lowland species in the sub-  
alpine habitat of western Norway.**

Eric Meineri

**Dissertation for the degree of philosophiae doctor (PhD)**

**University of Bergen, Norway**

**2011**

**Supervision:**

Vigdis Vandvik, University of Bergen, Norway.

Olav Skarpaas, The Norwegian Institute for Nature Research, Norway

UNIVERSITETET I BERGEN



**Contents:**

- Abstract ..... 2
- Acknowledgements ..... 4
- List of papers ..... 5
- Declaration ..... 6
- Introduction ..... 7
  - Species ranges and reproduction by seeds ..... 7
  - Complex climatic controls on reproductive life-stages ..... 9
  - Specific aims of this PhD thesis: ..... 10
- Sampling design ..... 10
- Studied species ..... 14
- Experimental and analytical approaches ..... 16
  - Paper I: ..... 16
  - Paper II: ..... 16
  - Paper III: ..... 17
- Results and discussion ..... 18
  - Reproductive life-stages and species climatic niche ..... 18
  - The complexity of climate control ..... 21
  - Biotic interactions at the rear edge of alpine species ..... 22
  - Further work and concluding remarks ..... 24
- References ..... 26
- Papers ..... 34

## **Abstract**

### **Aims and background:**

Species range shift is among the most well-documented responses to climate change. As a result, a growing number of studies model species climatic niches to predict how species ranges may displace in space and time (SDM studies). These studies are criticised because they do not include reproduction in their predictions. Other studies use empirical data to assess climatic control on reproductive life-stages. However, the climatic niche of reproductive life-stages may not determine the climatic niche of species, limiting the ability of both types of studies to assess the effect of climate change. In this synthesis, I compare the results of a SDM study (Paper I) with the results of two empirical studies focussing on flowering performance (Paper II) and seedling emergence (Paper III). The research focuses on the leading and rear altitudinal edges of lowland and alpine species ranges, respectively, as those are the two delimiting fronts that are expected to be specifically vulnerable to climate change.

Reproduction response to climate is a complex process because it involves several sub-stages that can be affected by climate in several ways. Therefore, the results included in this synthesis integrate several direct and size-dependent climatic effects on flowering performance and report on the importance of both the climate conditions occurring at the recruitment sites and those experienced by the source populations for seedling emergence.

### **Study area and species:**

This thesis makes use of the sub-alpine and alpine landscapes of western Norway to investigate climatic control on species occurrence and reproduction. This study area was chosen because it includes the leading altitudinal edge of lowland species' ranges and the rear altitudinal edge of alpine species' ranges. The research uses *Viola biflora* (alpine), *Viola palustris* (lowland), *Veronica alpina* (alpine), and *Veronica officinalis* (lowland) as study cases because these species are common in the study area and the study sites, and are representative of the alpine and lowland communities occurring at the studied sites.

### **Results and discussion:**

The climatic control on flowering performances and seedling emergence did not reflect the climatic niches of three out of four species, suggesting ontogenetic niche shift. These mismatches challenge the predictive ability of both SDMs and empirical studies focusing on reproductive life-stages.

Papers II and III highlight the complexity of climatic control on reproduction and show species-specific results. Flowering was both climate- and size-dependent for three species, but the way size-dependency was expressed differed between species. Seedling emergence was less species-specific although one species (*Veronica officinalis*) was found to be affected by the climate experienced by its source populations while the three other species were only responding to the climate of their sowing sites. This illustrates the importance of accounting for the complexity of reproduction to improve climate-change predictions on plant reproduction.

Finally, Papers I and II suggest a high importance of biotic interactions from the lowland flora for the two alpine species, stressing the importance of understanding plant-plant interactions to forecast climate-change impacts.

**Further research and conclusions:**

Structured population models can resolve some of the problems reported in this synthesis but further methodological developments are necessary to integrate local adaptation patterns and to accurately project the outputs of such models in space. Dispersal has been largely ignored in climate-change studies. Further research should also aim to improve knowledge on dispersal because quantifying dispersal and recruitment rates is required to predict accurately climate-change impacts on plant populations and potential range displacements. Individualistic responses to climate suggest drastic changes in plant communities over the coming years. Given the high importance of biotic interactions, increasing knowledge on species interactions will be an important step to better understand and predict the potential climate-change impacts. Since the climatic control of a given species may not relate to the climatic control of another species, more effort should be given to key and/or endangered species that may have specific value for conservation.

## ***Acknowledgements***

Doing a PhD is a long and difficult process that brings joys but often frustrations. During my PhD time, interactions with others have been very helpful. They helped me to keep a relatively high motivation and at the same time, to detect the strengths and the flaws in my work, allowing me to move forward.

First of all, I thank my supervisors Vigdis Vandvik and Olav Skarpaas for their guidance and also for their patience. They always supported and encouraged me, took a lot of time for my work, and were always eager to give helpful comments and suggestions on the papers. Although their inputs sometimes felt frustrating, they were important in improving my critical thinking, my writing ability, and my overall research. They successfully taught me what science was about and I am grateful for that.

My project co-workers Joachim Spindelböck and Kari Klanderud have also been of great help. They were interested in what I did and were always available when I needed to discuss my research. I also thank Debora Goldberg for her input into my papers during the SEEDCLIM meetings.

The many field assistants that we had over the last four summers were also a great help. Namely, Tessa Bargmann, Serge Farinas, Simon Le Mellec, Christine Pötsch, Keno Ferter, and Nina Mahler. This PhD would not have been possible without them.

I thank my colleagues at EECRG for their inputs during research group meetings and Jutta Kapfer as well as the other members of the 'UN office' for being supportive and listening to my confusions during lunch time.

My family have been supportive, listening to my complaints and helping me to keep my self-confidence; and friends in France and Norway have been helpful in listening and trying to understand my research.

Most importantly, thank you Lise. She is, and I hope will stay, my best supporter. Our discussions had great impact on my work and therefore a big part of this thesis belongs to her as well.

This work is funded by the NFR NORKLIMA SeedClim project (184912/S30) and "Olav Grolle Olsens" funding from the Bergen Museum.

## ***List of papers***

This thesis is based on the three following papers which will be referred by their roman numeral hereafter

**Paper I:** Meineri, E., Skarpaas, O., Vandvik, V. Modelling alpine plant distributions at the landscape scale: Do biotic interactions matter? Submitted to Ecological Modelling.

**Paper II:** Meineri, E. Skarpaas, O., Spindelbock, J., Bargmann, T., Vandvik, V. Direct and size-dependent climate effect on flowering performance in alpine and lowland herbaceous species. Submitted to Journal of Vegetation Science.

**Paper III:** Meineri, E., Spindelbock, J., Vandvik, V. Seedling emergence responds to the climate of both recruitment site and seed source - A climate change experiment combining transplant and gradient approaches. Submitted to Oecologia.



## ***Declaration***

**Paper I:** Meineri, E., Skarpaas, O., Vandvik, V. Modelling alpine plant distributions at the landscape scale: Do biotic interactions matter?

Meineri, E: Experimental design, analytical design, data processing, statistical analyses, writing

Skarpaas, O: Experimental design, inputs on analytical design, editing

Vandvik, V: Experimental design, inputs on analytical design, editing

**Paper II:** Meineri, E. Skarpaas, O., Spindelbock, J., Bargmann, T., Vandvik, V. Direct and size-dependent climate effects on flowering performance in alpine and lowland herbaceous species.

Meineri, E: Experimental design, field work, data processing, analytical design, main statistical analyses, writing

Skarpaas, O: Experimental design, field work, inputs on analytical design, statistical analyses, editing

Spindelbock, J: Experimental design, field work, data processing, inputs on analytical design, editing

Bargmann, T: Field work, laboratory work, data processing, editing

Vandvik, V: Experimental design, inputs on analytical design, editing

**Paper III:** Meineri, E., Spindelbock, J., Vandvik, V. Seedling emergence responds to the climate of both recruitment site and seed source - A climate change experiment combining transplant and gradient approaches.

