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Direct and indirect effects of climate change on alpine plant community diversity: the abiotic environment modifies species interactions

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Preface

This thesis is carried out at the Department of Ecology and Natural Resource Management (INA), Norwegian University of Life Sciences. The Norwegian Research Council provided financial support as a part of the programme 'Biologisk mangfold', The Norwegian Polar Institute provided support for the fieldwork in Svalbard, and INA financed some of the soil analyses.

My major thanks are to Ørjan Totland, who gave me the opportunity to work on this project, and who has supervised me through all stages with impressing enthusiasm, optimism, and efficiency. Always open for a dialogue, the working together has for me been inspiring and instructive.

Thanks also to all colleagues at INA who have been giving professional and social support. Ole Wiggo Røstad has been helpful with various kinds of computer challenges. Thanks to Erika Leslie and Harald Steen at Finse research station for all technical support and for their hospitality during five field seasons. I am indebted to Vibeke Arnesen, Ingunn Heggstad, and Jorunn Nyléhn, for field assistance, and to Wenche Eide, Francois Chalopin, and all the other students and researchers at the research station for all support, company and inspiration through long field seasons. I thank Einar Heegard and Jon-Arvid Grytnes for statistical advices, and Einar for helping with identifications of bryophytes.

Finally, I am grateful to my friends, family, and in particular Anne, for always being there, supporting me, and for reminding me of other aspects of life than work.

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PAPERS

LIST OF PAPERS

The thesis consists of the following papers, which will be referred to by their Roman numerals.

I. Klanderud K. and Totland Ø. 2004. Habitat dependent nurse effects of the dwarf shrub *Dryas octopetala* on alpine and arctic plant community structure. Ecoscience 11: 410-420.

II. Klanderud K. 2005. Climate change effects on species interactions in an alpine plant community. Journal of Ecology 93: 127-137.

III. Klanderud K. and Totland Ø. 2005. The relative importance of vegetation cover and abiotic environmental conditions for population dynamic parameters of two alpine plant species. Journal of Ecology: In press.

IV. Klanderud K. and Totland Ø. Simulated climate change altered dominance hierarchies and plant community diversity in an alpine biodiversity-hotspot. Ecology: In press.

V. Klanderud K. and Totland Ø. Invasibility, propagule availability and diversity of an alpine plant community under simulated climate change. Manuscript.

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ABSTRACT

Climate change is predicted to have large impacts on alpine ecosystem dynamics and diversity. However, little is yet known about which factors determine alpine plant community diversity and indeed, how alpine plant communities may respond to climate change. Climate change may affect plant community diversity through direct effects on individual species or through indirect effects by altering the dominance relationship among species and thus change the outcome of species interactions. One species that may have positive or negative effects on the performance of other species is *Dryas octopetala,* a dwarf shrub that is highly abundant in alpine and arctic *Dryas* heaths throughout the northern hemisphere. This thesis examines (1) which effects *Dryas* has on the population dynamics of other species, (2) how biotic impacts from *Dryas* and dispersal limitations of other species may determine local diversity, (3) how climate change may affect (1) and (2), and (4) how climate change may affect *Dryas* heath diversity. The main study site is Sandalsnuten (1550 m elevation) at Finse in the western part of Hardangervidda, southern Norway.

The results suggest that the role of *Dryas* on community structure and diversity may shift between habitats of contrasting environmental conditions. *Dryas* functioned as a nurse plant for some species in the high arctic Svalbard, but was mainly a competitor that reduced species diversity at alpine Finse. This supports the hypothesis of a shift from facilitative to competitive effects of neighbours along gradients of decreasing environmental severity. Removal manipulations in the *Dryas* heath at Finse showed that *Dryas* both protected other species from low temperatures, and at the same time competed for nutrients. Furthermore, interactions between the removal treatment and the environmental factors (warming and nutrients) suggested an increased role of competition from *Dryas* under climate change. However, an up-scaling of the simulated climate change from population- to community-level, showed that four years of nutrient addition and warming combined with nutrient addition, increased the abundances of graminoids and forbs at the expense of *Dryas*. Moreover, community diversity decreased dramatically, primarily due to losses of bryophytes and lichens, most likely because of the changes in dominance hierarchies from low-stature *Dryas* heaths to meadows of tall graminoids and forbs, which increased competition for light and space considerably.

Results from a propagule addition experiment showed that colonization and diversity of the *Dryas* heaths are strongly limited by both the dispersal abilities of the regional species and interspecific competition from *Dryas* and other species already established in the community. Experimental warming had only minor short-term effects on the colonization and diversity of the *Dryas* heaths. However, higher establishment frequency, increased colonization of bare soils, and increased competition from established plants on emerging seedlings under experimental warming, suggests that climate change effects on recruitment and on community-level interactions, may affect the long-term colonization processes and diversity of alpine plant communities.

This thesis shows that the *indirect* effects of climate change, such as changes in the biotic environment caused by changes in the abiotic environment, may be more important for alpine plant community structure and diversity than the *direct* effects of changed temperature and nutrient availability. Moreover, it highlights the importance of including species interactions in climate change experiments and models if we are to predict plant community responses to climate change with greater precision.

SAMMENDRAG

Det antas at klimaendringer vil ha store innvirkninger på samfunnsdynamikk og artsmangfold i alpine økosystemer. Likevel vet vi fortsatt lite om hvilke faktorer som regulerer artsmangfoldet i fjellet, og om hvordan alpine plantesamfunn vil respondere på

klimaendringer. Klimaendringer kan påvirke artsmangfoldet i et plantesamfunn ved *direkte* å påvirke enkeltarter og *indirekte* ved å endre dominansforholdet mellom arter, og dermed endre utfallet av samspillet mellom artene. En art som kan påvirke andre arter positivt eller negativt er reinrose (*Dryas octopetala*), en dvergbusk som er svært utbredt i alpine og arktiske områder. Denne avhandlingen studerer: (1) hvilke effekter reinrose har på andre arters populasjonsdynamikk, (2) hvordan biotiske effekter av reinrose og andre arters spredningsbegrensninger bestemmer lokalt artsmangfold, (3) hvordan klimaendringer vil påvirke (1) og (2), og (4) hvordan klimaendringer vil påvirke artsmangfoldet i reinroseheiene. Studieområdet er Sandalsnuten (1550 m.o.h.) på Finse, Hardangervidda, Sør-Norge.

Resultatene viser at reinrosens påvirkning av samfunnsstruktur og artsmangfold kan skifte mellom habitat av ulike abiotisk miljøforhold. Reinrose fungerte som beskyttelse for enkelte arter på Svalbard, mens den virket mer som en konkurrent på Finse, der den førte til redusert artsmangfold. Disse resultatene støtter hypotesen om at betydningen av fasilitering i forhold til konkurranse kan øke langs en gradient av tiltagende abiotisk stress.

Eksperimenter på Finse der reinrose ble fjernet, viste at reinrose både beskytter andre arter mot lave temperaturer, og samtidig konkurrerer om næring. Videre viser interaksjoner mellom reinrose-fjerning og de abiotiske miljøfaktorene (temperatur og næring) at konkurranse fra reinrose kan forsterkes dersom temperatur og næringstilgang øker i framtiden. Likevel, en oppskalering av simulerte klimaendringer fra populasjons- til samfunnsnivå, viser at økt næringstilgang, og høyere temperaturer, kombinert med økt næring økte forekomsten av graminoider (gress og starr) og urter på bekostning av reinrose. Samtidig minket artsmangfoldet dramatisk, mest på grunn av tap av moser og lav, fordi endringer i dominanshierarkiet, fra reinroseheier med lavtvoksende vegetasjon til enger av høye graminoider og urter, sannsynligvis førte til intensivert konkurranse om lys og tilgjengelige voksesteder.

Resultater fra eksperimentell utsåing av regionale arter viser at artsmangfoldet i reinroseheiene er regulert både av en begrenset spredningsevne til de regionale artene og av interspesifikk konkurranse fra reinrose og andre etablerte arter i reinrosesamfunnet, spesielt graminoider. En generelt høyere etableringsfrekvens, økt kolonisering av bar jord, og en sterkere konkurranse fra etablerte arter mot nye frøplanter under eksperimentell oppvarming, viser at effekter av klimaendringer på rekrutteringsprosesser, og på samspillet mellom arter i reinroseheiene, kan endre koloniseringsprosesser og artsmangfold i alpine plantesamfunn over et lengre tidsperspektiv.

Denne avhandlingen viser at endringer i det biotiske miljø, forårsaket av endringer i det abiotiske miljø, kan ha større betydning for alpine plantesamfunnsstrukturer og artsmangfold enn de direkte effektene av økt temperatur og næringstilgang. Videre viser resultatene at samspillet mellom arter må inkluderes i eksperimenter og modeller på klimaeffekter for at vi med bedre presisjon skal kunne forutsi hvordan plantesamfunn vil respondere på global oppvarming.

SYNOPSIS

How can climate change affect alpine plant community diversity?

Alpine and arctic ecosystems are predicted to be particularly vulnerable to climate change because they are believed to be largely controlled by climatic constraints and many species occur close to their climatic limits of survival (e.g. Mitchell et al. 1992, Maxwell 1992, Callaghan and Jonasson 1995, Guisan et al. 1995, Körner 1995, 1999). Moreover, many mountain plants are intolerant to competition (e.g. Dahl 1998). Thus, although the predicted changes in the abiotic environment (IPCC 2001) are thought to impose large *direct* effects on alpine plants, associated changes in the biotic environment may have even greater *indirect* effects on the performance of individual plant species, and secondary on the species composition, dynamics, and diversity of plant communities (e.g. Mooney 1991, Kingsolver 1993, Grabherr et al. 1995, Gottfried et al. 1998), and potentially on ecosystem processes, such as CO_2 fluxes (e.g. Shaver and Jonasson 1999). Previous climate change experiments have primarily studied the direct effects of abiotic environmental changes on individual plant species, and have found that the growth and reproduction of most alpine and arctic plants increase in response to increased temperature (Arft *et al*. 1999) and/or nutrient availability (Dormann and Woodin 2002). However, the responses to simulated climate change are not similar among species, suggesting that some species may benefit more than others to the direct changes in the abiotic environment. Because species respond with different speed and amplitude to abiotic environmental changes, the biotic environment experienced by most species in a community, such as biomass and canopy height, may also be altered. These indirect effects of climate change form the basic premises of this thesis.

The relative importance of the biotic and abiotic factors on community dynamics in any ecosystem (Huston and McBride 2002), or in low productive habitats of high abiotic stress, in particular (e.g. Hobbie et al. 1999) is far from clear. The traditional view has been that species interactions have less impact on community structure in areas of high abiotic stress because the physical environment is the main constrictor of plant growth here (e.g. Savile 1960, Billings and Mooney 1968, Grime 1977). Some ecologists have, however, predicted a great role of competition in these habitats because resource availability is particularly low here (e.g. Chapin and Shaver 1985, Tilman 1988), whereas others have claimed that the role of facilitation may be more important than competition because neighbour vegetation may improve the survival potential for individual plants (e.g. Callaghan and Emanuelson 1985, Bertness and Callaway 1994). Removal experiments are needed to demonstrate the relative role of abiotic and biotic factors, and the relative role of facilitation and competition on community structure. Only a few removal studies are done in cool habitats, and with conflicting results (see Hobbie et al. 1999, Bret-Harte et al. 2004, Dormann et al. 2004). Furthermore, even though species interactions may directly affect community structure, and may be modified by climate change, these effects are largely ignored in climate change experiments (but see Shevtsova et al. 1997, Hobbie et al. 1999, Bret-Harte et al. 2004, Dormann et al. 2004) and in models predicting responses to climate change (Mooney 1991, Pacala and Hurtt 1993, Davies et al. 1998).

The most prevalent species in a community may strongly influence the biotic conditions experienced by other species and is often an important driver of ecosystem function and community dynamics (Grime 1998). The dwarf shrub *Dryas octopetala* L. is a circumpolar species that may be highly abundant in alpine, subarctic, and arctic plant communities (Hultén 1959), with the alpine *Dryas* heaths characterised as biodiversity hot-spots compared to other alpine plant communities in northern Europe.

Climate change is predicted to be the most important driver of biodiversity change in alpine habitats (Sala et al. 2000). Moreover, an upward migration of species caused by climate change may decrease the abundances of locally rare and competitively weak species due to increased competition from the invaders (Grabherr et al. 1995, Gottfried et al. 1999, Klanderud and Birks 2003). Little is, however, known about which factors that determine alpine community diversity and how climate change may affect colonization processes and diversity. Moreover, climate change effects on plant community dynamics, as this project focus upon, is little studied. By better understand the interactions among species, and how these interactions may be modified under climate change, this may be better able to forecast how climate change will affect alpine plant community diversity.

Aims of this thesis

The main aim of this thesis is to examine how climate change may affect the diversity of *Dryas* heaths in alpine Norway. To answer this I examine:

1. The role of *Dryas* on community structure and if the role of *Dryas* may differ between contrasting environmental conditions (Paper I).
2. If *Dryas* affect population dynamics of other species (Paper II) and if this effect differs from the impacts of other neighbour species in the *Dryas* heath (Paper III).
3. The relative importance of dispersal limitations and local interactions on colonization and diversity of the *Dryas* heath (Paper V).
4. How climate change will affect (2) and (3) (Paper II, III, V).
5. How four years of simulated climate change affect *Dryas* heath diversity (Paper IV).

Material and methods

Study system

The main part of this project was conducted in a *Dryas octopetala* heath at ca 1550 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda in alpine southwest Norway (60° 36’ N, 7° 31’ E). Sandalsnuten is an exposed ridge, where the snow normally disappears in late May/early June. Mean summer (June, July, August) temperatures at 1222 m elevation at Finse is 6.3 °C (Aune 1993), and mean summer precipitation is 89 mm (Førland 1993). The study was conducted on the south exposed slope of Sandalsnuten.

Dryas octopetala is a ‘wintergreen’ (Welker et al. 1997) dwarf shrub in the Rosaceae familiy, and is highly abundant in *Dryas* heath communities throughout the northern hemisphere (Hultén 1959). It grows as dense compressed clones, which cover *c.* 35 % of the ground at Sandalsnuten (Paper I). The alpine *Dryas* heaths are associated with basic bedrocks, and are therefore particular species rich compared to other alpine plant communities in northern Europe. The relatively simple vegetation structure, with few and compressed vegetation layers, the presence of a high-abundant species, the high species diversity, and the predictions of large climate change effects on alpine species composition and diversity, make the alpine *Dryas* heaths an ideal arena to test questions related to species interactions and climate change.

This study has been part of the International Tundra Experiment (ITEX, http://www.itex-science.net), a research initiative that focuses on the possible effects of climate change on arctic and alpine plants and ecosystems. ITEX is organised within the International Geosphere Biosphere program (IGBP under the section Global Change and Terrestrial Ecosystems (GCTE). At present there are 10-15 active ITEX sites established world-wide in arctic and alpine areas in ten countries. (ITEX; see Global Change Biology, 1997, volume 3, supplement 1, and Arft et al. 1999).

Field methods

An optimal way to study the outcome of biotic interactions on plant communities under changing environmental conditions is to combine studies along natural gradients of environmental change with experimental manipulations. The results in this thesis are based on experimental manipulations, except Paper I, which is a comparative description of vegetation structure inside and outside *Dryas* mats in habitats of contrasting abiotic stress. Observations of how the vegetation structure associated with *Dryas* differ with changing environmental conditions across spatial scales, may reflect how this relationship will change under changed environmental conditions over temporal scales. Natural gradients may represent natural experiments where vegetation had time to adjust to environmental changes (Körner 1999), and may therefore be useful in creating hypothesis (Paper I) that can be tested through experimental manipulations (Paper II-IV).