Meineri, E: Experimental design, field work, data processing, analytical design, statistical analyses, writing

Spindelbock, J: Experimental design, inputs on analytical design, field work, editing

Vandvik, V: Experimental design, inputs on analytical design, editing

## **Introduction**

### **Species ranges and reproduction by seeds**

Over the last century, temperature has increased by, on average, 0.74°C, and precipitation has increased by 6 to 8% in the northern hemisphere. These climatic trends are expected to accelerate in the future (IPCC, 2007). Changes in temperature and precipitation induced by global warming are already influencing ecosystems world-wide (Walther *et al.*, 2002, Root *et al.*, 2003, IPCC, 2007). Species range shift (Table 1) is among the most well-documented responses to past (Huntley, 1991, Pitelka *et al.*, 1997, Muller & Richard, 2001) and present (Pitelka *et al.*, 1997, Kelly & Goulden, 2008, Lenoir *et al.*, 2008) climate changes.

A growing number of studies have been aiming to forecast species climatic niches (Table 1) in order to predict potential range displacements in the coming years (e.g. Bakkenes *et al.*, 2002, Thomas *et al.*, 2004, Thuiller *et al.*, 2005). This particular branch of spatial modelling exercises, known as “Species distribution models”, “Climate envelope modelling” or “Ecological niche models” (hereafter, referred to as SDM), correlate observations of species occurrence with climatic variables in order to extract species climatic niches. They then study how this climatic window may displace in space and time according to climate models’ predictions and assuming that the target species will track its climatic niche. These studies have been criticised because they disregard the biological processes that determine species ranges and which may or may not allow species range displacements (Clark, 2003, Higgins *et al.*, 2003, Pearson *et al.*, 2006, Thuiller *et al.*, 2008). For many species, successful reproduction by seeds is required to achieve range displacement because it allows for the production of the dispersal units. At the same time, seed production may allow for adaptation, limiting the need of range displacement. Thus, several studies have used empirical data to investigate how reproductive life-stages respond to variation in temperature (e.g. Gimenez-Benavides, Escudero & Iriondo, 2008, Milbau *et al.*, 2009, Shevtsova *et al.*, 2009, De Frenne *et al.*, 2010) and water availability (Shevtsova *et al.*, 2009, Graae *et al.*, 2011). Such an approach is interesting to improve the understanding of climatic control on sexual reproduction, but can only allow speculating on the potential climate-change impacts on plant populations. One of the reasons is that niche shift may occur among plant life development stages (i.e. ontogenetic niche shift, Table 1) (Eriksson, 2002, Thompson & Ceriani, 2003, Auffret *et al.*, 2010) and thus, climatic control on plant sexual reproduction may not necessarily shape species range (e.g. Gilman, 2006).

While predictions from SDMs may be biased because they ignore niche processes and plant sexual reproduction, predictions from empirical studies focussing on reproduction may be biased because their results may not be relevant throughout the species range. This paradoxical situation illustrates the necessity of investigating climate-change impact using several approaches and calls for comparisons between SDMs and empirical studies focussing on reproduction. Such comparisons are however difficult because the two types of study do not investigate the same organisms and empirical studies do not often link their results to the position of their study sites within the studied species' climatic niches (but Gimenez-Benavides, Escudero & Iriondo, 2007a, b, De Frenne *et al.*, 2009). This synthesis compares the results from one SDM study (Paper I) with the results of two empirical studies focussing on reproductive life-stages (Papers II and III). In all three papers, we used the same species and the same habitat allowing for comparison among approaches.

Comparing species' responses to climate using different approaches is especially important at the leading and rear edges of species ranges (see Table 1 and Hampe & Petit, 2005 for definition of leading and rear edges). This is because they are the two delimiting fronts of species ranges and therefore, the plasticity of the reproductive life-stages to climate at the leading and rear edges may be of overwhelming importance for range displacements. To shape species range, reproductive life-stages should respond to climate at the leading and rear edge according to predictions based on the 'centre-periphery' theory. This theory predicts less suitable conditions at the boundaries of species ranges (Lawton, 1993). However, while the lower species success at the leading edge is thought to be caused by high abiotic stress, increasing competition is thought to be of higher importance at the rear edge (Brown, Stevens & Kaufman, 1996, Choler, Michalet & Callaway, 2001, Callaway *et al.*, 2002). Although a decreasing reproductive success can be expected towards these two margins, the effect of rising temperature and precipitation should differ at the leading and rear edges. A temperature increase should reduce the abiotic stresses at the leading edge. This effect can be expected to improve reproductive success at a species' leading edge and thus facilitate range extension. In contrast, a temperature increase at the rear edge can be expected to decrease reproductive success because of increasing biotic interactions, or to have limited effect because of low abiotic stress. This would result in species retreat at their rear edge. Furthermore, lower reproductive success at the rear edge may also be caused by other abiotic factors. For example, several authors have suggested an increasing drought stress on reproduction toward the rear altitudinal edge of a species range (e.g. Gimenez-Benavides, Escudero & Iriondo, 2007a, Gimenez-Benavides, Escudero & Iriondo, 2008), highlighting potential interactions

between temperature and water availability. In such a scenario, the potential negative or limited effect of temperature increase that can be expected at the rear altitudinal edge may be counter-balanced by a positive effect of increasing precipitation.

In this synthesis, I used the results from Papers II and III to test the predictions stated above. These papers make use of the subalpine zone of western Norway to study how reproductive life-stages respond to temperature and precipitation. The subalpine zone encloses both the leading altitudinal edge of lowland species' ranges and the rear altitudinal edge of alpine species' ranges, and is therefore suitable for testing such predictions.

### **Complex climatic controls on reproductive life-stages**

One of the problems when investigating climatic effects on reproductive life-stages is that reproduction is a complex process that includes several sub-stages and each sub-stage can be affected by climate in several ways. Without being exhaustive, reproduction includes flowering and flower production, seed dormancy, germination and seedling emergence, and ultimately, establishment. In this thesis, I focus on flowering probability and flower production (Paper II, Table 1), and seedling emergence (Paper III, Table 1) responses to temperature and precipitation. The separation between these distinct stages seemed natural as it marks the differentiation between the reproductive organ, and the seed and its subsequent seedling. Furthermore, these stages were chosen because they can be investigated in the field and can therefore reflect the indirect climatic effects affecting reproduction.

Flowering probability and flower production can respond directly to climate or indirectly through plant-size. This is because flowering performance is often described as size-dependent (Obeso, 2002, Mendez & Karlsson, 2004, Pfeifer, Heinrich & Jetschke, 2006, Pfeifer *et al.*, 2006) and plant size is repeatedly shown to vary with climate (De Valpine & Harte, 2001, Zavaleta *et al.*, 2003, Bloor *et al.*, 2010, Kardol *et al.*, 2010). Furthermore, size-dependency for flowering performance plasticity to climate might well express itself in other ways, for instance, allocation to reproduction and minimum size for flowering have been shown to vary along climatic gradients (Ohlson, 1988, Welham & Setter, 1998, Mendez & Karlsson, 2004, Bonser & Aarssen, 2009).

Similarly, seedling emergence may respond to climatic changes in several different ways. First, seedling emergence may respond directly to the climatic conditions at the germination site as those may differently fulfil the requirements that are necessary to break seed dormancy and to trigger germination (Fenner & Thompson, 2005, see "sowing site climate" in Table 1). This reflects a plastic response to climate. Second, seedling emergence

may respond to the climate of the source population (see “seed-source climate” in Table 1), which can reflect a maternal environmental effect (Schmuths *et al.*, 2006), or a specific regeneration strategy such as a bet-hedging effect (Vandvik & Vange, 2003), or, simple differences in seed quality across populations experiencing different climate (Graae, Alsos & Ejrnaes, 2008). Third, seedling emergence can be adapted to the local climatic conditions via local adaptation or pre-conditioning environmental maternal effect (hereafter collectively referred to as adaptive seedling emergence, Table 1), depending on whether genetic differentiation occurs or not (Roach & Wulff, 1987, Kawecki & Ebert, 2004, Donohue, 2009). In Papers II and III, I decomposed these different climatic effects on flowering performance and seedling emergence to assess the complexity of climatic control on reproduction.

### **Specific aims of this PhD thesis:**

- 1) Assessing how the responses of reproductive life-stages to climate vary throughout the species range, and thus assessing the relationship between SDMs and empirical studies on reproductive life-stages.
- 2) Exploring the complexity of climate control on the occurrence, flowering, and seedling emergence of lowland and alpine species.
- 3) Exploring the importance of biotic interactions at the rear altitudinal edge of alpine species' ranges.

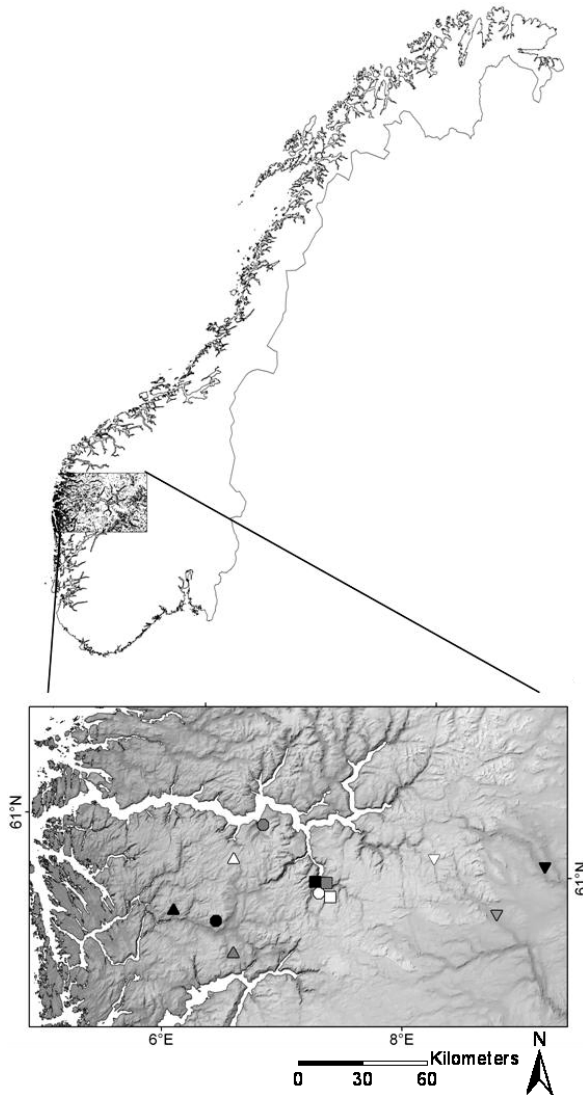
### ***Sampling design***

The three studies included in this thesis make use of the heterogeneous landscapes of western Norway (ca 4°50' - 8°45' E; 60°20' - 61°50' N). Steep altitudinal gradients are found throughout these landscapes, with elevation ranging from sea level on the west coast and along the fjords to 2469m a.s.l. at the top of the Jotunheimen mountain range situated in the north-eastern part of the area (Figure 1). Because of its oceanic geographical position and topography, this area covers a wide range of climatic conditions. Mean annual temperature, ranging from -8.22°C to 7.57°C, is driven primarily by elevation and continentality and is generally lower in the eastern mountains. Annual mean precipitation ranges from 379 mm in the east to 3836 mm in the west. Duration of snowcover varies from 0 to 8 months. Grazing by domestic and wild herbivores is common throughout the landscape.

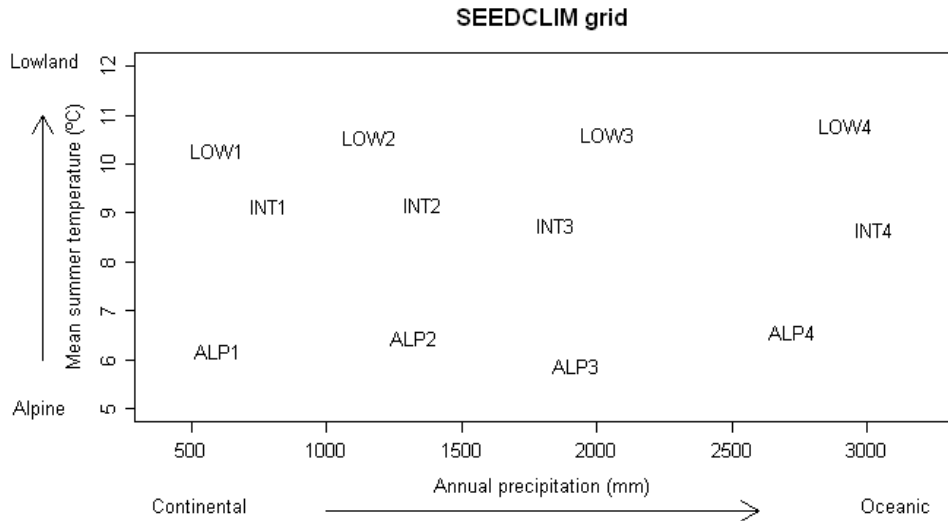
**Table 1:** Definitions of the terms commonly used in this synthesis.

<i>Term</i>	<i>Definition</i>
Species range	Physical geographical distribution of a species.
Climatic niche	Climatic window delimiting the species range (i.e. realised niche).
Ontogenetic niche shift	Realised niche shift among life history stages.
Leading altitudinal edge	Upper altitudinal front of the species range.
Rear altitudinal edge	Lower altitudinal front of the species range.
Flowering probability	Probability of flowering for a plant.
Flower production	Number of flowers on a flowering plant.
Seedling emergence	Seedling that germinated and survived at least one growing season.
Sowing-site climate	Climate experienced at the sowing site (i.e. experienced during seed dormancy, seed germination, and seedling first summer.
Seed-source climate	Climate occurring at site of seed collection (i.e. experienced by the source population, during seed maturation and by the mother plant).
Adaptive seedling emergence	Local adaptation or maternal environmental effect known as “pre-conditioning” depending on whether genetic differentiation occurs.

In Paper I, the strong climatic gradients found in western Norway are used to capture extensive parts of the target species’ ranges. For the purpose of Papers II and III, and other research within the SEEDCLIM project, we used that landscape to set up 12 calcareous grassland experimental sites in a “climate grid” design enabling us to decouple the effects of temperature and precipitation. The climate grid was designed to cover an approximately 6-degree gradient in mean annual temperature across the boreal to low-alpine zone transition. Mean summer temperature, defined in this synthesis and the related papers as the mean of the four warmest months, and annual precipitation were used to design and set up the climate grid (hereafter referred to as the SEEDCLIM grid). The SEEDCLIM grid combines four levels of annual precipitation (ca 600 (level 1), 1200 (level 2), 2000 (level 3) and 2700 (level 4) millimetres) with three levels of mean summer temperatures (ca 6.5 (ALP), 8.5 (INT), and 10.5°C (LOW) (see Figure 1 for geographic position of each site). The sites were selected to keep other factors such as grazing regime and history, bedrock, and vegetation structure in



**Figure 1:** Geographical location of the study area within Norway (top), SEEDCLIM experimental sites and topography of the study area (bottom). Experimental sites: White: alpine sites, grey: intermediate sites, black: lowland sites; ▼: dry sites, ■: mid-dry sites, ●: mid-wet sites, ▲: wet sites.