Open top chambers (OTCs, Fig. 1) were used to experimentally increase summer temperature over experimental plots (Paper II-V). On average, summer air temperature increased by 1.5-2.0 °C, which corresponds with the predicted increase of ca 1.5 °C in summer temperature over the next 75 years in southern Norway (IPCC 2001). The OTCs consist of six *c*. 40 cm high polycarbonate walls with qualities as described in Marion et al. (1997). There may be side-effects of the OTCs, such as reduced wind speed (personal observation), decreased pollination visitation rates to flowers (Totland and Eide 1999), and obstacles to seed dispersal (although to my knowledge not reported), but the OTCs have minor effects on atmospheric gas concentrations and ambient precipitation, and are commonly used in climate change experiments (Hollister and Webber 2000).

Warmer soils due to climate warming are predicted to increase the mobilization of soil nutrients and thus increase nutrient availability for plants in alpine and arctic habitats (e.g. Harte et al. 1995). Furthermore, the deposition of atmospheric nitrogen is predicted to fertilize alpine and arctic tundra. The magnitude of the predicted changes in available nitrogen for alpine plants is, however, unclear. Nutrient availability was manipulated by adding fertilizer (Paper II-IV), and to facilitate comparison of responses across habitats similar amounts were used (*c*. 10 mg N/m^2/year) as used in other climate change experiments (Chapin et al. 1995, Press et al. 1998, Shaver and Jonasson 1999). These amounts may be higher than what is realistic to expect as results of soil warming and anthropogenic nitrogen deposition. However, because the study site is situated on a slope and in an area with large rainfall and with a stony and well-drained soil, there was a risk that much of the nutrients would be washed away from experimental plots. Thus, these amounts were chosen to ensure that, if there were any responses to changes in nutrient availability in this system, this would be able to detect them over a relatively short time-span.

Many alpine plants are clonal, and the OTC-, nutrient-, and removal treatments conducted in the experiments may affect only some parts of a target individual, leaving other components of the individual unmanipulated. This may have dampened some of the treatment responses. However, the relatively distinct responses of most of the manipulations suggest that this was not a major problem in this study.

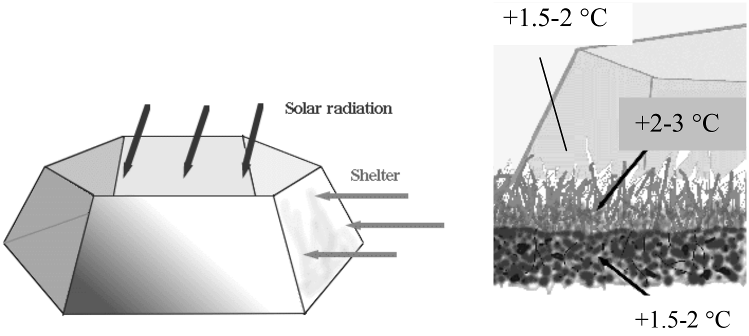

Fig 1. Open top chamber used to increase summer temperature at Finse. Approximate increases in air (*c*. 5 cm above ground), ground, and soil (*c*. 5 cm below ground) temperature across three experimental set-ups and during different time periods are shown. Drawing modified after Ulf Molau.

Results and discussion

Species interactions in alpine and arctic plant communities

This thesis highlights the ecological importance of species interactions in low productive habitats of high abiotic stress (e.g. Callaghan and Emanuelson 1985, Chapin and Shaver 1985, Tilman 1988, Bertness and Callaway 1994). Indeed, this show that that plant-plant interactions may be important determinants of plant population dynamics (Paper II-III), community structure (Paper I, IV), colonization processes (Paper V), and diversity (Paper IV-V) in the alpine region. Moreover, results from two removal experiments (Paper II-III) and one sowing experiment (Paper V) show that species interactions may be more important for plant population dynamics, and community invasibility and diversity than the abiotic environment. This is in sharp contrast to the traditional view claiming that physical factors are the main controllers of species composition and dynamics in environmentally harsh habitats (e.g. Savile 1960, Billings and Mooney 1968, Grime 1977). However, these results are in line with a growing number of studies from sub-alpine (e.g. Callaway 1998, Kikvidze et al. 2001, Totland and Esaete 2002), alpine (e.g. Choler et al. 2001, Callaway 2002), sub-arctic (Shevtsova 1995, 1997), and arctic (Dormann et al. 2004) communities, showing that biotic interactions affect plant growth and community dynamics in these systems, although several authors report few effects of species interactions in the arctic (see Hobbie et al. 1999 and references therein, Callaway et al. 2002, Bret-Harte et al. 2004).

The comparisons of species composition and diversity inside and outside *Dryas octopetala* mats in the high arctic Svalbard and at alpine Finse (Paper I), suggested that the role of *Dryas* shifted from being a nurse plant, at least for some species, in habitats of high abiotic stress, to a stronger competitive role under more benign environmental conditions. This supports the hypothesis of a shift from facilitative to competitive effects of neighbours along gradients of decreasing environmental severity (e.g. Callaghan and Emanuelson 1985, Bertness and Callaway 1994, Choler et al. 2001). Thus, based on these results I predict that the current relationship between effects of facilitation and competition in alpine plant communities may shift under global warming (see also Callaway et al. 2002, Paper I).

Removal experiments in the *Dryas* heaths at Finse showed that *Dryas* (Paper II) and other species (Paper III) protected neighbours from stressful low temperatures at Finse, but at the same time there was interspecific competition for nutrients. Furthermore, a larger effect of the *Dryas* removal (Paper II) than of the removal of the general neighbour vegetation (Paper III) on the population dynamic parameters of two abundant species in the *Dryas* heath (*Thalictrum alpinum* L. and *Carex vaginata* Tausch.), suggest that one highly abundant species may have larger effects on the population dynamics of other species than the combined net effect of all the other species in the community (Paper III).

Climate change effects on species interactions

Four years of simulated climate change in the *Dryas* heaths at Finse showed that the biotic changes caused by the changes in the abiotic environment might be more important for community structure and diversity than the direct effects of warming and nutrient addition (Paper IV). Both temperature and nutrient conditions limited plant growth in the *Dryas* heaths at Finse, with the largest effects of nutrients, or of synergistic effects of warming and nutrients (Paper II, III, IV). Experimental warming alone had only minor effect on the population dynamics of *Thalictrum alpinum* and *Carex vaginata* (Paper II-III), community diversity (Paper IV), and colonization processes (Paper V), which is in line with climate change experiments from the arctic, where nutrients are found to be the major limiting factor for plant growth (e.g. Chapin and Shaver 1985, Chapin et al. 1995, Robinson et al. 1998, Shaver and Jonasson 1999, Dormann and Woodin 2002). However, see Klein et al. (2004) for negative effects of experimental warming on species richness on the Tibetan Plateau.

Interactions between neighbour removal (*Dryas* Paper II; other species, Paper III) and the manipulated warming and nutrient addition on the population dynamic parameters of *Thalictrum* and *Carex*, showed that environmental change may alter the outcome of species interactions. Indeed, the effects of climate change simulations on these interactions suggested that the role of competition, in particular from *Dryas,* may be more important under climate change (Paper II-III). When the climate change simulations were conducted on a community-scale (Paper IV), *Dryas* maintained dominance in the control plots and in plots with only warming. Under increased nutrient availability on the other hand, graminoids and forbs increased their abundances at the expense of *Dryas,* suggesting that these functional groups may be stronger competitors than *Dryas.* A shift in dominance hierarchies from heaths previously dominated by the low-stature *Dryas* to meadows dominated by tall graminoids and forbs after four years of warming combined with nutrient addition, likely altered the biotic interactions towards an increased role of competition for light and space. This change in competition hierarchy resulted in a dramatic decrease in community diversity, primarily due to losses and decreased abundances of bryophytes and lichens (Paper IV).

Changes in nutrient regimes caused by higher soil temperature and increased nitrogen mineralization are predicted to increase the role of species interactions, which may result in altered competition hierarchies in alpine and arctic plant communities (Chapin et al. 1995, Shaver and Jonassen 1999, Dormann and Woodin 2002, Gough et al. 2002). This study is the first to demonstrate the combined effects of warming and nutrient addition in an alpine plant community (but see Theodose and Bowman 1997 for nutrient treatment, and Klein et al. 2004 for warming and grazing:).

Colonization and diversity of alpine plant communities

The results of an experimental addition of propagules of 27 regional species into the *Dryas* heath showed that both dispersal limitations of the regional species and community-level interactions control the diversity of the alpine *Dryas* heaths (Paper V). This is in line with results obtained from various temperate terrestrial and aquatic habitats (see Tilman 1997 and references therein), and supports the hypothesis that propagule availability is an important determinant of local diversity (e.g. Taylor et al. 1990, Cornell and Lawton 1992, Eriksson 1993). This study is, however, the first to verify this hypothesis for an alpine plant community. Indeed, propagule availability and competition from *Dryas* and other species established in the community (in particular graminoids), had a greater role on colonization processes and diversity than the availability of safe germination sites, facilitation, and simulated warming. These results from the alpine are in sharp contrast to results from a study in the high arctic, where Cooper et al. (2004) suggested that the availability of safe germination sites with protecting vegetation was more important for recruitment to the *Dryas* heaths than the lack of seeds. Thus, the processes that control colonization and diversity may vary between alpine and arctic sites, with higher importance of safe microsites and facilitation for species recruitment under more extreme climatic conditions in the arctic (Coulson et al. 1993, Eriksson & Fröborg 1996).

The highly significant increase in community diversity after the propagule addition shows that, despite the relatively high diversity, the *Dryas* heaths are not saturated with species. Thus, vacant sites occur that may be colonized if dispersal limitations of species are overcome (Paper V).

Dryas *heath diversity under climate change*

Germination, seedling survival and establishment success may increase for some local and regional species if summer temperature increase in the future (Paper V). However, the strongly limited dispersal abilities of the regional species, and the small effect of climate warming on colonization processes and diversity, suggest that global warming alone may not increase the invasion of new species into the *Dryas* heaths, at least not in the short term (Paper V). If dispersal limitations are overcome, on the other hand, vacant patches in the *Dryas* heath may be colonized, resulting in a denser vegetation cover. However, an increased role of competition from established vascular species, in particular graminoids, on emerging seedlings under experimental warming (Paper V), suggests that climate change effects on species interactions may affect long-term colonization processes and diversity of alpine plant communities. Recent uphill migration of species on European mountains has been explained by recent climate change (e.g. Grabherr et al. 1994, Kullmann 2002, Klanderud and Birks 2003), whereas four years of experimental warming had only minor effects on the establishment success of potential invading species at Finse (Paper V). This may suggest that climate is an important driver of species migration along elevation gradients on large temporal and spatial scales, whereas over shorter time scales and smaller spatial scales, on the other hand, local interactions and the lack of propagules limit the colonization processes. Four years of climate change simulations showed that if soil warming and/or nitrogen deposition enhance nutrient availability for alpine plants, the currently high *Dryas* heath diversity may be reduced by increased competition from nitrophilous graminoids and forbs (Paper IV). Decreases in *Dryas* cover with increased nutrient availability and increased abundances of graminoids (McGraw 1985, Fox 1992, Paper IV), suggest that *Dryas* may be a stress tolerator more than a competitor. The current dominance of *Dryas* on exposed ridges with basic bedrock and low nitrogen levels in the soil is likely depending on the lack of competition from more nitrophilous species. Thus, in spite of harsh environmental conditions, such as extreme wind and thin snow cover, graminoid and forb species may increase their abundances at the expense of both *Dryas* and several other species if nutrient limitation is overcome, resulting in a decline in species diversity and a shift in species composition.

Concluding remarks

This thesis shows that interspecific competition may be more important for community structure and dynamics than previously predicted for alpine systems. Furthermore, it underlines that processes controlling community diversity may differ between alpine and arctic habitats, with higher importance of physical factors and facilitation in the climatically more extreme arctic. This thesis also highlights the difficulties of extrapolating climate change responses of individual species or populations to the community-level because the complexity of ecological interactions, such as positive and negative effects of neighbours, may be modified under environmental change and thus affect the whole community. Moreover, biotic interactions and their responses to environmental changes may alter the direct effects of changes in the abiotic conditions. Climate change may increase the role of competition in alpine plant communities, which may reduce species diversity dramatically. Indeed, this thesis suggests that changes in biotic interactions caused by climate change may be more important for community composition and diversity than the direct effects of changes in temperature and nutrient conditions. These results emphasize that species interactions must be considered in climate change experiments and in models predicting climate change effects in order to predict future responses to global warming with greater precision.

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Paper I

ÉCOSCIENCE
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Habitat dependent nurse effects of the dwarf-shrub *Dryas octopetala* on alpine and arctic plant community structure[1]

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Abstract: Some species may increase community diversity by modifying the local environment for co-occurring species. This is most common in habitats of high abiotic stress. To explore whether the mat-forming dwarf shrub *Dryas octopetala* functions as a nurse plant in alpine and arctic plant communities of contrasting but generally stressful environmental conditions, we measured species diversity, richness, cover, and composition of different functional groups (vascular plants, bryophytes, and lichens) inside and outside *Dryas* mats at sites differing in environmental severity at Finse, alpine Norway, and in arctic Svalbard. *Dryas* appears to function as a nurse plant primarily for bryophytes, and mainly at the most severe sites in Svalbard. At the more benign sites at Finse, total diversity (Shannon's index) and richness, and richness of all functional groups, were lower inside *Dryas* than outside, suggesting that *Dryas* has no nurse plant function on diversity parameters there. Species composition, however, differed inside and outside *Dryas* in all the communities, due to both presence/absence and abundance differences at Finse, and primarily due to differences in species abundances in Svalbard. This may suggest that *Dryas* functions as a nurse plant for individual species of all of the three functional groups in all the communities, even if competitive impacts of *Dryas* may overrule the positive effects on a whole-community level. Finally, our results show that *Dryas* may shift from being a nurse plant to being a competitor when its cover increases, but only under relatively low abiotic stress.

Keywords: competition, facilitation, functional groups, Norway, species composition, species diversity.

Résumé : Certaines espèces peuvent accroître la diversité des communautés en modifiant l'environnement local des espèces voisines. Ce phénomène est commun surtout dans les habitats où les stress d'origine abiotique sont élevés. Nous avons voulu vérifier si le *Dryas octopetala*, un arbuste nain qui forme des tapis, agit en tant que plante compagne dans des communautés alpines et arctiques où les conditions environnementales sont contrastées et en général stressantes. Nous avons mesuré la diversité en espèces, la richesse, le recouvrement et la composition des groupes fonctionnels (plantes vasculaires, bryophytes et lichens) se trouvant à l'intérieur et à l'extérieur des tapis de *Dryas* dans plusieurs sites où la sévérité des conditions environnementales est variable. L'étude s'est déroulée à Finse, dans une zone alpine de la Norvège, et dans l'archipel de Svalbard, dans l'Arctique. Le *Dryas* servirait de plante compagne surtout pour les bryophytes et essentiellement dans les sites aux conditions environnementales les plus sévères de l'archipel de Svalbard. Aux sites plus cléments de Finse, la diversité totale (indice de Shannon) et la richesse, ainsi que la richesse de tous les groupes fonctionnels, sont moins élevées à l'intérieur des tapis de *Dryas* qu'à l'extérieur, ce qui suggère que le *Dryas* n'agirait pas comme plante compagne sur les paramètres de la diversité à cet endroit. La composition en espèces au sein des tapis de *Dryas* diffère de ce que l'on trouve à l'extérieur des tapis dans toutes les communautés, que ce soit au niveau de la présence et de l'abondance des espèces à Finse, ou de l'abondance des espèces dans l'archipel de Svalbard. Le *Dryas* servirait donc de plante compagne chez des espèces des trois groupes fonctionnels dans toutes les communautés, bien que les effets compétitifs que le *Dryas* entraîne puissent annuler les effets positifs de cette plante compagne au niveau de la communauté. Enfin, il semble que le *Dryas* puisse également devenir une plante compétitrice lorsque son couvert augmente, mais seulement en présence de bas niveaux de stress d'origine abiotique.