**Figure 2:** Position of each site within the SEEDCLIM climate grid. Altitude is the main driver for changes in mean summer temperature and continentality is the main driver for changes in annual precipitation within the grid, but there are interactions between the two and sites are therefore positioned in geographical space so as to decouple the two gradients as far as possible

terms of local scale species richness, and slope and exposure, as constant as possible across sites. Specifically, we targeted grazed intermediate-rich meadows (*Potentillo-Festucetum ovinae*; G8 *sensu*, Fremstad, 1997) with relatively rich bedrock in term of nutrient availability, preferably phyllitic or calcareous, and occurring on south-facing, shallow slopes (5-20°) (see Papers II and III for details on site selection). Hereafter, I refer to the 12 selected grassland sites as LOW1, INT1, ALP1, LOW2, INT2, ALP2, LOW3, INT3, ALP3, LOW4, INT4, ALP4 to reflect their temperature (lowland, intermediate, alpine) and precipitation (1=low to 4=high) levels within the grid (see Figure 2 for site position within the SEEDCLIM grid). The SEEDCLIM grid was set-up during the summer 2008. All sites were fenced in spring 2009 to prevent animal disturbance. The vegetation was cut yearly at ca 10cm above the ground from the summer season 2009 as a standardised grazing/mowing treatment across sites.

At each site, five blocks of approximately 5 m<sup>2</sup> were selected within a grassland area of approximately 30 m<sup>2</sup>. Blocks were chosen to be as similar as possible in terms of vegetation structure, slope, and exposure. Within each block, we established the study plots



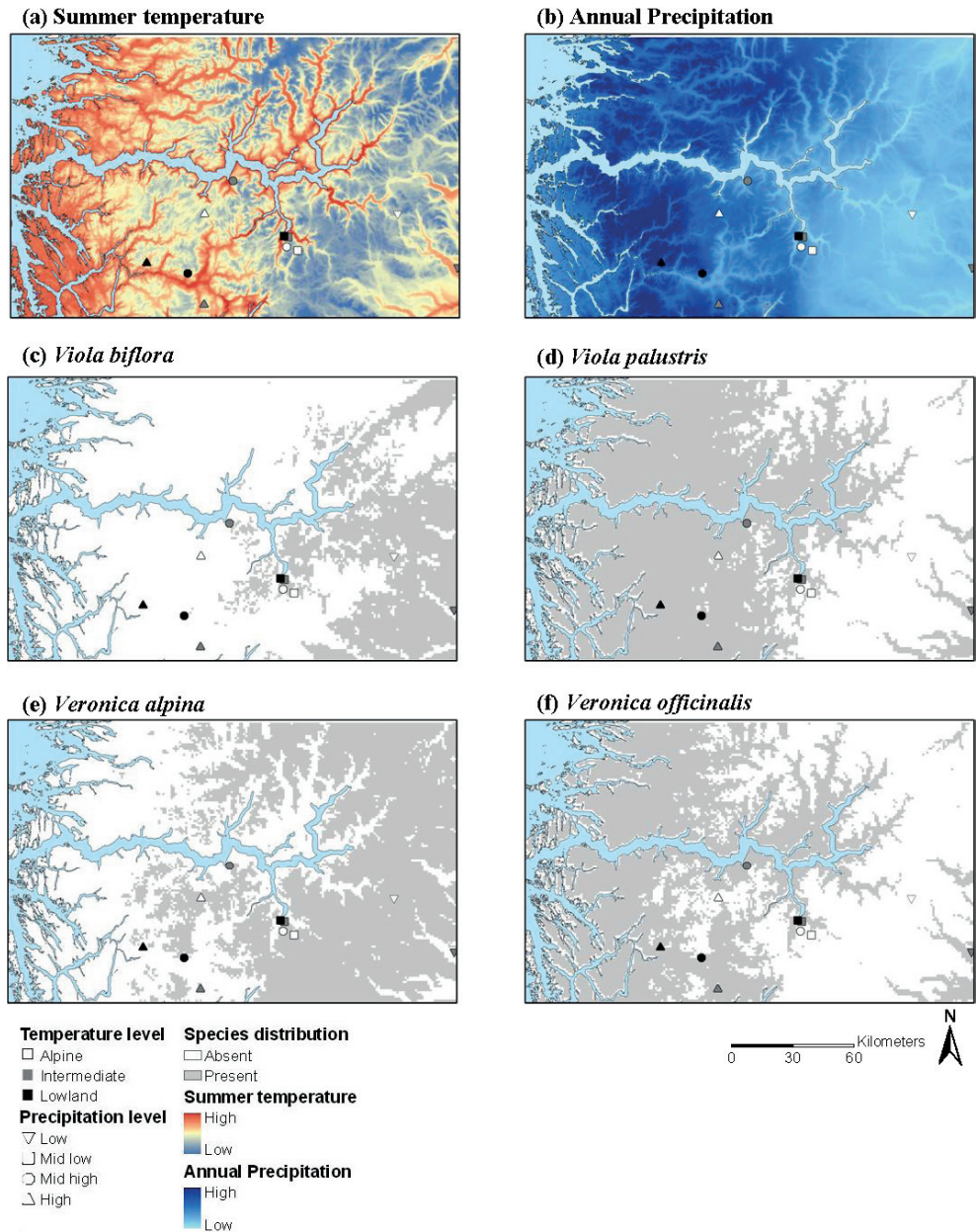
that were used to study flowering performance and seedling emergence in Papers II and III, respectively (see Papers II and III for specific plot design within the blocks).

Interpolated temperature and precipitation data from the normal period 1961-1990 with a resolution of 100m (met.no, 2009) (see Tveito *et al.*, 2000, Tveito *et al.*, 2001, Tveito *et al.*, 2005 for method description) were used to aid site selection and for statistical analyses. The interpolated mean summer temperatures for the normal period were highly correlated (Pearson correlation 0.98, n=12) with local mean summer temperatures in 2009 (data for subsequent years are not available yet) calculated from on-site temperature measurements (hourly temperature at two metres high monitored with UTL-3 Scientific Dataloggers, GEOTEST/SLF, www.utl.ch). Precipitation measurements were also set up locally, but the recordings contained too many measurement errors to be used within this PhD.

### **Studied species**

Two alpine-lowland species pairs, *Viola biflora*-*Viola palustris* and *Veronica alpina*-*Veronica officinalis*, were chosen for the three studies. These species were chosen so that the climate grid would cover the rear altitudinal edge of the two alpine species and the leading altitudinal edge of the two lowland species as confirmed by the models developed in Paper I (Figure 3, Paper I). These four species were also chosen because they were common in the 12 sites and were judged as good representatives of the targeted communities of the SEEDCLIM sites. This species choice also allowed us to maximise the number of sites where the species occurred individually, and the number of sites where both species of a pair occurred simultaneously. Working with species pairs with similar branching structures was chosen to allow for easier comparison between alpine and lowland species.

*Viola biflora* is common in moist and relatively nutrient rich mountain habitats and is found in snowbeds and leesides, grazed upland pastures, stream banks, and birch forests. *Viola palustris* grows on moist soils and is common in moist pastures, meadows, and forests, mires, and stream banks. *Veronica alpina* is found in a wide range of upland habitats and is common in snowbeds, upland forests, grasslands, and stream banks. *Veronica officinalis* is often found on shallow well-drained soils within pastures and meadows, along road verges, and in grazed forests and uplands (Lid & Lid, 2005, Mossberg & Stenberg, 2007)



**Figure 3:** Maps showing a) summer temperature, b) annual precipitation, and c-f) modelled species distribution (according to their climatic niche) of the four studied species within the study area (Paper I). The locations of the experimental sites are plotted on each map. The site LOW1 is not represented as it is outside the study area of Paper I.

## ***Experimental and analytical approaches***

### **Paper I:**

This paper explores how climate controls species occurrence in western Norway. In this study, logistic models were used to predict the climatic niches of the four target species. For the two alpine species, these models were designed to account for both climate and biotic interactions with the lowland flora. For each alpine species, the lowland flora was represented by their respective lowland species congener. By doing such, we did not intend to include the effect of the two interacting species *per se* but rather the influence from the lowland communities in which these lowland species are dominant. The inclusion of competing organisms in SDMs may reflect important abiotic parameters for the modelled species that are already accounted for by the other variables (Guisan & Thuiller, 2005, Elith & Graham, 2009). Interactions with competing organisms are thus partly included, and adding competitors' occurrences or abundances can lead to numerical problems caused by collinearity between abiotic and biotic predictors. Such collinearity is likely to have a strong effect in the case of alpine-lowland species interactions since the strength of the interaction is linked to altitude and thus to temperature. I therefore developed an alternative method where the potential competing species effect is estimated in an independent set of models that are used to re-predict the landscape parts where the alpine and lowland target species are predicted to co-occur by a SDM based on climatic parameters only.

### **Paper II:**

This study is a gradient analysis using plant size and reproductive measurement of individuals occurring within the 12 sites of the SEEDCLIM grid to decompose direct and size-dependent climate effects on flowering performance. In this study, we used a sequence of logistic and log-linear mixed effect models to study flowering probability and flower production respectively. In these models, direct climate effects were indicated by a statistical effect of temperature or precipitation on the flowering rates studied. An indirect climate effect through plant size was indicated by a statistical effect of plant size in logistic and/or log-linear models describing flowering probability and flowering performance respectively, in addition to a significant effect of climate on plant size in another set of linear models. A change in minimum size for reproduction was indicated by additive effects of size and climate in the logistic models. This is because a statistical effect of climate induces variation in the X-intercept in the logistic curve describing flowering probability response to size. Variation in

reproductive investment (allocation to reproduction) was indicated by an interaction between size and climate in log-linear and/or logistic models as such interactions induce variation in the slope describing the relationship between plant size and flowering performance.

### **Paper III:**

This study is a seed-sowing experiment that includes both gradient and experimental approaches to investigate how seedling emergence is affected by the climate conditions occurring at the sowing sites and experienced by the seed-source populations. For this study, we transplanted mature seeds from site to site within the SEEDCLIM grid. Hence, seeds from each source population were sown *in situ* in their site of origin as well as *ex situ* in three different sites where the climate was 1) one step warmer, 2) wetter, and 3) warmer and wetter relative to the seed-source site.

In the experimental approach, we used nested ANOVAs where we adapted the random structure to the hypothesis tested. The random structure of a mixed model is normally used to describe the structure of data and so the contrast between control and treatment groups. In this study, we modified the random structure of these models to change control and treatment groups according to the hypothesis tested. Hence, models nested on source site were used to compare the emergence of seeds sown at home versus the emergence of seeds sown away. In contrast, models nested on sowing site were used to compare the emergence of foreign seeds versus the emergence of seeds of the local populations. This allowed the separation of the effect of the sowing-site climate from the effect of the seed-source climate.

In the gradient approach, log-linear regressions were used to analyse how seedling emergence responds along the extended temperature and precipitation gradients of the SEEDCLIM grid. The effect of the sowing-site climate and the effect of the seed-source climate could be studied separately by excluding the emergence scores of the seeds sown at home, thus experiencing similar sowing-site and seed-source climate.

Using both experimental and gradient approaches allowed us to not only compare local responses to gradient-wide patterns but also to identify signs of adaptive seedling emergence (local adaptation or pre-conditioning maternal environmental effect). In the experimental approach, adaptive seedling emergence was indicated by higher seedling emergence for the seeds sown at home compared to seeds sown away (home vs. away criterion in Kawecki & Ebert, 2004) and higher emergence for the local seeds of a sowing site compared to the foreign seeds (local vs. foreign criterion in Kawecki & Ebert, 2004). However, the gradient approach was necessary to confirm that this effect was not caused by

potential negative effects of the sowing-site climate since the transplants were only made in a single direction.

## **Results and discussion**

### **Reproductive life-stages and species climatic niche**

This thesis shows an overwhelming climate control on the four studied organisms. Climate affected species occurrence, flowering performance, and seedling emergence of the two *Veronica* species and *Viola biflora* and affected the occurrence and the seedling emergence of *Viola palustris* (Papers I, II, and III). However, the results tended to be species-specific within the three papers and the climatic control on flowering performance and seedling emergence only partially reflected the position of the sites within the climatic niches of the four study species (rear vs. leading edge) (see Table 2). Hereafter, I first detail the results per species and later discuss the implications of these results.

*Viola biflora* flowering performance was not affected by changes in temperature but increased slightly with higher precipitation at its rear altitudinal edge (Table 2, Paper II). In contrast, increasing temperature reduced the species seedling emergence while increasing precipitation increased it (Table 2, Paper III). These results suggest an overall negative effect of increasing temperature, in contrast to an overall positive effect of increasing precipitation. If both temperature and precipitation increase, as suggested by the climate predictions for this study system (Hanssen-Bauer *et al.*, 2009), global warming may have a limited impact on the reproduction of *Viola biflora* in its rear altitudinal edge as the two effects may cancel each other out. On the one hand, these results are in line with the predictions from the center-periphery theory that forecast a negative or limited effect of increasing temperature and precipitation at species rear edge. On the other hand, these results do not completely match with the results from Paper I, as the SDM predicted *Viola biflora* occurrence to decrease with increasing precipitation in western Norway, while results on reproductive life-stages suggest the opposite pattern (Table 2). This suggests that the responses of reproductive life stages to climate only partially shape the species' range.

Although we found similar results regarding the seedling emergence of *Veronica alpina* (Table 2, Paper III), the flowering response to climate differed between the two alpine species (Table 2, Paper II). *Veronica alpina* flowering performance was predicted to increase with higher temperature at its rear edge (Table 1, Paper II). *Veronica alpina* reproduction may

thus be improved in a warmer and wetter climate if the negative effect of temperature and the positive effect of precipitation on seedling emergence cancel each other out. These results corroborate neither the predictions based on the center-periphery theory nor the results obtained in Paper I since both suggest a negative effect of increasing temperature at the species' rear edge. This indicates that a potential species retreat in the coming years at the species' rear edge may not be caused by reproductive plasticity to climate.

The results from the leading edge of the two lowland species were also mixed. *Veronica officinalis* was predicted to increase both flower production (Table 2, Paper II) and seedling emergence (Table 2, Paper III) with increasing temperature. These results are in line with predictions based on the center-periphery theory and reflect the results of Paper I. However, the species seedling emergence was not affected by the climatic conditions at the sowing sites as was found for the other three species, but by the climatic conditions experienced by the source populations and was always higher in similar climatic conditions to the one experienced by the source populations. If such effects are not maternal effects but are adaptive (see Roach & Wulff, 1987, Donohue *et al.*, 2010 for discussion on maternal effects and adaptation), the benefit of increasing temperature may be limited if the species cannot adapt fast enough (Paper III).

In contrast, the flowering performance of *Viola palustris* was not affected by climate (Table 2, Paper II) while its seedling emergence was found to decrease with higher temperature and increase with higher precipitation, as was observed for the two alpine plants (Table 2, Paper III). This suggests a limited impact of global warming on reproduction as the effect of temperature and precipitation on seedling emergence may cancel each other out. The predicted increase in reproductive performance at the species' leading edge caused by increasing temperature was therefore not confirmed. *Viola palustris* seems to have a slightly more cold-tolerant temperature range than *Veronica officinalis* (Paper I, Figure 3). Indeed, the species occurred in plots of two of our alpine sites (ALP 3 and ALP 4) and could be found in nearby surroundings of the other alpine sites. It is therefore possible that our intermediate and lowland sites are too close to the centre of the species' climatic niche to detect a temperature effect.

**Table 2:** Effect of increasing temperature and precipitation at lowland species leading and alpine species rear altitudinal edge according to the three papers included in this synthesis. +: positive effect, - negative effect, +- unimodal relationship, 0: no effect (not significant or effects cancelling out each other). For flowering performance, the effects are calculated for the warmest driest site of the SEEDCLIM grid for alpine species and for the coldest wettest site for the lowland species.