Mots-clés : compétition, composition en espèces, diversité en espèces, facilitation, groupes fonctionnels, Norvège.

Nomenclature: Nyholm, 1986-1993; Smith, 1990; Krog, Osthagen & Tonsberg, 1994; Lid & Lid, 1994; Hallingbäck & Holmåsen, 1995.

Introduction

Dominant species are often important drivers of ecosystem function and community dynamics (Power & Mills, 1995; Grime, 1998) and may have both positive and negative effects on other species. Some species function as nurse plants by facilitating establishment of others and thereby increase community diversity (Niering, Whittaker & Lowe, 1963; Yarranton & Morrison, 1974; Callaway, 1995). On the other hand, dominant species may also reduce species diversity through resource competition (Connell & Slatyer, 1977; Vitousek & Walker, 1987; Walker, 1993).

Nurse plant effects appear to be particularly common in habitats of high abiotic stress. Here, any improvement of environmental conditions caused by the presence of a nurse plant may enhance growth and survival to the extent that it outweighs the competitive effects of growing in dense associations (Bertness & Callaway, 1994). Competition, on the other hand, is predicted to be most

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important in more productive habitats (Grime, 1979), although some ecologists claim that competition intensity is higher in low-productive communities simply due to the resource scarcity itself (Tilman, 1988). Facilitation and competition most likely occur simultaneously within plant communities (Callaway, 1995; Kikvidze *et al.*, 2001; Dormann & Brooker, 2002), and the relative importance of plant-plant interactions and the interactions between abiotic stress and functional attributes of neighbouring species in determining plant community structure is still unclear (Callaway & Walker, 1997).

Alpine and arctic ecosystems are characterized by a high level of abiotic stress, such as low temperatures, strong winds, and desiccation, which may intensify facilitation and thus the importance of nurse plants (Brooker & Callaghan, 1998). One species that potentially may function as a nurse plant in alpine and arctic plant communities is *Dryas octopetala,* a widespread circumpolar tundra dwarf shrub forming dense compressed mats. Manipulative experiments have shown that dwarf shrubs may provide shelter from wind (Carlsson & Callaghan, 1991), and nurse effects have been reported for other species of this genus (Chapin *et al.*, 1994). For example, as an early succession species in Glacier Bay, Alaska, *Dryas drummondii* modifies the environment by increased input of organic matter with associated nitrogen, making the habitat more suitable for the establishment of other species (Chapin *et al.*, 1994) and thus functioning as a nurse plant in these habitats. *Dryas* may, on the other hand, also have negative effects on other species because it may reduce space availability considerably. In addition, since *Dryas* produces a dense cover of leaves and litter, it may inhibit germination and seedling establishment of other species (K. Klanderud & Ø. Totland, unpubl. data).

Thus, the role of species as nurse plants may vary between habitats of contrasting abiotic stress and during succession. In addition, both the properties and cover of the potential nurse species (Callaway & Walker, 1997) and the functional attributes of the associated species may be important for a species' role as a nurse plant (Dormann & Brooker, 2002). Different functional groups differ in their competitive abilities (Goldberg & Werner, 1983) and most likely respond differently to the abiotic environment and to the presence of other species (Wilson & Whittaker, 1995). Therefore, in this study we examine whether *Dryas* functions as a nurse plant and whether this nurse plant role (if any) differs between habitats of contrasting abiotic stress and between different functional groups. We accomplish this by assessing species diversity in general and richness, cover, and composition of vascular, bryophyte, and lichen species in particular, inside and outside *Dryas* mats. We did this at two alpine sites differing in environmental severity in southern Norway and at two contrasting sites in arctic Svalbard.

Methods

STUDY AREA

The study was done in *Dryas* heaths close to Longyearbyen in arctic Svalbard (*ca* 78° N) and at Finse, in the northern part of Hardangervidda (*ca* 60° N) in alpine southwest Norway. We selected two sites of contrasting climatic severity at each locality. The more severe site in Svalbard was situated at *ca* 250 m elevation on a north-exposed ridge facing Isfjorden, *ca* 1.5 km south of Longyearbyen airport. The ground is stony and sparsely vegetated. The more benign site in Svalbard is more protected, at the exterior of Adventdalen at *ca* 25 m elevation, *ca* 1.5 km east of Longyearbyen, northeast exposed, and facing away from Isfjorden. The vegetation cover is denser at this site compared to the other, suggesting that environmental conditions are more benign. Reindeer graze at both sites. The more severe site at Finse was situated on a south-exposed ridge at 1,550 m elevation at Sandalsnuten, where wind speed is high and snow disappears early. The more benign site at Finse is more protected from the wind, at *ca* 1,250 m elevation and *ca* 2 km east of Finse railway station, facing south. Sheep may graze at the low-elevation site. Total species numbers for the sites are given in Figure 1 (for species abundances see Appendix I).

To document differences in environmental conditions, we measured temperature 5 cm above ground during the period of fieldwork in 2001 (the first 2 weeks of August in Svalbard and the last 2 weeks of August at Finse) by using four data loggers (Tinytag 12 Plus G, INTAB Interface-Teknik AB, Stenkullen, Sweden). The average temperature was 7.0 °C (SE = 0.05) at the high-elevation and 9.2 °C (SE = 0.15) at the low-elevation site in Svalbard, and 7.9 °C (SE = 0.08) at the high-elevation and 8.9 °C (SE = 0.09) at the low-elevation site at Finse. Mean summer temperature (June, July, August) is 6.3 °C at 1,222 m elevation at Finse (Aune, 1993) and 4.3 °C at *ca* 25 m at Svalbard Airport (Hanssen-Bauer, Kristensen Solås & Steffensen, 1990), and mean precipitation for the same months is 89 mm at Finse (Førland, 1993) and 17 mm in the Longyearbyen area (Svalbard Airport) (Hanssen-Bauer, Kristensen Solås & Steffensen, 1990).

SAMPLING AND SOIL ANALYSES

To study whether community diversity and composition differed between inside and outside *Dryas octopetala* mats, we randomly positioned two parallel 30-m long transects along a topographic gradient from a dry ridge to a more moist lee-slope at each of the four sites. At every second metre along the transects we positioned a 30- × 30-cm square inside the closest *Dryas* mat and another one outside the same *Dryas* mat (*ca* 30 cm from the edge of the *Dryas* mat), making a total of 15 plot pairs per transect and a total of 30 plot pairs per site. We estimated the abundances of vascular, bryophyte, and lichen species inside sub-squares of 10 × 10 cm, on a scale from 0 to 3, where 0 = absent, 1 = rare (cover < *ca* 12%), 2 = frequent (cover *ca* 13-50%), and 3 = dominant (cover > *ca* 50%). By adding abundance estimates from each of the sub-squares, we obtained a species abundance estimate ranging from 0-27 for each 30- × 30-cm square. We estimated *Dryas* cover as percentage cover within each sub-square. To examine if soil pH, nutrient, water, and organic matter content differed inside and outside *Dryas* mats, we collected one pair of soil samples at *ca* 5 cm below ground inside and outside *Dryas* mats at the top and the bottom of the transects at each of the four sites. The soil was immediately placed in a freezer and kept frozen until analyses were done at JORDFORSK, Ås, Norway. Easily soluble P and K were analyzed from soil extractions with ammonium lactate solution by inductive coupled plasma atom emission spectrometry (ICP-AES) (Egnér, Riehm & Domingo, 1960). Mg, Ca, and Na were also measured by ICP-AES, but from dissolution of a mixture of concentrated HNO_3 and HCl (1:3) (ns-EN ISO 11885). NO_3^- and NH_4^+ concentrations were determined from soil and water extractions by a spectrophotometer method (AV 14 and AV 16, modified versions of ns 4745 and ns 4746 for NO_3^- and NH_4^+, respectively). To estimate water content, the soil was dried at 105 °C for 6 h. The number of soil samples was too low to conduct statistical tests on differences between inside and outside *Dryas* mats and between the sites.

STATISTICAL ANALYSES

The data were normally distributed and the variances were equal. Initial two-way ANOVAs showed complex interactions between locality (Finse, Svalbard) and the effect of *Dryas* on total species richness, species diversity (Shannon's index, Ludwig & Reynolds, 1988), and number of vascular, bryophyte, and lichen species, indicating that the differences in community structure between plots inside and outside *Dryas* differed between the alpine and the arctic communities. We therefore conducted separate ANOVAs for Finse and Svalbard to test whether the community parameters differed between plots inside and outside *Dryas* and between the sites (within locality). These models included the inside/outside *Dryas* factor and elevation (high, low) as fixed effects and the two transects within each elevation as a random factor nested under the elevation factor, examining interactions between the inside/outside and elevation factors and the inside/outside and transect factors. The mean squares were compared sequentially, as shown for such nested models in Montgomery (1997).

To examine whether the position of plots along the transects had any effect on the difference in species richness and diversity between plots inside and outside *Dryas*, we included transect position as a co-variable in ANCOVAs with inside/outside *Dryas* as a fixed factor.

We used linear regressions to examine whether *Dryas* cover explained the differences between plots outside and inside *Dryas* mats in species richness, diversity, number of vascular, bryophyte, and lichen species, and species composition (see below). The mean percentage of *Dryas* cover within each 30- × 30-cm square was used as a predictor within each elevation site, whereas the response variables were obtained by subtracting the variable values inside *Dryas* from the values outside the *Dryas* mats for each plot pair. The ANOVAs and regressions were done in SYSTAT 10 for Windows (Wilkinson, 2000).

We used redundancy analysis (RDA, ter Braak & Smilauer, 1998) to examine whether species composition differed between plots inside and outside *Dryas*. We chose RDA because detrended correspondence analyses (DCAs, ter Braak & Smilauer, 1998) showed small composition differences (total variation less than 2 SD) for some of the functional groups in some of the communities, suggesting that a method based on linear species responses is most appropriate for these data (ter Braak & Prentice, 1988). To obtain comparable results of the ordinations, we therefore used linear methods for all functional groups in all the communities. We analyzed the four sites separately because of large differences in species composition between them. The ordinations were constrained by the inside/outside *Dryas* factor as an environmental variable, and the eigenvalues therefore reflect the variance in species composition that can be attributed to the *Dryas* effect. The abundance data were log-transformed, and the ordinations made by default settings in CANOCO 4 for Windows (ter Braak & Smilauer, 1998). We used a split-plot constrained Monte Carlo permutation test (999 permutations) to obtain the significance of the difference in species composition inside and outside *Dryas*. Species composition did not differ significantly between or within transects, indicating that such variations did not influence the statistical tests (ter Braak & Smilauer, 1998). Therefore, data from both transects within a site were pooled and the permutations were constrained to randomize only within one pair of samples (inside and outside *Dryas*). To examine whether differences in species composition inside and outside *Dryas* were due to species turnovers or simply due to abundance differences, we used RDA with the same options as above, but with presence/absence data instead of abundance data.

We used a principal components analysis (PCA, ter Braak & Smilauer, 1998) with inter-sample distance in CANOCO 4 for Windows (ter Braak & Smilauer, 1998) to estimate the difference in species composition between plots inside and outside *Dryas* by measuring the distance between the two samples' scores from plot pairs (inside/outside) along the first four axes. We weighted the sample scores by multiplying each score with the eigenvalue of the corresponding axis prior to measuring the distances. To ensure the robustness of interpretation of this analysis we ranked the plot pairs according to the difference in sample-score between plot pair members prior to regression analyses of relationships between *Dryas* cover (predictor) and the differences in species composition.

To examine whether the cover of each species differed between plots inside and outside *Dryas*, we tested each species within each community separately by using the nonparametric Mann-Whitney *U*-test. Plot pairs not including the particular species tested were removed from the dataset before testing.

Results

No differences occurred in soil pH between plots inside and outside *Dryas* in any of the localities, whereas organic matter (LOI) and soil water contents were higher inside compared to outside *Dryas* mats (Table I). Most of the nutrients were also more abundant inside *Dryas*, in particular NH_4^+ and Ca. These differences were most pronounced at Finse (Table I).

At the low-elevation site at Finse, 94% of the total species number there occurred outside and 90% inside the *Dryas* mats, whereas at the high-elevation site, 94% occurred outside and 82% inside *Dryas*. At the low-elevation site in Svalbard, 91% of the species occurred outside and 88% inside the *Dryas* mats, whereas at the high-elevation site, 81% occurred outside and 92% inside *Dryas*. The nested ANOVAs showed that mean total species richness per plot (F = 31.6, P = 0.03) and species diversity (F = 21.5, P = 0.005) were significantly higher outside than inside *Dryas* mats at the low- and high-elevation sites at alpine Finse, whereas no effects of *Dryas* on community parameters were evident in Svalbard (Figures 1a and b). Separate analyses of each functional group indicated that the number of vascular species was slightly higher outside than inside *Dryas* at Finse (Figure 1c), but nested ANOVA showed that *Dryas* had no statistically significant effect on vascular richness in any of the communities (F < 6.35, P > 0.13 in all cases). Bryophyte and lichen richness, on the other hand, were slightly higher outside than inside *Dryas* at Finse (F = 16.4, P = 0.056; F = 15.7, P = 0.058, respectively; Figures 1d and e), whereas no differences were evident in Svalbard (F < 4.05, P > 0.18 in all cases), except for a slightly higher bryophyte richness inside compared to outside *Dryas* at the high-elevation site (Figure 1d).

TABLE I. Mean values of soil variables from inside and outside *Dryas octopetala* mats at Finse and Svalbard. Numbers in parentheses are minimum and maximum values, respectively.

Soil variables	Finse		Svalbard	
	Inside	Outside	Inside	Outside
pH	6.3	6.3	6.1	6.0
	(6.1-6.8)	(6.0-6.5)	(5.7-6.5)	(5.6-6.2)
LOI (%)[1]	13.9	8.7	9.5	7.5
	(7.0-27.3)	(5.5-15.1)	(3.5-13.3)	(6.2-9.1)
H_2O (%)	39.5	29.3	24.0	14.9
	(29.1-59.2)	(21.7-39.8)	(11.7-34.5)	(9.0-20.1)
P ($mg \cdot 100\ g^{-1}$)	0.7	0.5	1.4	1.4
	(0.5-1.1)	(0.3-0.8)	(0.5-2.2)	(0.7-2.4)
K ($mg \cdot 100\ g^{-1}$)	6.3	4.1	10.0	11.9
	(3.5-8.1)	(2.4-6.5)	(5.8-13.8)	(8.5-14.4)
Mg ($mg \cdot kg^{-1}$)	9.2	5.9	37.2	37.4
	(6.0-17.5)	(3.0-13.1)	(22.0-44.0)	(26.1-44.7)
Na ($mg \cdot kg^{-1}$)	1.3	1.0	4.4	5.9
	(0.9-2.1)	(0.7-1.5)	(1.7-7.1)	(2.2-10.9)
NO_3^- ($mg \cdot kg^{-1}$)	1.0	1.0	0.6	0.5
	(0.8-1.5)	(0.6-2.1)	(0.3-0.9)	(0.5-0.6)
NH_4^+ ($mg \cdot kg^{-1}$)	5.9	3.2	4.5	1.8
	(2.8-9.7)	(1.7-6.1)	(0.7-8.4)	(0.8-3.4)
Ca ($mg \cdot kg^{-1}$)	315.0	177.1	193.9	156.6
	(149.0-521.0)	(68.4-355.0)	(90.5-267.0)	(97.3-199.0)

[1] LOI: soil organic matter.