	Alpine species		Lowland species	
	<i>Viola biflora</i>	<i>Veronica alpina</i>	<i>Viola palustris</i>	<i>Veronica officinalis</i>
<b>Temperature increase</b>				
<i>Species occurrence</i>	-	-	+	+
<i>Flowering performance</i>				
Direct effects	0	+	0	+
Indirect effects	0	0	0	+
Minimum size for reproduction	0	0	0	0
Reproductive investment	0	-	0	0
<b>Total</b>	<b>0</b>	<b>+</b>	<b>0</b>	<b>+</b>
<i>Seedling emergence</i>				
Sowing-site climate	-	-	-	0
Seed-source climate	0	0	0	+
<b>Total</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>+</b>
<b>Precipitation increase</b>				
<i>Species occurrence</i>	-	<b>0</b>	+	<b>0</b>
<i>Flowering performance</i>				
Direct effects	+ -	0	0	+
Indirect effects	0	0	0	0
Minimum size for reproduction	-	0	0	0
Reproductive investment	+	0	0	-
<b>Total</b>	<b>+</b>	<b>0</b>	<b>0</b>	<b>0</b>
<i>Seedling emergence</i>				
Sowing-site climate	+	+	+	0
Seed-source climate	0	0	0	0
<b>Total</b>	<b>+</b>	<b>+</b>	<b>+</b>	<b>0</b>

The climatic control on flowering performance and seedling emergence did not reflect the climatic niches of three out of four species (see Table 2). This suggests an ontogenetic niche shift. Earlier studies have shown differences between recruitment and adult niche (Eriksson, 2002, Thompson & Ceriani, 2003, Gilman, 2006, Auffret *et al.*, 2010). In this thesis, I find similar patterns, but also a mismatch between flowering performance and seedling emergence responses to climate as well as between flowering performance and adult occurrence. Such mismatches in species response to climate across life stages challenge the predictive ability of both SDMs and empirical studies focusing on reproduction. Indeed, predictions in time from SDMs are likely to be biased if species ranges are not determined by the reproductive life-stages' response to climate. This is because species range displacement most often requires seed production and seedling emergence. Similarly, the ability of empirical studies focusing on reproductive life-stages to investigate climate-change impact or at least net consequences of climate change for population dynamics and persistence may be limited if reproduction plasticity to climate does not affect species ranges.

An interesting approach to circumvent the problems caused by ontogenetic niche shift is the use of structured population models (e.g. population matrix model, internal projection model, see Tuljapurkar & Caswell, 1997). Such models assess how each of the life stages contributes to the growth rate of populations and indicate whether a population is growing or shrinking in a given site. At the moment, structured population models studies covering entire species ranges or part of them, and questioning how climate affects growth rate along species climatic niches are still scarce (but see Stokes, Bullock & Watkinson, 2004, Souther & McGraw, 2011). The results of this thesis suggest that such models may be one of the most appropriate approaches to predict climate-change impacts on plant populations because they allow the assessment of how climate affects each life stage and how each life stage affects population growth rate in the different parts of species climatic niches.

### **The complexity of climate control**

The results of Papers II and III show how complex are reproductive responses to climate. The results of Paper II show that flowering performance was size- and climate-dependent for three out of the four species. However, the way climate and size affected flowering differed among species. For instance, indirect climate effects mediated through plant size were detected for *Veronica officinalis* only, climatically driven variation in minimum size for reproduction was



detected for *Viola biflora* only, and variations in reproductive investment with temperature was detected for *Veronica alpina* only (see Table 2, Paper II).

Seedling emergence responses to climate were more consistent across species (Paper III). However, while plastic responses to the sowing-site temperature and precipitation were detected for the two *Viola* species and *Veronica alpina*, *Veronica officinalis* seedling emergence was found to rank according to the temperature experienced by the seed-source populations, and to be pre-conditioned, or locally adapted, to the local climatic conditions (Table 2, Paper III).

The importance of these different climate effects on flowering performance (Mendez & Karlsson, 2004, Bonser & Aarssen, 2009) and seedling emergence (Roach & Wulff, 1987, Donohue *et al.*, 2010) are well known. Nevertheless, studies investigating climate effect on flowering while controlling for plant size are still scarce (but see Mendez & Karlsson, 2004, Pfeifer, Heinrich & Jetschke, 2006, Gimenez-Benavides, Escudero & Iriondo, 2007b, Milla *et al.*, 2009); and germination or seedling-emergence studies integrating the effects of both the climate of the the sowing sites and the seed-source populations are most often carried out in a controlled environment (e.g Schmuths *et al.*, 2006, Blodner *et al.*, 2007) (but see Gimenez-Benavides, Escudero & Iriondo, 2007a). This thesis stresses the importance of integrating a higher level of complexity in field studies assessing climate effects on reproductive life-stages because it shows that not accounting for plant size for flowering, or not accounting for the climatic conditions of the seed-source populations for seedling emergence, may lead to a biased or incomplete assessment of climate effects on reproduction.

### **Biotic interactions at the rear edge of alpine species**

The results of Paper I point to the high importance of biotic interactions for alpine species at their rear altitudinal edge. Accounting for potential interactions with the lowland flora improved the predictions of the landscape-scale distribution of both alpine species, although this was significant for *Viola biflora* only (Paper I). This is in line with earlier descriptive (ordination approach; Heegaard, 2002, Heegaard & Vandvik, 2004) and experimental (removal approach; Choler, Michalet & Callaway, 2001, Olofsson, 2004) studies and suggests that competition with lowland flora is an important factor partly shaping the rear altitudinal edge of alpine plants distributions. Furthermore, the importance of biotic interactions for alpine plants seems to be reflected in some of the results from Paper II. In particular, reproductive investment (allocation to reproduction) was found to decrease towards the warmest sites for *Veronica alpina* and towards the wettest sites for *Viola biflora*. Reducing

allocation to reproduction and thus increasing vegetative growth at these sites may allow the two species to increase their competitive abilities. For both species, these patterns fit the hypothesis of an increasing importance of biotic pressure as abiotic stress decreases: temperature for *Veronica alpina* and drought for *Viola biflora* (see Paper I).

In Paper I, the lowland species were chosen from among the dominant ones in grassland lowland habitats so that they would be representative of the lowland communities of the specific system. Here, we did not project the model in time because such predictions may be biased if species-specific responses to climate change result in a disruption of these lowland plant communities (e.g. Walther *et al.*, 2002, Williams & Jackson, 2007, Lenoir *et al.*, 2008). However, increasing competition between alpine and lowland species can be expected in the coming years. This is because climatically suitable areas for alpine species' range expansion may not be found at the upper altitudinal limits of species ranges (i.e. hard boundary). Thus, alpine species can be expected to concentrate towards the lower altitudinal limits of their range, where interactions with lowland species occur. The negative effect of competition from lowland species on alpine species' rear edge is therefore likely to be exacerbated in the coming years. This prediction stresses the importance of understanding plant-plant interactions to better forecast climate-change impacts. To do so, it is necessary to have empirical data describing which specific lowland species are problematic for target alpine plants (e.g. Choler, Michalet & Callaway, 2001, Pellissier *et al.*, 2010), what life history stages are more vulnerable to such competition processes, and what resources are alpine and lowland plants competing for.

In Paper I, I developed a method where abiotic and biotic models were combined to predict the two alpine species' ranges (abiotic + biotic model). This approach was designed to solve numerical issues caused by collinearity between climatic and biotic parameters. In addition, models were run using a more conventional approach. These models included both climatic and biotic parameters as covariates (covariate model). For the two alpine species, the best results were obtained with the combined modelling approach, while the covariate approach had worse accuracy than models including only climatic parameters for *Veronica alpina* and failed for *Viola biflora*. This methodological comparison shows that the abiotic + biotic modelling approach is robust and can be used to control for biotic interactions in other study cases. With empirical data, the method will also be able to project species range in time while accounting for biotic interactions. This may give us important information on the strength of species interactions in the coming years and thus allow for better climate change assessments and predictions.