There were no interactions between inside/outside *Dryas* and elevation or inside/outside *Dryas* and transect for any of the community parameters, showing that total species diversity and richness of all the functional groups inside and outside *Dryas* did not differ between the high- and low-elevation sites or within the sites (between the transects) either in Svalbard or at Finse. ANCOVAs showed no significant interactions between transect position and the inside/outside *Dryas* factor at Finse or in Svalbard, indicating that the differences in community parameters inside/outside *Dryas* were unaffected by the contrasting environmental conditions along the ridge-lee-side gradient within a site.

Redundancy analyses (RDA) with species abundances showed that species composition differed significantly between plots inside and outside *Dryas* for all functional groups at all four sites (P < 0.05 in all cases). At Finse, RDA with presence/absence values resulted in approximately equal eigenvalues (λ) and P-values (λ = 0.02-0.05; P < 0.005 in all cases) as the RDA with species abundances (λ = 0.03-0.07; P < 0.001 in all cases). In Svalbard on the other hand, RDA with presence/absence data had lower eigenvalues and higher P-values (λ = 0.004-0.03; P < 0.971 in all cases), than the RDA with

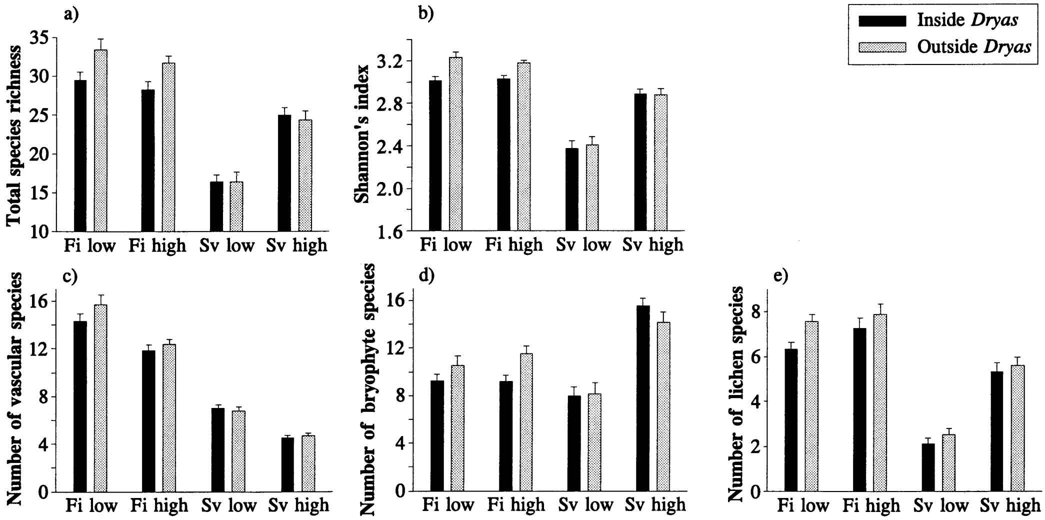

FIGURE 1. Mean + SE (vertical lines) of a) total species richness, b) Shannon's diversity index, c) number of vascular plant species, d) number of bryophyte species, and e) number of lichen species per plot (30 x 30 cm) inside and outside *Dryas octopetala* in four communities differing in abiotic severity (high and low elevation) at Finse (Fi) and in Svalbard (Sv) in 2001.

abundance data ($\lambda = 0.01\text{-}0.27$; $P < 0.05$ in all cases). This indicates that different species occur inside and outside *Dryas* at Finse, and that the abundances of the species may differ between plots inside and outside *Dryas* here. In Svalbard, on the other hand, the same species mainly occur both inside and outside *Dryas*, but they may differ in their abundances. For all the functional groups, the severe site in Svalbard had higher abundance data eigenvalues (λ) than the other sites ($\lambda_{\text{all species}} = 0.05$; $\lambda_{\text{vascular}} = 0.27$; $\lambda_{\text{bryophytes}} = 0.15$; $\lambda_{\text{lichens}} = 0.21$; $P = 0.001$ in all cases), indicating that the effect of *Dryas* explained more of the species composition here than in the other communities.

Most of the vascular, bryophyte, and lichen species had equal cover inside and outside *Dryas* at both Finse and Svalbard (Table II). Only a few vascular species (none in Svalbard) had a statistically significant ($P < 0.05$, Mann-Whitney *U*-test) higher cover inside compared to outside *Dryas,* whereas a higher percentage had a higher cover outside than inside, in particular at the low-elevation site at Finse (Table II). More bryophyte species had a higher cover inside *Dryas* compared to vascular plants and lichens (Table II). A relatively large percentage of the lichen species had a higher cover outside than inside *Dryas* in all the communities, but in particular at Finse. No lichen species were more abundant inside than outside *Dryas*, except at the highest-elevation site in Svalbard, where one species (*Peltigera aphtosa*) had a significantly higher cover inside *Dryas* than outside (Appendix I).

On average *Dryas* covered 67% (SE = 2.24) per plot at the low-elevation site and 67% (SE = 2.96) at the high-elevation site at Finse and 59% (SE = 1.58) at the low-elevation and 53% (SE = 2.33) at the high-elevation site in Svalbard. Linear regressions showed that *Dryas* cover had no effect on the differences in any of the community parameters inside and outside *Dryas* at any site in Svalbard ($P > 0.11$ in all cases). At the low-elevation site at Finse, on the other hand, there were significant positive relationships between *Dryas* cover and the differences in species diversity, total species richness, number of vascular and bryophyte species, and total species composition between plots outside and inside *Dryas* (Figures 2a-e). In this community, there were larger differences in composition of all functional groups between plots inside and outside *Dryas* than in more open mats. At the high-elevation site at Finse, the effect of *Dryas* cover was only significant for the difference in the number of lichen species between plots inside and outside *Dryas* mats (Figure 2f).

Discussion

There was little overall evidence for a nurse plant effect from *Dryas octopetala* on species diversity in the examined communities. Indeed, in the environmentally harsh sites in Svalbard, *Dryas* had no impact on community diversity, whereas in the relatively benign communities at Finse, total species richness, diversity, and richness of bryophyte and lichen species were actually lower inside compared to outside *Dryas,* while no differences occurred for vascular plants. Thus, the possible shelter effect and the higher soil moisture and nutrient content inside *Dryas* mats, which are considered important nurse plant effects in alpine habitats (Griggs, 1956; Pysek & Lyska, 1991; Nuñez, Aizen & Ezcurra, 1999), may be overruled by negative effects of *Dryas* in these communities. This result is in line with other studies (Bertness & Shumway, 1993; Bertness & Yeh, 1994) suggesting that competition is an important factor affecting community structure in relatively benign environments with relatively low abiotic stress. Furthermore, our results support the hypothesis of decreased diversity when early succession nurse plants attain higher cover in relatively productive habitats and thus dominate resource use (Connell & Slatyer, 1977; Vitousek & Walker, 1987; Walker, 1993).

Thus, the diversity parameters inside and outside *Dryas* suggested competitive effects of *Dryas* rather than nurse effects, but only in the alpine communities. Species composition, on the other hand, differed substantially between plots inside and outside *Dryas* for all three functional groups both at Finse and in Svalbard, indicating species-specific responses to the possible net positive and negative interactions from *Dryas*. At Finse, both presence/absence of the species and their cover differed between plots inside and outside *Dryas*, showing that

Table II. Total species number and the percentage of species with a significantly ($P < 0.05$, Mann Whitney *U*-test) higher cover outside or inside *Dryas*, and the percentage of species with no significant differences in cover inside or outside *Dryas* at the low- and high-elevation sites at Finse and in Svalbard. (Data are shown for each functional group and for each community studied).

Functional group	Variable	Finse Low	Finse High	Svalbard Low	Svalbard High
Vascular plants	Total species number	49	39	26	20
	% species with higher cover outside *Dryas*	30.6	12.8	7.7	20.0
	% species with higher cover inside *Dryas*	2.0	2.5	0	0
	% species with no difference in cover inside *versus* outside *Dryas*	67.4	84.7	92.3	80.0
Bryophytes	Total species number	55	50	48	55
	% species with higher cover outside *Dryas*	16.4	26.0	14.6	7.2
	% species with higher cover inside *Dryas*	9.1	8.0	6.3	5.5
	% species with no difference in cover inside *versus* outside *Dryas*	74.5	66.0	79.2	87.3
Lichens	Total species number	15	18	10	16
	% species with higher cover outside *Dryas*	33.3	33.3	20.0	25.0
	% species with higher cover inside *Dryas*	0	0	0	6.3
	% species with no difference in cover inside *versus* outside *Dryas*	66.7	66.7	80.0	68.7

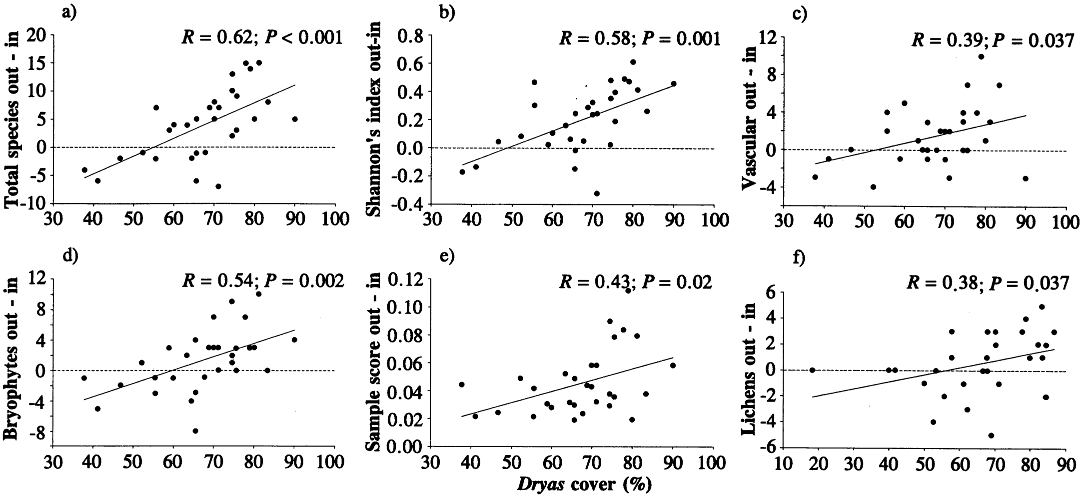

FIGURE 2. Relationship between mean *Dryas octopetala* cover (%) per plot (30 x 30 cm) and the difference between plots outside and inside *Dryas* in a) total species richness, b) Shannon's diversity index, c) number of vascular plant species, d) number of bryophytes, and e) the ranked difference in sample scores from a principal components analysis (PCA) of all species in the most benign community at Finse, and f) the difference in the number of lichen species from outside to inside *Dryas* in the most severe community at Finse. Only significant relationships are shown. Plots below zero (dotted line) have a higher species richness or diversity inside *Dryas*, whereas plots above zero have a higher species richness or diversity outside *Dryas*. Standardized regression coefficients (*R*) and significance values (*P*) are given. All sample sizes are 30.

Dryas influences the actual identity of which species are growing inside the mats. In Svalbard, on the other hand, the same species often occur both inside and outside *Dryas,* whereas their cover may differ substantially. Since competition and facilitation most likely occur simultaneously within plant communities (Callaway & Walker, 1997; Callaway, 1998; Kikvidze *et al.*, 2001), it is often difficult to assess which has the greatest role for community structure. In our study, the decrease in species diversity, richness, and cover of all functional groups inside *Dryas* at the most benign sites at Finse indicates that competitive impacts from *Dryas* may have the greatest role in determining differences in species composition in these communities, even if a sub-set of species may be facilitated by *Dryas*. In Svalbard, on the other hand, the slightly higher bryophyte richness inside *Dryas* at the high-elevation site and the neutral effect of *Dryas* on total diversity and vascular and lichen richness suggest that nurse effects from *Dryas* on some individual species may be important in producing the differences in species composition.

The different functional groups differed in their abundances inside and outside *Dryas*, and between the alpine and arctic communities. Bryophytes, for example, were generally more abundant inside *Dryas* compared to the other functional groups, in particular in Svalbard. Vascular plants and lichens, on the other hand, generally had higher abundances outside *Dryas*, even if nurse effects may occur for a sub-set of species. These results are in line with Kikvidze *et al.* (2001), who found that competition was the prevailing type of interaction on vegetative biomass in a species-rich sub-alpine meadow, but that facilitation balanced or outweighed the effects of competition for some of the species.

The cover of *Dryas* had a significant negative relationship with community parameters only at the environmentally most benign site (low elevation at Finse, and high elevation at Finse for lichens). There, mats of high *Dryas* cover contained significantly lower total species richness, diversity, and number of vascular and bryophyte species and had a larger difference in species composition between plots inside and outside *Dryas* compared to more open mats, which appeared to have a positive relationship with the same community parameters. This suggests an interaction between *Dryas* cover and abiotic stress, where the function of *Dryas* shifts from being a nurse plant to becoming a competitor when *Dryas* cover increases, but only under relatively benign climatic conditions. This partially supports Callaway and Walker (1997), who found that increasing age, size, or density of the nurse plant increased competition under benign physical conditions, whereas facilitation was most prominent under harsh conditions, irrespective of age, size, or density. This result is also in line with Cornelissen *et al.* (2001), who found a negative relationship between lichen abundances and vascular biomass in sub- and mid-Arctic sites, but no relationship in the cooler high Arctic.

Callaway *et al.* (2002) found that increased temperature led to a shift from positive to negative effects of neighbouring species and predicted that global warming may change the current balance between facilitative and competitive plant-plant interactions. Thus, the effects of *Dryas* may become more competitive, as suggested in the more benign communities, if global temperatures continue to rise. However, Callaway *et al.* (2002) found relatively weak facilitative effects of neighbouring plants in the Arctic that were most pronounced in the driest sites. This may suggest that other stress factors, such as, for example, wind and desiccation, may be more important for positive plant-plant interactions than low temperatures.

Dryas appears to be more important as a nurse plant for bryophytes than for vascular plants or lichens, although the differences in species composition between plots inside and outside the *Dryas* mats may suggest that *Dryas* functions as a nurse plant for specific individual species of all functional groups. These findings underline the importance of incorporating different functional groups to detect ecosystem dynamics, and they also underline the uncertainty in scaling-up results from studies of a few target species to the whole-community level.

Although this work is non-experimental, we believe that an optimal way to study the outcome of positive and negative interactions on plant community level under changing environmental conditions is to combine studies in natural habitats of contrasting environmental stress with experimental manipulations. We are currently experimentally assessing how *Dryas octopetala* affects a sub-set of species under contrasting environmental conditions in our study system.

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APPENDIX I. The mean abundances of vascular, bryophyte, and lichen species inside and outside *Dryas octopetala* mats at the low- and high-elevation sites at Finse and in Svalbard, 2001. Abundances are expressed on a scale from 0-27 based on visual estimates. An open cell for a species denotes that the species did not occur in that community.

	Finse				Svalbard			
	Low		High		Low		High	
Species	In	Out	In	Out	In	Out	In	Out
VASCULAR PLANTS								
Alopecurus borealis					0.27	0.53		
Antennaria dioica	2.47	3.23	0.57	0.4				
Anthoxanthum odoratum	0.63	0.73						
Arabis alpina			0	0.13				
Astragalus alpinus	0	0.07						
Bartsia alpina	0.57	0.73	1.4	2.13				
Bistorta vivipara	10.83	13.43	15	14.67	7.3	8.7	1.17	4.07
Campanula rotundifolia	0.3	1.53	1.33	1.97				
Carex atrofusca	0.13	0.7	0.07	0.4				
Cardamine belidifolia			0.07	0	0.03	0.03	0.04	0.1
Carex bigelowii			0.53	0.63				
Carex capillaris	0.87	3.8	0.2	0.53				
Carex rupestris	11.17	11.33	9.26	11.67	3.2	5.03		
Carex spp.	6.17	8.8	10.47	10.73				
Carex vaginata	1.43	1.9	0.73	0.2				
Cassiope hypnoides	0	0.47	0	0.13				
Cassiope tetragona					0.07	0	0.7	1.27
Cerastium alpinum	0.5	0.57	0.6	0.6				
Cerastium arcticum							0.4	0.33
Draba arctica					0.1	0.33		
Draba lactea					0.33	1.1	0.27	0.9
Draba spp.	0	0.2			0.27	0.23	0	0.03
Erigeron uniflorus	2.63	5.13	0.43	0.17				
Euphrasia frigida	0.53	2.33	0.5	2.2				
Empetrum nigrum	0.4	0.93	0	1.03				
Equisetum variegatum	0.4	1.33						
Festuca ovina ssp. *ovina*	6.33	6.27	0.13	0.77				
Festuca rubra ssp. *arctica*					2.43	1.83		
Festuca rubra ssp. *rubra*	1.1	1.4						
Festuca vivipara	0.07	0	1.07	2.47				
Festuca sp.	0	0.33	2.2	2.47				
Gentianella campestris	0.07	0.8						
Gentiana nivalis	0.57	0.67						
Hieracium alpinum					0.43	0.2		
Hupertzia selago			0	0.07				
Juncus trifidus	0.6	0.73	0.07	0.23				
Kobresia simplicifolia	0.33	0.53						
Leontodon autumnalis	0.3	0.33						
Luzula arctica					0.53	0.77		
Luzula confusa					7.03	5.37	1.9	5.13
Luzula spicata	0.3	0.63	0.93	1.14				
Lychnis alpina	0.07	0.27	0.1	0				
Minuartia biflora	0.2	0.1			0.03	0.37		
Minuartia rubella					0.07	0.33		
Omalotheca supina	0	0.07						
Oxyria digyna	0	0.03			1	0.73	0.07	0
Oxytropis lapponica	0.27	0.77	1.9	0.83				
Papaver dahlianum					0.13	0.03		
Parnassia palustris	1.77	1.53						
Pedicularis hirsuta					0.33	0.3	0.1	0.2
Pedicularis lanata					0.7	0.03	0.07	0.47
Poa alpina	0.67	0.57	0.17	0.1	0	0.13	0	0.03
Poa arctica					3.23	3.37	1.77	1.33
Poa glauca					0.57	0.33		
Potentilla crantzii	3.07	4.47	1.93	2.3				
Rhodiola rosea			0	0.07				
Salix herbacea	0.4	0.4	5.07	10.23				
Salix polaris					13.3	12.13	15.1	15.43
Salix reticulata	3.67	4.83	6.63	7.03				
Saussurea alpina	1.8	3.13	4.67	5.17				
Saxifraga cernua					0.27	0.27	0	0.3
Saxifraga cespitosa			0.03	0			0	0.07
Saxifraga nivalis							0	0.03
Saxifraga oppositifolia	0.3	0.4	1.4	0.87	2.03	2.4	0.07	0.33

APPENDIX I. Continued.

	Finse				Svalbard			
	Low		High		Low		High	
Species	In	Out	In	Out	In	Out	In	Out
Selaginella selaginoides	4.7	8.73	2.33	3.07				
Sibbaldia procumbens	0.13	0.2						
SILENE ACAULIS	4.17	7.17	5.9	10.03				
Silene uralensis ssp. *arctica*					0.07	0		
Stellaria crassipes					2.7	2.13	1.03	1.17
Stellaria longipes							0.53	0
Thalictrum alpinum	10.63	14.27	12.13	13.37				
Tofielda pusilla	1.53	2.47	0.13	0				
Vaccinium uliginosum	0.27	0	0.87	1.53				
Vaccinium vitis-idaea	0.6	0.3						
Veronica alpina	0.47	0.33						
BRYOPHYTES								
Anthelia juratzkana	0	0.07			0.07	0.2	0.8	1.93
Aulacomnium turgidum					4.3	3.1	8.13	4.6
Barbilophozia hatcheri	0.93	0.5	0.13	0.13	0	0.07	1.27	2.47
Barbilophozia kunzeana	0.43	1	0.93	1.4	0.27	0.07		
Barbilophozia lycopodioides	1.87	1.6						
Bartramia ithyphylla	0	0.87	0.6	0.33	0.73	0.47	1.87	2
Barbula sp.					0.07	0.27	1.2	1.13
Blepharostoma trichophyllum	0.4	0.73	0.07	0.4	0.13	0.6	0.4	1.2
Brachytecium albicans	2.17	0.53	0.07	0				
Brachytecium collinum			0	0.07				
Brachytecium erythrorrhizon	2.67	1.33	2.6	2.73				
Brachytecium turgidum					0.07	0	0.4	0
Brachytecium spp.	0.67	0.27	0.8	0	0	0.13	0.2	0
Bryum spp.	3.07	6.67	1.47	4.87	1.67	4.37	5.07	7.47
Campylium stellatum	1.53	3.27	0.7	3.07	1.93	0.8	1.13	1
Cephalozia ambigua							0.07	0
Cephaloziella arctica					0.27	0.07	0.13	0
Cephaloziella divaricata	0.2	0.27	0.13	0.87				
Ceratodon antarcticus					0.33	0.93		
Conostomum tetragonum	0.07	0.07					0.2	0.07
Cynodontium spp.							0	0.47
Dichodontium pellucidum							0.4	0
Dicranella crispa							0.4	0
Dicranum fuscescens	11.93	9.93	14.13	12.97	0.33	1.2	6.77	7.6
Dicranum sp.	0.07	0.97						
Dicranoweisia crispula	0.13	9.93	0	0.33			1.4	1.07
Distichium capillaceum	4.87	6.07	5.6	5.93	7.33	7.07	4.13	3.13
Ditricum flexicaule	0.07	0.53	2.93	4.47	0.4	0.4	8.37	5.5
Drepanocladus uncinata	2.2	1.87			17.2	10.13	14.2	6.87
Encalypta rhaptocarpa					0.33	1	0.8	1.07
Fissidens osmundioides	0.07	0.53						
Fissidens sp.			0	0.13				
Gymnomitrion corallioides	0.2	0	0	0.33	0	0.2	1.9	6.13
Hylocomium splendens	0.27	0	1.67	0.87	0.7	0.27	11.87	5.47
Hypnum bambergii	1.53	0.8			0	0.07	0.2	0
Hypnum recurvatum	0.13	0.07	0	0.27				0.67
Hypnum revolutum	0.13	0	1	1.47	0.13	0.6	0.67	
Jungermannia spp.					0.4	0.6	0.3	0.46
Lophozia spp.	0.93	2.13	0.33	0.73	0.34	0.27	0.6	1.4
Marchantia alpestris	0.3	0.73						
Marsupella sp.	0	0.27	0.27	0.13				
Meesia uliginosa	0.07	0.3	0	0.2				
Mnium blyttii			0	0.07				
Mnium marginatum			0.07	0.53				
Mnium thomsoni					0.33	0		
Myurella julacea	0.13	0			0.47	0.33		
Myurella tenerrima	0.13	0.13	0.07	0.47	0.07	0.07		
Odontoschisma macounii	0.37	0.53	0.7	1.47	0.07	0	0.13	0.3
Oncophorus virens					0	0.33	2.2	2.27
Oncophorus wahlenbergii	2.33	4.73	2.2	4.6	0.13	0.47	1.13	1.4
Pohlia cruda	0.33	0.93	0	0.63	2	2.27	6.53	6.17
Pohlia drumondii					0.133	0.13	0.2	0.13
Pohlia nutans	0.07	0.33	0	0.07	0.2	0.87	0.27	0.4
Pohlia spp.	0.73	1.73	0.67	0.53	0.53	0.13	1.66	0.6
Polytrichum alpinum			0.67	0.07	1.73	0.87	0.67	0.7

APPENDIX I. Continued.

	Finse				Svalbard			
	Low		High		Low		High	
Species	In	Out	In	Out	In	Out	In	Out
Polytrichum juniperinum	0.77	1.47	2.93	6.87	1.6	4.43	8.2	7
Polytrichum longisetum	0	0.47	5	2.43				
Polytrichum piliferum			0.33	0.07			1	3.67
Ptilidium ciliare	6.13	3.13	4.53	1.73			0.7	0.6
Racomitrium canescens	0.4	0.07	0.27	0.47	0	0.2	0.47	0
Racomitrium lanuginosum	0.27	1.4	5.93	7.77	0.13	1.8	8.73	10.5
Rhizomnium andrewsianum							0.2	0
Rhytidium rugosum	0.67	0.33	2.93	0.67				
Saelania glaucescens	0	0.07						
Scapania aequiloba	0.47	1.6	0.07	0.4				
Scapania curta			0.13	0.33	0.27	0.07	0.33	1.13
Scapania obcordata	1.07	1.93					1.07	2.17
Scapania scandica	0.87	1.6	0.27	1.2				
Scapania sp.							1.8	0.4
Timmia austriaca					4.73	1.4	6.77	3.8
Tortella fragilis			0	0.27				
Tortella tortuosa	0.07	0.2	0	0.37				
Tortula ruralis	0.87	0.07	0.53	0.47	0.2	0	2.27	1.93
Tomentypnum nitens	0	0.13	0.27	0	6.67	5.33	0.2	0
Trichostomum arcticum					0.2	0.13		
Trichostomum crispulum	0.13	0.8	0	0.13				
LICHENS								
Alectoria ocroleuca	0.37	0.13	2	4.2				
Bryocaulon divergens	0.53	2.07	3.13	6.17	0.07	0.47	1.7	2.87
Cetraria aculeata					0.7	1.17	0.07	0.07
Cetraria delisei	0.2	0.73	0.2	0.07			0.47	1.53
Cetraria islandica	14.7	15.77	14.97	15.67	0.37	0.3	1.73	4.87
Cetraria juniperina			0.57	2.57				
Cetraria muricata							0	0.03
Cetraria nivalis	7.73	10.83	9.7	10.43			0.5	0.33
Cladonia gracilis	0.1	0.1						
Cladonia arbuscula	10.73	13.27	2.87	4.07				
Cladonia rangiferina			0	0.2				
Cladonia uncialis	5.77	9.83	2.37	3.47	0	0.07	0.73	1.03
Cladonia spp.	8.27	10.77	4.53	5.7	0.27	0.5	3.07	4.97
Ochrolechia frigida	2.17	8.5	2.1	8.93	2.8	12.13	5.3	15.4
Peltigera aphtosa	0.67	1.93	0.77	1.43	0.4	0.33	3.07	0.93
Peltigera lepidophora							0.03	0
Physconia muscigena			0.07	0				
Sphaerophorus fragilis							0.47	0.6
Sphaerophorus globosus	0.07	0.4	0.47	0.9	0	0.1	0.2	0.7
Stereocaulon spp.	2.33	3.73	1.13	1.6	0.8	0.97	8.33	7.57
Thamnolia vermicularis	5.2	3.9	6.27	6.8	1.3	1.67	1.37	0.97

Paper II

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Climate change effects on species interactions in an alpine plant community

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Summary

1 I examined the role of species interactions on the population dynamics of the herb *Thalictrum alpinum* and the sedge *Carex vaginata* by removing the dwarf shrub *Dryas octopetala* over four growing seasons at Finse, in the alpine region of south Norway, Furthermore, by increasing temperature (open top chambers) and nutrient availability (nutrient addition), I assessed the effects of climate warming on biotic interactions.

2 *Dryas* removal increased the number of *Thalictrum* and *Carex* leaves, and flowering frequency of *Carex*. Flower stems and leaf stalks of *Thalictrum*, and the leaves of *Carex*, became significantly shorter following *Dryas* removal. Warming and nutrient addition increased vegetative plant growth, whereas warming alone had positive effects on sexual reproductive effort of the target species. My results suggest that there is both competition for nutrients, and a facilitative shelter effect of *Dryas* on its neighbours.

3 Species interactions affected population dynamics of *Thalictrum* and *Carex*. Interactions between the impacts of *Dryas* removal and abiotic factors on leaf production, suggested that interactions between *Dryas* and neighbouring species might be modified if temperature and, in particular, nutrient availability increase under global warming.

4 This study shows that both biotic interactions and abiotic environmental conditions may affect alpine plant population dynamics. Furthermore, it shows that climate change may modify species interactions.

5 Species interaction effects should be included in climate change experiments and in future models predicting plant community changes under global warming.

Key-words: biotic and abiotic factors, competition, dominant species, *Dryas octopetala*, facilitation, nutrient availability, plant functional types, population dynamics, removal experiment, warming

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Introduction

Both biotic factors, such as species properties and species interactions, and abiotic factors, such as climate and soil characteristics, affect ecosystem structure and processes (Huston & McBride 2002). However, the relative importance of the biotic and abiotic factors for community dynamics in habitats of contrasting environmental severity and productivity is far from clear (Callaway & Walker 1997). Competition appears to play an important role in structuring plant communities of high productivity (e.g. Grime 1979), but there is still a debate about the role of biotic interactions when productivity is low, such as in alpine and arctic plant communities of high abiotic stress. Competition may be strong here because resources are scarce (e.g. Chapin & Shaver 1985; Tilman 1988), or facilitation may be stronger, with neighbouring vegetation improving the survival potential for individual plants (e.g. Callaghan & Emanuelson 1985; Bertness & Callaway 1994). Alternatively, species interactions may have less impact on community composition in areas of high abiotic stress because plant growth here is primarily limited by the environmental conditions (e.g. Savile 1960; Billings & Mooney 1968; Grime 1977).

Global warming may modify abiotic conditions that influence individual plant performance, with alpine and arctic ecosystems predicted to be particularly affected (e.g. Callaghan & Jonasson 1995; Guisan *et al.* 1995; Körner 1995, 1999). Climate change may alter soil moisture and increase nutrient availability and, in

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combination with the direct warming effect, these factors may impact the growth, reproduction and resource allocation of the plants. However, functional groups (Arft *et al.* 1999; Dormann & Woodin 2002; Brooker & van der Wal 2003) or individual plant species (see Henry & Molau 1997) may differ in their responses to environmental changes. Furthermore, changes in the performance of one species or a functional group may change any current relationship between positive and negative plant–plant interactions, i.e. changes in competition or facilitation hierarchies between co-occurring species or growth forms.