## Further work and concluding remarks

The results of the papers included in this thesis highlight the complexity of climatic control on plants. Earlier in this synthesis, I suggested the structured population models as important tools that can incorporate greater complexity to better predict climate-change impacts on populations growth and spread (e.g. Jongejans, 2011). These tools can resolve problems caused by ontogenetic niche shifts, can include plant-size dependency for flowering, and can include reproduction responses to climate (see Childs *et al.*, 2004, Ellner & Rees, 2006). Still, two problems remain. First, such an approach may not be able to accurately predict in time the growth rate for locally adapted populations under changing climate. This is an important limitation because our results and earlier studies suggest that local adaptation may be an important driver of a species response to climate (Paper III, see Donohue *et al.*, 2010 for review). This issue could be resolved by transplanting locally adapted populations and assessing whether the populations can adapt fast enough to the new conditions. Second, collecting the data that are necessary to feed such models is excessively time consuming and can only be done for a limited number of populations during a single growing season (personal field observations). To be able to spatialise the output of such model, one would need a considerable number of populations experiencing a large range of climatic conditions. This is an important limitation because it questions the feasibility of the method. In my opinion, those aspects should not be ignored because they may constitute the next challenges for assessing climate impact on plant populations.

Dispersal is required for species range displacements. However, information on dispersal capacity are only available for a few species (see Walck *et al.*, 2011 for examples) and so far, most SDM-based studies assume unlimited dispersal capacity (but Engler *et al.*, 2009). Assessing seed production and seedling emergence plasticity to climate at the leading and rear edges of species ranges is a first step as it gives valuable information on species persistence and invasive ability at the rear and leading edge, respectively. Nevertheless, such information is of limited use if the dispersal capacity of the studied organisms does not allow the species to track their climate niches. I suggest that increasing knowledge on seed dispersal together with quantifying dispersal and recruitment rates is required to predict accurately climate change impacts on plant populations and potential range displacements.

The results of the three papers included in this thesis show species-specific responses to climate. The four studied species were not affected by the same climate variables, were not affected by the same biological possesses, and the responses to climate were also found to differ among the life stages of a single species. Such individualistic responses to climate

suggest drastic changes in plant communities in the coming years. Given the high importance of biotic interactions, increasing knowledge on species interactions and their effects will be an important step to understand and predict accurately the potential climate-change impacts. This is especially required for alpine species for which the lower altitudinal limit seems to be highly dependent on the presence and abundance of lowland competitors.

Individualistic species responses to climate also question our ability to generalise the effects of global warming on plant populations. Since the climatic controls of a given species may not relate to the climatic controls of another species, more effort should be given to key and/or endangered species that may have specific values for conservation.

### ***Acknowledgements***

Vigdis Vandvik and Olav Skarpaas provided helpful comments on the text and Cathy Jenks provided language corrections.

## References

- Auffret, A. G., Meineri, E., Bruun, H. H., Ejrnaes, R. & Graae, B. J. (2010) Ontogenetic niche shifts in three *Vaccinium* species on a sub-alpine mountain side. *Plant Ecology & Diversity*, **3**, 131-139.
- Bakkenes, M., Alkemade, J. R. M., Ihle, F., Leemans, R. & Latour, J. B. (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology*, **8**, 390-407.
- Blodner, C., Goebel, C., Feussner, I., Gatz, C. & Polle, A. (2007) Warm and cold parental reproductive environments affect seed properties, fitness, and cold responsiveness in *Arabidopsis thaliana* progenies. *Plant Cell and Environment*, **30**, 165-175.
- Bloor, J. M. G., Pichon, P., Falcimagne, R., Leadley, P. & Soussana, J. F. (2010) Effects of Warming, Summer Drought, and CO<sub>2</sub> Enrichment on Aboveground Biomass Production, Flowering Phenology, and Community Structure in an Upland Grassland Ecosystem. *Ecosystems*, **13**, 888-900.
- Bonser, S. P. & Aarssen, L. W. (2009) Interpreting reproductive allometry: Individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspectives in Plant Ecology Evolution and Systematics*, **11**, 31-40.
- Brown, J. H., Stevens, G. C. & Kaufman, D. M. (1996) The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597-623.
- Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D. & Cook, B. J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844-848.
- Childs, D. Z., Rees, M., Rose, K. E., Grubb, P. J. & Ellner, S. P. (2004) Evolution of size-dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 425-434.
- Choler, P., Michalet, R. & Callaway, R. M. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295-3308.
- Clark, J. S. (2003) Uncertainty in ecological inference and forecasting. *Ecology*, **84**, 1349-1350.

- De Frenne, P., Graae, B. J., Kolb, A., Brunet, J., Chabrerie, O., Cousins, S. A. O., Decocq, G., Dhondt, R., Diekmann, M., Eriksson, O., Heinken, T., Hermy, M., Jogar, U., Saguez, R., Shevtsova, A., Stanton, S., Zindel, R., Zobel, M. & Verheyen, K. (2010) Significant effects of temperature on the reproductive output of the forest herb *Anemone nemorosa* L. *Forest Ecology and Management*, **259**, 809-817.
- De Frenne, P., Kolb, A., Verheyen, K., Brunet, J., Chabrerie, O., Decocq, G., Diekmann, M., Eriksson, O., Heinken, T., Hermy, M., Jogar, U., Stanton, S., Quataert, P., Zindel, R., Zobel, M. & Graae, B. J. (2009) Unravelling the effects of temperature, latitude and local environment on the reproduction of forest herbs. *Global Ecology and Biogeography*, **18**, 641-651.
- De Valpine, P. & Harte, J. (2001) Plant responses to experimental warming in a montane meadow. *Ecology*, **82**, 637-648.
- Donohue, K. (2009) Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 1059-1074.
- Donohue, K., de Casas, R. R., Burghardt, L., Kovach, K. & Willis, C. G. (2010) Germination, Postgermination Adaptation, and Species Ecological Ranges. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41, **41**, 293-319.
- Elith, J. & Graham, C. H. (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66-77.
- Ellner, S. P. & Rees, M. (2006) Integral projection models for species with complex demography. *American Naturalist*, **167**, 410-428.
- Engler, R., Randin, C. F., Vittoz, P., Czaka, T., Beniston, M., Zimmermann, N. E. & Guisan, A. (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, **32**, 34-45.
- Eriksson, O. (2002) Ontogenetic niche shifts and their implications for recruitment in three clonal *Vaccinium* shrubs: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Vaccinium oxycoccus*. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **80**, 635-641.
- Fenner, M. & Thompson, K. (2005) *The Ecology of Seeds*. Cambridge University Press, Cambridge.
- Fremstad, E. (1997) Vegetasjonstyper i Norge. *NINA Temahefte*, **12**, 1-279.

- Gilman, S. E. (2006) The northern geographic range limit of the intertidal limpet *Collisella scabra*: a test of performance, recruitment, and temperature hypotheses. *Ecography*, **29**, 709-720.
- Gimenez-Benavides, L., Escudero, A. & Iriondo, J. M. (2007a) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of Botany*, **99**, 723-734.
- Gimenez-Benavides, L., Escudero, A. & Iriondo, J. M. (2007b) Reproductive limits of a late-flowering high-mountain Mediterranean plant along an elevational climate gradient. *New Phytologist*, **173**, 367-382.
- Gimenez-Benavides, L., Escudero, A. & Iriondo, J. M. (2008) What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. *Ecography*, **31**, 731-740.
- Graae, B. J., Alsos, I. G. & Ejrnaes, R. (2008) The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites *Plant Ecology*, **198**, 275-284.
- Graae, B. J., Ejrnaes, R., Lang, S. I., Meineri, E., Ibarra, P. T. & Bruun, H. H. (2011) Strong microsite control of seedling recruitment in tundra. *Oecologia*, **166**, 565-576.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.
- Hampe, A. & Petit, R. J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461-467.
- Hanssen-Bauer, I., Drange, H., Førland, E. J., Roald, L. A., Børsheim, K. Y., Hisdal, H., Lawrence, D., Nesje, A., Sandven, S., Sorteberg, A., Sundby, S., Vasskog, K. & Ådlandsvik, B. (2009) Klima i Norge 2100, Bakgrunnsmateriale til NOU Klimatilpassing. Norsk klimasenter, Oslo.
- Heegaard, E. (2002) A model of alpine species distribution in relation to snowmelt time and altitude. *Journal of Vegetation Science*, **13**, 493-504.
- Heegaard, E. & Vandvik, V. (2004) Climate change affects the outcome of competitive interactions - an application of principal response curves. *Oecologia*, **139**, 459-466.
- Higgins, S. I., Clark, J. S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J. M. V., Aguiar, M. R., Ribbens, E. & Lavorel, S. (2003) Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology*, **91**, 341-347.
- Huntley, B. (1991) How Plants Respond to Climate Change - Migration Rates, Individualism and the Consequences for Plant-Communities. *Annals of Botany*, **67**, 15-22.

- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. (eds R. K. Pachauri & A. Reisinger). IPCC, Geneva.
- Jongejans, E., Shea, K., Skarpaas, O., Kelly, D. & Ellner, S. P. (2011) Importance of individual and environmental variation for invasive species spread: a spatial integral projection model. *Ecology*, **92**, 86-97.
- Kardol, P., Campany, C. E., Souza, L., Norby, R. J., Weltzin, J. F. & Classen, A. T. (2010) Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology*, **16**, 2676-2687.
- Kawecki, T. J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225-1241.
- Kelly, A. E. & Goulden, M. L. (2008) Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11823-11826.
- Lawton, J. H. (1993) Range, Population Abundance and Conservation. *Trends in Ecology & Evolution*, **8**, 409-413.
- Lenoir, J., Gegout, J. C., Marquet, P. A., De Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768-1771.
- Lid, J. & Lid, D. T. (2005) *Norsk flora. Det norske samlaget*. Oslo.
- Mendez, M. & Karlsson, P. S. (2004) Between-population variation in size-dependent reproduction and reproductive allocation in *Pinguicula vulgaris* (Lentibulariaceae) and its environmental correlates. *Oikos*, **104**, 59-70.
- met.no (2009) Norwegian Meteorological Institute.
- Milbau, A., Graae, B. J., Shevtsova, A. & Nijs, I. (2009) Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany*, **104**, 287-296.
- Milla, R., Gimenez-Benavides, L., Escudero, A. & Reich, P. B. (2009) Intra- and interspecific performance in growth and reproduction increase with altitude: a case study with two *Saxifraga* species from northern Spain. *Functional Ecology*, **23**, 111-118.
- Mossberg, B. & Stenberg, L. (2007) *Gyldendals store nordiske flora, revidert og utvidet utgave*. Gyldendal.
- Muller, S. D. & Richard, P. J. H. (2001) Post-glacial vegetation migration in conterminous Montreal lowlands, southern Quebec. *Journal of Biogeography*, **28**, 1169-1193.



- Obeso, J. R. (2002) The costs of reproduction in plants. *New Phytologist*, **155**, 321-348.
- Ohlson, M. (1988) Size-dependent reproductive effort in 3 populations of *Saxifraga-hirculus* in Sweden. *Journal of Ecology*, **76**, 1007-1016.
- Olofsson, J. (2004) Positive and negative plant-plant interactions in two contrasting arctic-alpine plant communities. *Arctic, Antarctic, and Alpine Research*, **36**, 464-467.
- Pearson, R. G., Thuiller, W., Araujo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T. P. & Lees, D. C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704-1711.
- Pellissier, L., Brathen, K. A., Pottier, J., Randin, C., Vittoz, P., Dubuis, A., Yoccoz, N. G., Alm, T., Zimmerman, N. E. & Guisan, A. (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography*, **33**, 1004-1014.
- Pfeifer, M., Heinrich, W. & Jetschke, G. (2006) Climate, size and flowering history determine flowering pattern of an orchid. *Botanical Journal of the Linnean Society*, **151**, 511-526.
- Pfeifer, M., Wiegand, K., Heinrich, W. & Jetschke, G. (2006) Long-term demographic fluctuations in an orchid species driven by weather: implications for conservation planning. *Journal of Applied Ecology*, **43**, 313-324.
- Pitelka, L. F., Gardner, R. H., Ash, J., Berry, S., Gitay, H., Noble, I. R., Saunders, A., Bradshaw, R. H. W., Brubaker, L., Clark, J. S., Davis, M. B., Sugita, S., Dyer, J. M., Hengeveld, R., Hope, G., Huntley, B., King, G. A., Lavorel, S., Mack, R. N., Malanson, G. P., McGlone, M., Prentice, I. C. & Rejmanek, M. (1997) Plant migration and climate change. *American Scientist*, **85**, 464-473.
- Roach, D. A. & Wulff, R. D. (1987) Maternal Effects in Plants. *Annual Review of Ecology and Systematics*, **18**, 209-235.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57-60.
- Schmuths, H., Bachmann, K., Weber, W. E., Horres, R. & Hoffmann, M. H. (2006) Effects of preconditioning and temperature during germination of 73 natural accessions of *Arabidopsis thaliana*. *Annals of Botany*, **97**, 623-634.
- Shevtsova, A., Graae, B. J., Jochum, T., Milbau, A., Kockelbergh, F., Beyens, L. & Nijs, I. (2009) Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology*, **15**, 2662-2680.

- Souther, S. & McGraw, J. B. (2011) Evidence of Local Adaptation in the Demographic Response of American Ginseng to Interannual Temperature Variation. *Conservation Biology*, **25**, 922-931.
- Stokes, K. E., Bullock, J. M. & Watkinson, A. R. (2004) Population dynamics across a parapatric range boundary: *Ulex gallii* and *Ulex minor*. *Journal of Ecology*, **92**, 142-155.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L. & Williams, S. E. (2004) Extinction risk from climate change. *Nature*, **427**, 145-148.
- Thompson, K. & Ceriani, R. M. (2003) No relationship between range size and germination niche width in the UK herbaceous flora. *Functional Ecology*, **17**, 335-339.
- Thuiller, W., Albert, C., Araujo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Guy, F. M., Paterson, J., Schurr, F. M., Sykes, M. T. & Zimmermann, N. E. (2008) Predicting global impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137-152.
- Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T. & Prentice, I. C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences, USA*, **102**, 8245-8250.
- Tuljapurkar, S. & Caswell, H. (1997) *Structured-population models in marine, terrestrial, and freshwater systems*. Chapman and Hal.
- Tveito, O. E., Bjordal, I., Skjelvag, A. O. & Aune, B. (2005) A GIS-based agro-ecological decision system based on gridded climatology. *Meteorological Applications*, **12**, 57-68.
- Tveito, O. E., Førland, E. J., Heino, R., Hanssen-Bauer, I., Alexandersson, H., Dalström, B., Drebs, A., Kern-Hansen, C., Jónsson, T., Vaarby Laursen, E. & Westman, Y. (2000) Nordic temperature maps. No. 09/00. *DNMI-klima*.
- Tveito, O. E., Førland, E. J., Heino, R., Hanssen-Bauer, I., Alexandersson, H., Dalström, B., Drebs, A., Kern-Hansen, C., Jónsson, T., Vaarby Laursen, E. & Westman, Y. (2001) Nordic temperature maps. No. 06/01. *DNMI-klima*.
- Vandvik, V. & Vange, V. (2003) Germination ecology of the clonal herb *Knautia arvensis*: Regeneration strategy and geographic variation. *Journal of Vegetation Science*, **14**, 591-600.

- Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K. & Poschlod, P. (2011) Climate change and plant regeneration from seed. *Global Change Biology*, **17**, 2145-2161.
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389-395.
- Welham, C. V. J. & Setter, R. A. (1998) Comparison of size-dependent reproductive effort in two dandelion (*Taraxacum officinale*) populations. *Canadian Journal of Botany-Revue Canadienne De Botanique*, **76**, 166-173.
- Williams, J. W. & Jackson, S. T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, **5**, 475-482.
- Zavaleta, E. S., Shaw, M. R., Chiariello, N. R., Thomas, B. D., Cleland, E. E., Field, C. B. & Mooney, H. A. (2003) Grassland responses to three years of elevated temperature, CO<sub>2</sub>, precipitation, and N deposition. *Ecological Monographs*, **73**, 585-604.