The role of species interactions in structuring tundra plant communities differs between sites (see Hobbie *et al.* 1999). Moreover, effects of climate change on plant–plant interactions are rarely studied (but see Shevtsova *et al.* 1997; Hobbie *et al.* 1999), and species interactions are mostly ignored in models predicting how plant communities or ecosystems respond to climate change (Mooney 1991; Pacala & Hurtt 1993). Bertness & Callaway (1994) predicted a shift from facilitative to competitive effects of neighbouring plant species along gradients of decreasing abiotic severity and, in a study of 11 alpine sites, Callaway *et al.* (2002) found that species interactions shifted from positive to negative when summer temperatures increased along latitudinal and altitudinal gradients. They predicted that such shifts may speed changes in community composition and diversity compared with more physiologically based climate change models, and concluded that there is a need for more experiments on climate change effects on individual plant–plant interactions. There is also a lack of knowledge about how plant interactions affect resource allocation to reproduction vs. vegetative growth. Studies show contrasting results, which may indicate that both competition and facilitation may contribute to higher reproductive effort, though with varying responses between species (Kikvidze *et al.* 2001).

The aim of this study is to assess the relative impacts of biotic and abiotic factors on the growth and reproduction of two plant species in a *Dryas* heath community in alpine south Norway, and to gain an understanding of how interspecific interactions may be modified by abiotic conditions predicted to change under global warming. Hobbie *et al.* (1999) manipulated air temperature and the presence of seven dominant species in Alaskan tussock tundra, and found that the environmental conditions were more important for plant growth and biomass production than the impacts of species interactions. Moreover, as they found no interactions between warming and species removal, they concluded that global warming might not alter species interactions in tundra. In northern Finland, on the other hand, Shevtsova *et al.* (1997) found a number of interactions between environmental conditions (temperature and water) and species removal on the growth of sub-arctic dwarf shrubs, suggesting that community composition may modify the effects of climate change here. The contrasting results between the Alaskan tundra and the European sub-arctic site suggest that there is a need for more research on species interactions and their responses to climate change. Moreover, none of these studies assessed the impact of increased nutrient availability resulting from climate warming (but see Bret-Harte *et al.* 2004), although this is predicted to provide the largest effects on tundra plant community composition (e.g. Chapin *et al.* 1995; Shaver & Jonasson 1999; Dormann & Woodin 2002).

Dryas heaths are plant diversity ‘hot spots’ in the Scandinavian mountains, dominated by the long-lived ‘wintergreen’ dwarf shrub *Dryas octopetala* L. (*Dryas* hereafter). *Dryas* grows in dense clones that may have positive or negative impacts on community diversity (Klanderud & Totland, in press). The relatively simple vegetation structure, with few and compressed vegetation layers, as well as predictions of large climatic impacts on species composition in alpine areas, make this an ideal arena to test questions related to species interactions and climate change. I used experimental removal of *Dryas*, warming (open top chambers, OTCs) and nutrient addition, to examine the role of these factors on the population dynamics of *Thalictrum alpinum* L. and *Carex vaginata* Tausch. Furthermore, I assessed if species interactions might be modified under climate warming. *Thalictrum* and *Carex* are abundant in the alpine *Dryas* heaths, and they belong to different functional groups (herbs and sedges, respectively) that may contrast in their responses to other species and to the abiotic environment (e.g. Wilson & Whittaker 1995; Dormann & Woodin 2002; Brooker & van der Wal 2003). Three predictions were addressed. (i) The two target species will differ in their responses to *Dryas* removal and to changes in the abiotic environment. (ii) Higher productivity at our site will lead to plant–plant interactions playing a greater role in plant community dynamics than reported in the Alaskan tundra (Hobbie *et al.* 1999; Bret-Harte *et al.* 2004). (iii) Species interactions will be modified by increased temperatures and nutrient availability.

Methods

STUDY SYSTEM

The experiment started in early July 2000 and lasted until the end of the growing season (late August) in 2003. The study site was situated on a south-west exposed slope of a *Dryas octopetala* L. heath at *c.* 1500 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (60° N, 7° E) in alpine south-west Norway. The snow normally disappears in late May/early June. Mean summer (June, July, August) temperature at 1222 m elevation at Finse is 6.3 °C (Aune 1993), and mean summer precipitation is 89 mm (Førland 1993).

The dwarf shrub *Dryas octopetala* is widely distributed in alpine and arctic areas. At Sandalsnuten, dense *Dryas* mats cover *c.* 35% of the ground of the *Dryas* heath community (Klanderud & Totland, in press). Other abundant species here are the herbs *Thalictrum alpinum* L., *Potentilla crantzii* Crantz., *Bistorta vivipara* L. and *Cerastium alpinum* L., the dwarf-shrub *Salix reticulata* L., the grasses *Festuca vivipara* L. and *Poa alpina* L., and the sedges *Carex vaginata* Tausch., *C. atrofusca* Schkuhr, *C. rupestris* All. and *Luzula* spp. (nomenclature follows Lid & Lid 1994), in addition to a number of bryophytes and a few lichens.

Vegetative regeneration is common for alpine plants. *Thalictrum alpinum* and *Carex vaginata* grow clonally by producing new ramets from below-ground rhizomes, and seedlings of these species are rarely found at Sandalsnuten. Therefore I studied the responses of mature individuals rather than seedling responses.

EXPERIMENTAL DESIGN

To assess the possible effects of removal of *Dryas*, warming and increased nutrient availability on the population dynamics of *Thalictrum alpinum* and *Carex vaginata*, and whether environmental conditions affected any species interactions, I randomly selected 20 plots within a relatively homogenous area of the *Dryas* heath. I placed OTCs upon 10 of these plots and left the 10 others as controls. The OTC/control plots are the main-plots in a split-plot design with 10 replicates (see, e.g. Underwood 2001). In each of the 20 main-plots, I selected eight *Thalictrum* and eight *Carex* ramets growing inside *Dryas* mats, and inserted half a slow-dissolving NPK-fertilizer stick into the soil *c.* 1 cm upslope of half of the individuals of each species immediately after snowmelt and again in late July (*c.* 0.2 g N, 0.04 g P and 0.17 g K per ramet/growing season). Ramets receiving fertilizer were selected so that the added nutrients could not move to unfertilized ramets, i.e. they were grouped, or situated down-slope from other ramets. Thereafter, I clipped the above-ground parts of neighbouring *Dryas*, and carefully removed below-ground parts that could be pulled up with minimal soil disturbance, from a diameter of *c.* 10 cm around half of the fertilized ramets and around half of the ramets not receiving any fertilizer. I removed re-growth twice during each of the four growing seasons. This provided a split-plot design with temperature treatment as a fixed factor conducted on main-plot level, 20 plots as a random factor nested within the main-plot factor (temperature), and nutrient addition and removal treatments as fixed factors conducted on subplot level. Thus, for each of the 10 replicates, two ramets of each of the two target species in each temperature treatment (inside and outside OTCs) received nutrient addition, two experienced *Dryas* removal, two nutrient addition and *Dryas* removal, and two were untreated controls. The responses of the two individuals receiving similar treatments were averaged prior to statistical analysis.

Removal experiments may be problematic for several reasons. Removal of above-ground biomass may leave dead roots to decompose and increase soil nutrient levels (Putwain & Harper 1970; Berendse 1983). However, these resources have most likely been obtained by competition in the past, and their release may benefit those plants that have been denied these resources earlier (Aarssen & Epp 1990). Vegetation removal may also disturb the soil, resulting in a nutrient flush. However, the primary removal in this study was of above-ground *Dryas* shoots, and there were probably only minor effects on below-ground processes and soil disturbance.

The OTCs are hexagonally shaped polycarbonate chambers with an inside diameter of *c.* 1 m, and with qualities as described in Marion *et al.* (1997). OTCs are commonly used to raise the temperature in climate change experiments (e.g. Marion *et al.* 1997; Hollister & Webber 2000). The chambers did not affect the duration of snow cover (personal observation) and were therefore left in place throughout the experiment. The site was fenced to inhibit sheep grazing.

ABIOTIC MEASUREMENTS

Air (*c.* 5 cm above ground) and ground surface temperatures were measured with a Grant Squirrel data logger during 10 days of late July/early August 2000, and soil (*c.* 5 cm below ground) temperatures were measured with Tinytag 12 Plus G data loggers (Intab Interface-Teknik AB, Stenkullen, Sweden) from early June to late August 2002, inside and outside the OTCs, in plots where *Dryas* had been removed, and in undisturbed plots. Leaf surface temperature of *Dryas* inside and outside the OTCs was measured using an infrared thermometer (FLUKE 65, Fluke Corporation, Everett, USA). Soil moisture was measured at the end of the final growing season by inserting a 6 cm long sensor (Theta Probe, Delta-T Devices Ltd, Cambridge, England) into the soil immediately beneath each target ramet (averaging three measurements per ramet).

GROWTH MEASUREMENTS

I measured growth and reproductive variables of *Thalictrum alpinum* and *Carex vaginata* in late August after the first (2000), second (2001), third (2002) and fourth (2003, reproductive variables only) growing seasons. To assess differences in within-season growth rates, I also measured the growth variables in late May (before any growth had started), late June, and again in late July during the second and the third growing season. However, to limit possible legacy effects of the removal treatment, only the 2002 and 2003 measurements are used in the analyses, with the 2000 measurements as covariables.

Sexually reproductive *Carex* ramets normally die the year after flowering, with new tillers growing out from the old ramet (*Carex vaginata*, K. Klanderud, personal observation; *C. bigelowii*, see Brooker *et al.* 2001). To simplify interpretation of growth and sexual reproduction independently of flowering year, I obtained target ramets at similar developmental stages by selecting flowering *Carex* individuals at the start of the experiment.

To obtain an estimate of vegetative growth of *Thalictrum* and *Carex*, I counted the number of green leaves on each target ramet and the total number of leaves on new tillers growing out from the target ramet. The data from the target ramet and daughter tillers are pooled in the statistical analyses. As number of leaves is not reported per tiller, possible changes may be due either to increased tillering or increased size of the tillers. Furthermore, I measured the length and the width of the largest and the smallest leaf and the length of their leaf stalk (*Thalictrum*), and the length of the longest leaf (*Carex*), using a digital caliper. I calculated an approximate leaf area of *Thalictrum* leaves by multiplying the width by the length and then calculated the average area of the smallest and the biggest leaf. Leaf number, average leaf area of the largest and the smallest leaf, and the length of their leaf stalks, are parameters commonly used for herbs, whereas leaf number and the length of the longest leaf are commonly used for sedges to obtain non-destructive measures of vegetative growth (Molau & Edlund 1996; Arft *et al.* 1999). To estimate mortality I recorded dead target ramets. Measuring mortality on clonal plants is, however, not easily applied because individuals usually persist, and only parts of the plants die. The data for *Carex* are not analysed because mortality here coincides with sexual reproduction.

SEXUAL REPRODUCTION MEASUREMENTS

To estimate the sexual reproductive effort of *Thalictrum* and *Carex*, I measured the height of flower stems and collected mature infructescences at the end of each season and recorded the number of flowers and number and weight of dried seeds. There were not enough flowering *Carex* individuals to test for seed production and seed weight. Arctic and alpine plants normally do not produce flowers each year (Sonesson & Callaghan 1991) and the same ramet did not reproduce more than once during the experiment for either of the two species. To increase the sample size, I therefore pooled all flowering individuals from 2002 to 2003 to estimate flowering frequency for both species, as well as height of flower stem and number of flowers and seeds for *Thalictrum.* There were too few mature seeds to conduct statistical tests on seed weight.

STATISTICAL ANALYSES

Data on the number of leaves, leaf area (*Thalictrum*) and leaf length (*Carex*) were log transformed to fulfil the ANCOVA assumptions of normality and equal variances. All graphs are shown with untransformed data. To determine if warming, nutrient addition and removal of *Dryas* had any impact on the vegetative growth of *Thalictrum* and *Carex*, and whether possible species interactions were affected by the environmental factors, I used general linear models (GLM, SYSTAT 10) with the temperature treatment (main-plot factor), nutrient addition, removal of *Dryas*, and their interactions (subplot factors) as fixed factors, and plot nested within temperature as a random factor in a split-plot ANCOVA. I used the first year (2000) measurements as covariables in the analyses to increase the model's ability to detect treatment effects. The effect of temperature was tested over the plot error (main-plot term), whereas all other effects were tested over the model error (subplot term) (see, for example, Underwood 2001). Analyses were conducted separately for the two species. To examine if the removal of *Dryas* or the environmental factors had any impact on the combination of growth phenology and absolute size differences of *Carex* and *Thalictrum* during the third (2002) growing season after experimental onset, I used repeated-measures ANOVA with the same factors as above, and with ramet identity during three measurements throughout the season (time) as the repeated measures factor. A significant interaction between time and treatment may then indicate that treatments differ in the pattern of growth during the season.

Because of low sample sizes for reproductive parameters, I used the Mann–Whitney *U*-test to assess significant differences in height of flower stem, number of flowers per ramet and number of seeds per flower within each treatment separately (temperature vs. control, nutrient addition vs. natural, removal vs. undisturbed). I used Pearsons chi-square test to assess significant differences in flowering frequency for *Thalictrum* and *Carex* and mortality for *Thalictrum*, between the same treatments as above. The small sample sizes for sexual reproduction may result in conservative results.

Results

ABIOTIC FACTORS

The OTCs increased mean *Dryas* leaf temperature and air temperature by 1.5 °C, and ground temperature by 2.5 °C (Table 1). When soil temperature was measured, the OTCs increased values in undisturbed vegetation by 1.5 °C, while *Dryas* removal caused a decrease of 0.5 °C inside the OTCs, and an increase of 0.5 °C outside (Table 1).

VEGETATIVE GROWTH

Removal of *Dryas octopetala* increased the number of leaves of *Thalictrum alpinum* by 79.2% and of *Carex vaginata* by 56.4% across all treatments (Table 2, Figs 1a and 2a). The *Thalictrum* leaves became 35.1% smaller and the *Carex* leaves became 14.1% shorter after *Dryas* removal, although this was only statistically significant for *Carex* (Table 2, Figs 1b and 2b). The length of *Thalictrum* leaf stalks decreased by 49.3% after *Dryas* removal, although a close to significant three-way interaction indicated that temperature, nutrient addition and removal treatment all affected each other (Table 2, Fig. 1c). Significant measures from 2000 suggested treatment effects on *Thalictrum* leaf stalks after the first growing season.

Table 1 Mean temperature of *Dryas* leaf surface, air (*c*. 5 cm above ground), ground surface and soil (*c*. 5 cm below ground) where vegetation was experimentally removed or intact, and soil moisture, outside (control) and inside OTCs at alpine Finse. Standard errors, minimum and maximum measures are given

	Control		OTC	
	Mean ± SE	Minimum–Maximum	Mean ± SE	Minimum–Maximum
Dryas leaf surface (°C)	12.1 ± 0.1	9.7–14	13.6 ± 0.2	12.1–16.2
Air (°C)	7.8 ± 0.2	−2.2–28.1	9.3 ± 0.2	−2.5–36.9
Ground (°C)	10.4 ± 0.4	−2.1–45.1	12.9 ± 0.5	−2.5–55
Soil, *Dryas* removal (°C)	9.2 ± 0.1	2.1–18.2	9.6 ± 0.1	2.7–18.6
Soil, no removal (°C)	8.7 ± 0.1	2.3–17.0	10.2 ± 0.1	2.8–22.3
Soil moisture (%)	28.2 ± 0.6	17.9–44.2	27.9 ± 0.8	11.8–42.5

Table 2 $F_{\text{d.f.}}$ and P values (significant at < 0.05 in bold, < 0.1 in bold italics) of treatments performed in alpine *Dryas octopetala* heaths; T = temperature (OTC vs. control, main-plot fixed factor), N = nutrient addition (increased vs. ambient, subplot fixed factor), R = removal of *Dryas* (yes vs. no, subplot fixed factor), their interactions, plot nested in T (random factor), and measurements from 2000 included as covariables in split-plot ANCOVAS on number of leaves of *Thalictrum alpinum* and *Carex vaginata*, average leaf area and length of leaf stalk of the biggest and the smallest leaf of *Thalictrum*, and length of the longest leaf of *Carex*. $n = 10$ for each treatment

Sources of Variation	Number of leaves		Leaf area/length		Leaf stalk	
	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P
Thalictrum alpinum						
T	$0.33_{1,18}$	0.572	$0.16_{1,18}$	0.695	$1.14_{1,18}$	0.300
N	**4.91**$_{1,46}$	**0.032**	$1.41_{1,46}$	0.242	**5.35**$_{1,46}$	**0.025**
R	**22.13**$_{1,46}$	**< 0.001**	$2.08_{1,46}$	0.156	**15.51**$_{1,46}$	**< 0.001**
T × N	**9.90**$_{1,46}$	**0.003**	$2.23_{1,46}$	0.142	$0.49_{1,46}$	0.486
T × R	$0.59_{1,46}$	0.447	$0.48_{1,46}$	0.494	$1.57_{1,46}$	0.217
N × R	$1.84_{1,46}$	0.181	$0.00_{1,46}$	0.982	$0.57_{1,46}$	0.454
T × N × R	$0.11_{1,46}$	0.744	$1.64_{1,46}$	0.206	***3.38***$_{1,46}$	***0.073***
Plot (T)	***1.78***$_{1,46}$	***0.059***	$0.97_{1,46}$	0.511	$1.12_{1,46}$	0.368
2000 measure	$1.39_{1,46}$	0.244	***2.96***$_{1,46}$	***0.092***	**5.17**$_{1,46}$	**0.028**
Carex vaginata						
T	$1.50_{1,18}$	0.237	$0.37_{1,18}$	0.552		
N	**6.59**$_{1,38}$	**0.014**	$1.93_{1,38}$	0.173		
R	**4.74**$_{1,38}$	**0.036**	**4.75**$_{1,38}$	**0.036**		
T × N	***2.98***$_{1,38}$	***0.092***	$1.48_{1,38}$	0.231		
T × R	$0.25_{1,38}$	0.619	$0.19_{1,38}$	0.667		
N × R	$2.12_{1,38}$	0.153	$0.36_{1,38}$	0.552		
T × N × R	$0.02_{1,38}$	0.896	$0.04_{1,38}$	0.850		
Plot (T)	$1.23_{1,38}$	0.288	$1.22_{1,38}$	0.295		
2000 measure	$0.11_{1,38}$	0.74	$1.79_{1,38}$	0.189		

Nutrient addition increased the number of *Thalictrum* leaves by 32.3% and the number of *Carex* leaves by 59.1%, with interactions (only marginally significant for *Carex*) between temperature and nutrient addition suggesting that the number of leaves increased on ramets receiving both warming and nutrients, whereas there were no significant effects of either of these treatments separately (Table 2, Figs 1a and 2a). Warming and nutrient addition increased *Thalictrum* leaf area by 21.4% and 18.6%, respectively, and *Carex* leaf lengths by 8.7% and 10.8%, although these responses were not statistically significant (Table 2, Figs 1b and 2b).

GROWTH PHENOLOGY

The increased number of *Thalictrum* leaves after *Dryas* removal (Table 2, Fig. 1a) was primarily caused by production of more leaves early in the season (May, June), and again later in the growing season (August). This was particularly pronounced when nutrients were added in combination with *Dryas* removal, suggesting that removal of a competitor increased the benefit of the additional nutrient availability for *Thalictrum* (significant time × nutrients × removal, Fig. 3a). A significant interaction (time × temperature × nutrients, Fig. 3b) on *Thalictrum* leaf area indicated that leaves on fertilized plants, which in mid-June were bigger than leaves in all other treatments, decreased significantly in mean size from mid-July outside the OTCs, but remained bigger than all other leaves throughout August inside OTCs. *Thalictrum* leaf stalks, which also were longest on fertilized leaves, declined by the end of the growing season in most treatments except where *Dryas* was removed inside the OTCs, where they continued to

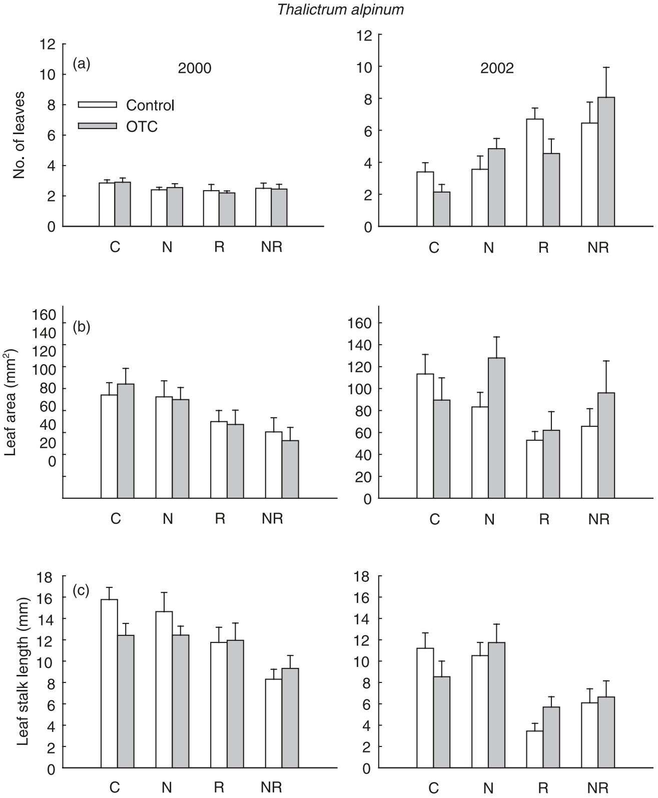

Fig. 1 Means and standard errors of (a) the number of leaves, (b) leaf area, and (c) length of leaf stalks of *Thalictrum alpinum* measured at the start of the experiment in 2000 (ANCOVA pre-treatment values) and by the end of the 2002 growing season in a *Dryas octopetala* heath outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway. $n = 10$ for each treatment.

grow throughout the season (significant time × removal, and time × temperature × nutrients, Fig. 3c).

For *Carex*, the combination of *Dryas* removal and nutrient addition clearly increased the number of leaves, primarily because of late season growth (July, August) when leaf production in the other treatments had terminated (significant time × removal × nutrients, Fig. 4a). No other seasonal growth pattern differed significantly between treatments on the vegetative growth of *Carex.*

SEXUAL REPRODUCTION AND MORTALITY

For the *Thalictrum* ramets, 2.5%, 5.0%, 37.5% and 3.8% reproduced sexually in 2000, 2001, 2002 and 2003, respectively. *Dryas* removal or nutrient addition had no effect on flowering frequency of *Thalictrum* (Pearsons $\chi^2 < 0.001$, $P > 0.10$ in both cases). Warming on the other hand, decreased flowering frequency by 32.5% (Pearsons $\chi^2 = 8.90$, $P = 0.003$) but increased the height of the flower stems of *Thalictrum* by 36.2% (Mann–Whitney $U = 89$, $P = 0.061$, Fig. 5a). There were no effects of any of the treatments on number of flowers per ramet (Mann–Whitney $U < 71$, $P > 0.311$ in all cases, Fig. 5b), whereas nutrient addition marginally decreased the number of seeds per flower by 25.5% (Mann–Whitney $U = 86$, $P = 0.093$, Fig. 5c).

For *Carex*, 95%, 2.5%, 2.5% and 5.0% of the target ramets reproduced sexually in 2000, 2001, 2002 and 2003, respectively. *Dryas* removal and warming increased flowering frequency by 13.6% (Pearsons $\chi^2 = 5.97$, $P = 0.015$) and 11.3% (Pearsons $\chi^2 = 3.82$, $P = 0.051$), respectively. Nutrient addition had no effect on flowering frequency of *Carex* (Pearsons $\chi^2 = 2.22$, $P = 0.136$). None of the treatments had any effects on the height of flower stem of *Carex* (Mann–Whitney < 80, $P > 0.100$ in all cases).

Thalictrum mortality decreased by 2.5%, 12.5% and 7.5% due to *Dryas* removal, warming and nutrient addition, respectively, although none of these responses were statistically significant (Pearsons $\chi^2 < 0.001$, $P > 0.98$ in all cases).

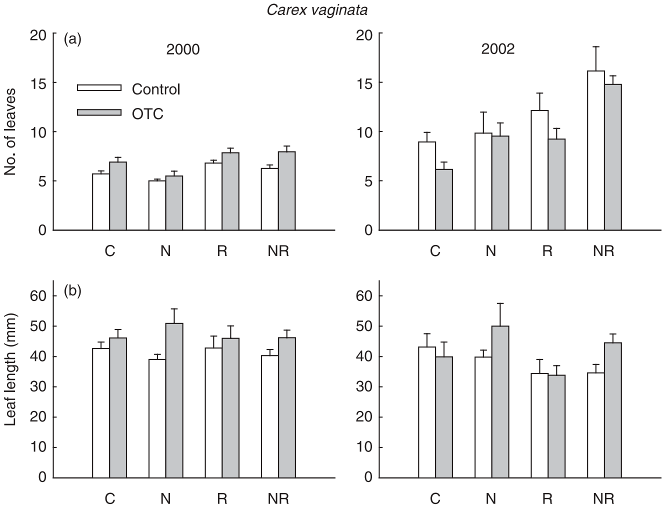

Fig. 2 Means and standard errors of (a) the number of leaves and (b) leaf length of *Carex vaginata* measured in a *Dryas octopetala* heath by the end of the 2000 and 2002 growing season outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway. $n = 10$ for each treatment.

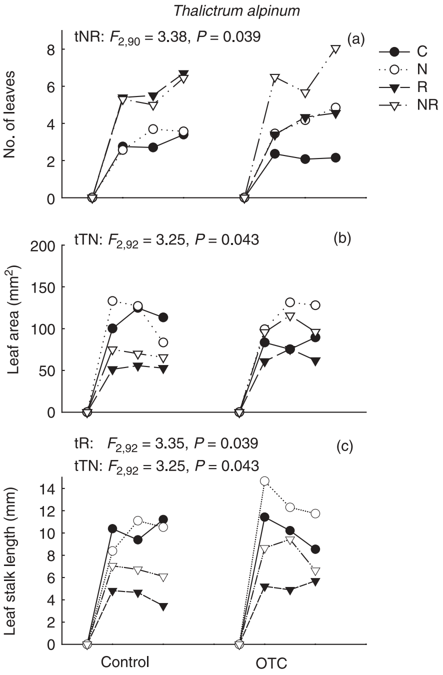

Fig. 3 Means of the number of leaves (a), leaf area (b) and leaf stalk length (c) of *Thalictrum alpinum* measured in a *Dryas octopetala* heath in late May, late June, late July and late August, outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway in 2002. F values, degrees of freedom and P values are shown for significant time (t) × treatment interactions, as tested by repeated measures ANOVA. To improve readability, standard errors are not shown. $n = 10$ for each treatment.

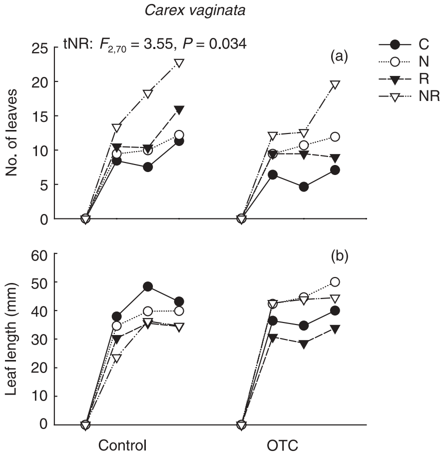

Fig. 4 Means of numbers (a) and length (b) of *Carex vaginata* leaves measured in late May, late June, late July and late August, in a *Dryas octopetala* heath, outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway in 2002. F values, degrees of freedom and P values are shown for significant time (t) × treatment interactions, as tested by repeated measures ANOVA. To improve readability, standard errors are not shown. $n = 10$ for each treatment.

Discussion

BIOTIC EFFECTS

Species interactions clearly affected plant growth, and thus could potentially influence population dynamics, of *Thalictrum alpinum* and *Carex vaginata* at alpine

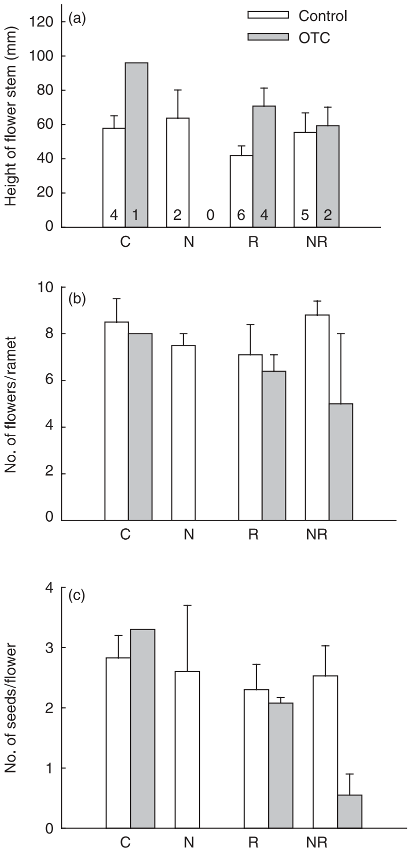

Fig. 5 Means and standard errors of (a) the height of flower stems, (b) number of flowers per ramet, and (c) number of seeds per flower of *Thalictrum alpinum* measured in a *Dryas octopetala* heath by the end of the 2002 and 2003 growing season outside (controls) and inside OTCs, on ramets receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway. Numbers in the columns are sample sizes for each treatment.

Finse, which is in contrast to Hobbie *et al.* (1999), who found no effects of removal treatments on the remaining species in Arctic tundra, and thus no evidence for species interactions.

Removal of *Dryas* increased the number of leaves of *Thalictrum alpinum* and *Carex vaginata*, and flowering frequency of *Carex* (Table 3). On the other hand, leaf stalks of *Thalictrum* and leaves of *Carex* became significantly shorter, suggesting a shift in internal resource allocation in both species after *Dryas* removal. The increased number of leaves (*Thalictrum* and *Carex*) and flowering frequency (*Carex*) after removal of *Dryas*, suggest competitive rather than facilitative impacts of *Dryas* at Finse. This is in line with Klanderud & Totland (in press), who found that *Dryas* decreased plant community diversity at Finse, and it is in line with other removal experiments detecting negative plant–plant interactions in alpine and subarctic sites (Aarssen & Epp 1990; Shevtsova *et al.* 1995). The same neighbour may, however, have multiple effects (Aarssen & Epp 1990), and the reduced length of *Thalictrum* leaf stalks and *Carex* leaves after *Dryas* removal may be caused by a loss of facilitative shelter against low temperature and strong winds. Bret-Harte *et al.* (2004) found possible facilitation of *Ledum palustre* on one forb in the Alaskan tundra. Moreover, Shevtsova *et al.* (1995) found decreased shoot length in some species after neighbour removal in sub-arctic Finland, which they suggested could be due to either a loss of facilitative protection or a release from negative shading effects. Shading may be considerable at high latitudes with low angle of sunlight and low annual solar input (Shevtsova *et al.* 1995), and the plants may produce larger leaves (e.g. Dormann & Woodin 2002; Totland & Esaete 2002), or longer shoots, to compensate for shading or to position flowers, seeds or photosynthetically active tissue above neighbouring plants (Grime 1979). When associated vegetation is removed, the influx of solar radiation increases, and the plants no longer need to compensate, or escape from shading, and this may result in shorter leaves and leaf stalks. However, the positive warming effects on various growth and reproductive parameters at Finse suggest that loss of facilitation effects may explain these responses, at least in part.

Dryas had similar effects on the vegetative growth of *Thalictrum* and *Carex*, although leaf production for *Thalictrum* increased proportionally more than for *Carex* after *Dryas* removal, suggesting a stronger role of competition from *Dryas* on *Thalictrum*. For sexual reproduction on the other hand, no *Dryas* effects were detected for *Thalictrum*, whereas competition from *Dryas* reduced the sexual reproductive effort of *Carex*.

ABIOTIC EFFECTS

Warming had positive effects on sexual reproductive parameters of the two target species, such as the height of flower stems of *Thalictrum alpinum* and flowering frequency of *Carex vaginata* (Table 3). Nutrients, on the other hand, increased the vegetative growth of both *Thalictrum* and *Carex*, although in most cases only in combination with warming. This shows that both warming and nutrient availability limited vegetative growth of these species at Finse (Table 3). Increased nutrient availability had no effect on the sexual reproduction of the target species, except a close to significant negative effect on the number of seeds of *Thalictrum*. These results are in line with other climate change experiments, showing that nutrients limit plant growth in alpine and arctic environments, with only minor effects of temperature alone, but often with synergistic effects of warming and nutrients (e.g. Chapin & Shaver 1985; Robinson *et al.* 1998; K. Klanderud & Ø. Totland, unpublished data). Warming, on the other hand, has been shown to increase the reproductive effort of several alpine and arctic species (Arft *et al.* 1999). These

Table 3 Summary responses of treatments with significant effects ($P < 0.05$, $P > 0.05$ in parentheses) on growth and reproductive parameters of *Thalictrum alpinum* and *Carex vaginata* growing in alpine *Dryas octopetala* heaths, as tested by different methods (see text). + = positive response; – = negative response; empty cells indicate no response ($P \geq 0.1$), and dots (.) indicate that no tests are done. Treatment abbreviations as in Table 2

Species and parameters	Treatments and responses						
	+ T	+ N	+ R	+ T + N	+ N + R	+ T + R	+ T + N + R
Thalictrum alpinum							
No. of leaves			+	+			
Leaf area							
Length of leaf stalk		+	–				(–)
Height of flower stem	(+)			.	.	.	.
No. of flowers				.	.	.	.
No. of seeds		(–)		.	.	.	.
Flowering frequency	–			.	.	.	.
Mortality				.	.	.	.
Carex vaginata							
No. of leaves		+	+	(+)			
Leaf length			–				
Height of flower stem				.	.	.	.
Flowering frequency	+		+	.	.	.	.

results are also in line with the meta-analysis of Dormann & Woodin (2002), although they found that nutrients also limit reproduction of arctic plants.

Vegetative growth increased more after nutrient addition in *Carex* than in *Thalictrum*, which is also in line with a number of experiments showing that graminoids respond more to increased nutrient availability than other functional groups (e.g. Jonasson 1992; Dormann & Woodin 2002; Bret-Harte *et al.* 2004; K. Klanderud & Ø. Totland, unpublished data).

SPECIES INTERACTIONS

Increased nutrient availability caused by climate change may modify the interactions between *Dryas* and other species at Finse. Nutrients appeared to be a limiting factor for plant growth at Finse, and the increase in late season leaf production of *Thalictrum* and *Carex* after *Dryas* removal combined with nutrient addition, suggests that these species benefit more from the increased nutrient availability when *Dryas* was removed. This is in line with Bret-Harte *et al.* (2004) who found increased graminoid biomass after removal treatment combined with fertilization, probably in response to increased nutrient availability when neighbours were removed. My results indicate that *Dryas* is a stronger competitor for nutrients than *Thalictrum* and *Carex*, which again may suggest that the role of competition from *Dryas* may be greater if nutrient availability increases under global warming.

Furthermore, warming reduced *Thalictrum* flowering frequency, while nutrient addition slightly decreased the number of seeds of *Thalictrum*, which may suggest that the possible negative effects of growing inside a *Dryas* mat may be greater when resources increase, most likely because of increased competition from *Dryas*. This is in line with findings of a greater role of competition under higher productivity (e.g. Bertness & Shumway 1993; Callaway 1998; Choler *et al.* 2001; Klanderud & Totland, in press), and it corresponds with Callaway *et al.* (2002), who found shifts from positive to negative species interactions of alpine plants when temperatures increased along latitudinal and altitudinal gradients.

The predicted response to increased nutrient availability varies among functional groups (e.g. Dormann & Woodin 2002). Grasses have been shown to respond strongly to nutrient addition, and increased nutrient availability caused by climate change may influence competition hierarchies, and thus species composition of plant communities. This is in line with Grime (1977) and others, who have found altered competition hierarchies in several ecosystems after changes in nutrient conditions (Austin & Austin 1986; DiTomasso & Aarssen 1989; Gurevitch & Unnasch 1989), whereas species interactions have not changed after short-term warming treatments alone (Hobbie *et al.* 1999). Overall, *Dryas* appeared to protect other species from low temperatures at Finse, but at the same time, there may be interspecific competition for nutrients. Thus, global warming may result in a shift towards increased competition, because increased nutrient availability may change competition hierarchies, resulting in more competition for light and space.

IMPLICATIONS FOR CLIMATE CHANGE MODELS

Previous climate change experiments have primarily focused on abiotic effects on plant growth, and most climate change models tend to ignore species interactions (Mooney 1991; Pacala & Hurtt 1993; Davies *et al.* 1998). This study clearly shows that both biotic and abiotic conditions affect alpine plant growth and possible population dynamics. Furthermore, climate change may alter species interactions, e.g. the role of competition from *Dryas* or other species may become greater in a future with more resources. Thus, species interactions should be considered in climate change experiments and in models predicting future plant community responses to global warming.

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Paper III

The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species

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Running headline*: Neighbour and abiotic factor effects in the alpine*

Summary

1. Vegetation removal manipulations over four growing seasons in an alpine *Dryas* heath at Finse, south Norway, were used to examine the role of neighbour vegetation for the population dynamics of the herb *Thalictrum alpinum* and the sedge *Carex vaginata.* We also increased temperature (by open top chambers) and nutrient availability to assess if effects of surrounding vegetation may be modified by environmental change.

2. Removal of neighbour vegetation increased the number of leaves of *Thalictrum* and *Carex,* whereas flowering stems and leaf stalks of *Thalictrum* became significantly shorter. Furthermore, increased plant growth after nutrient addition and warming suggests that both abiotic environmental conditions and biotic interactions limit plant growth at Finse.

3. Our results suggest that there is competition for nutrients at Finse, but that surrounding vegetation may also have facilitative sheltering effects on other species.

4. Interactions between vegetation removal and abiotic factors on population dynamic parameters of *Thalictrum* suggest that plant-plant interactions may be modified if temperature and nutrient availability increase under climate change.

5. The responses of the two target species to the removal of the general neighbour vegetation were less pronounced than their responses to the removal of the dominant *Dryas octopetala* examined in a previous study. This suggests that one dominant species may affect the population dynamics of other species more than the net effect of all the other species in the community in concert.

6. Our results show that biotic interactions may affect alpine plant populations and thereby structure alpine plant communities. Furthermore, the effect of neighbours and abiotic environmental changes on alpine plant growth may depend on the species identity of the neighbours.

Key-words: Carex vaginata, climate change, competition, *Dryas* heath, facilitation, nutrient availability, vegetation removal, species interactions, *Thalictrum alpinum,* warming

Introduction

The relative importance of species interactions and abiotic environmental factors for community structure and processes in areas of contrasting abiotic severity and productivity is unclear (Callaway & Walker 1997; Huston & Mc Bride 2002). Grime (1979) proposed that competition plays an important role in structuring species composition in plant communities where primary production is high. However, the effects of interactions in areas of low productivity, such as in alpine and arctic plant communities of high abiotic stress, are heavily debated. Under such conditions, competition may have an important role for the population dynamic of individual species because soil resources are in limited supply (e.g. Chapin & Shaver 1985; Tilman 1988; Körner 1999). Alternatively, some ecologists propose that facilitation may have a more important role than competition in environmentally severe habitats because neighbour vegetation may ameliorate the physical environment and thereby improve the survival, growth, and reproduction of individual plants (e.g. Callaghan & Emanuelson 1985; Bertness & Callaway 1994). It is also possible that interactions (positive or negative) from other species have a low impact on population dynamics compared to direct impacts from abiotic environmental conditions (e.g. Savile 1960; Billings & Mooney 1968; Grime 1977).

Climate change is predicted to have large effects on alpine and arctic plant communities (e.g. Callaghan & Jonasson 1995; Guisan *et al.* 1995; Körner 1995; 1999), and may directly modify abiotic conditions that influence individual plant performance (Arft et al. 1999), such as soil moisture and nutrient availability (e.g. Nadelhoffer *et al.* 1991; Harte *et al.*

1995). In combination with the direct warming effect, these factors may impact the internal processes of individual plants, such as growth, reproduction and resource allocation (Arft et al. 1999; Dormann & Woodin 2002), with potential cascading effects on the dynamics of populations and the species composition and diversity of plant communities. Moreover, since individual plant species (see for example Henry & Molau 1997) may respond differently to environmental change, global warming may indirectly change the current balance between positive and negative plant-plant interactions and thereby alter dominance hierarchies in plant communities. Thus, a more complete understanding of climate change effects requires that we consider the relative importance of changes in direct abiotic effects versus indirect biotic effects on important parameters of the population dynamics of species in concert.

The impact of neighbour vegetation on plant community structure, through its impacts on the population dynamic of individual species, may differ spatially and among species (see Hobbie *et al.* 1999; Dormann *et al.* 2004). Moreover, even though interactions from neighbouring vegetation may directly affect community structure, and may be modified by climate change, this effect is largely ignored in models predicting plant community or ecosystem responses to climate change (Mooney 1991; Pacala & Hurtt 1993; Davies *et al.* 1998; Dormann & Woodin 2002). Only a few climate change experiments have focused on species interactions (but see Shevtsova *et al*. 1997; Hobbie *et al.* 1999; Bret-Harte *et al*. 2004; Dormann *et al.* 2004; Klanderud 2005), and most of these have assessed the effects of only one or a few selected species on neighbours (but see Bret-Harte *et al*. 2004). In the natural biota, however, several species may simultaneously impact each other (Bret-Harte *et al.* 2004). Furthermore, climate change may affect all the possible interactions between all the species in a community.

In this study, we first examine the possible effects of removal of all neighbour vegetation on population dynamic parameters of two species (*Thalictrum alpinum* L. and

Carex vaginata Tausch.) in an alpine plant community. Second, we compare results from this study with effects of removal of only the dominant dwarf shrub, *Dryas octopetala* L. (Klanderud 2005), using the same experimental set-up. This will enable us to assess if removal of the dominant species and removal of the general neighbour vegetation have similar or different impacts on the two target species. We use experimental removal of neighbours, warming (open top chambers, OTCs) and nutrient addition to examine the relative role of neighbour vegetation and abiotic environmental conditions on the population dynamics of *Thalictrum alpinum* and *Carex vaginata* and thus to assess whether species interactions may be modified under climate warming. We predict that removal of the whole neighbour vegetation may have greater effect on the target species than removal of only *Dryas* (Klanderud 2005), because numerous species and functional groups in concert are likely to utilize the available resources more completely (e.g. MacArthur 1970, Tilman 1996) than one single species, despite this species being dominant.

Methods

STUDY SYSTEM

The experiment was initiated in early July 2000 and continued until the end of the growing season (late August) in 2003. The study site was situated in a southwest exposed slope of a *Dryas octopetala* heath at ca 1500 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (60° N, 7° E) in alpine southwest Norway. The mean summer (June, July, August) temperature at 1222 m elevation at Finse is 6.3 °C (Aune 1993), and mean summer precipitation is 89 mm (Førland 1993). Abundant vascular species in the *Dryas* heath, besides *Dryas octopetala*, are the herbs *Thalictrum alpinum* L.*,* *Potentilla crantzii* Crantz., *Bistorta vivipara* L.*,* and *Cerastium alpinum* L.*,* the dwarf shrub *Salix reticulata* L., the grasses

Festuca vivipara L. and *Poa alpina* L., and the sedges *Carex vaginata* Tausch.*, C. atrofusca* Schkuhr*, C. rupestris*, and *Luzula spicata* L. (nomenclature follows Lid & Lid 1994).

EXPERIMENTAL DESIGN

To assess if warming, increased nutrient availability and removal of neighbour vegetation have any effects on components of the population dynamics of *Thalictrum alpinum* and *Carex vaginata*, and if environmental conditions may modify any effect of the surrounding vegetation, we randomly selected twenty plots. We randomly placed OTCs upon ten of these plots and left the ten others as controls (ambient).

In each of the twenty main-plots, we selected eight *Thalictrum* and eight *Carex* tillers growing at least 10 cm away from any *Dryas* plant, and inserted half a slow-dissolving NPK-fertilizer stick into the soil *c.* 1 cm upslope of half the individuals of each species immediately after snowmelt and in late July (*c.* 0.2 g N, 0.04 g P, and 0.17 g K per tiller/growing season). Thereafter, we clipped the aboveground parts of all neighbour species, and carefully removed belowground parts that could be pulled up with minimal soil disturbance, from a radius of *c.* 5 cm around half of the fertilized tillers and around half of the tillers not receiving any fertilizer. We removed re-growth (mainly bryophytes with minimal belowground biomass) twice during each of the four growing seasons. This provides a split-plot design (Underwood 2001) with temperature treatment as a fixed factor conducted at main-plot level, 20 plots as a random factor nested within the main-plot factor (temperature), and nutrient addition and removal treatments as fixed factors conducted at sub-plot level. Thus, within each plot, whether with or without an OTC, two tillers of each of the two target species received each of the possible treatments; nutrient addition, removal of neighbours, nutrient addition and neighbour removal, and control. The responses of these two individuals were averaged prior to statistical analysis.

Experiments with removal of aboveground biomass may be problematic because it leaves roots to decompose, resulting in increased soil nutrients (Putwain & Harper 1970; Berendse 1983). However, these resources have most likely been obtained by competition in the past, and their release may benefit those plants that have previously been denied access to them (Aarssen & Epp 1990). Vegetation removal may also disturb the soil, resulting in a nutrient flush, but here there were probably only minor effects on belowground processes and soil disturbance.

The OTCs are hexagonally shaped polycarbonate chambers with an inside diagonal of *c.*1 m, and with qualities as described in Marion *et al.* (1997). OTCs are commonly used in climate change experiments to raise the temperature while minimizing secondary experimental effects, such as changes in atmospheric gas concentrations and ambient precipitation (e.g. Marion *et al.* 1997; Hollister & Webber 2000). The chambers did not affect the duration of snow cover (personal observation) and were therefore left in place during winter throughout the experiment. The OTCs increased summer air temperature *c.* 5 cm above ground by *c.* 1.5 °C, and ground temperature by *c.* 2.5 °C. In undisturbed vegetation, the OTCs increased soil temperature *c.* 5 cm below ground by *c.* 1.5 °C (see Klanderud 2005 for further details).

We fenced the site to prevent sheep grazing.

GROWTH MEASUREMENTS

We measured growth and reproductive variables of *Thalictrum alpinum* and *Carex vaginata* in late August after the first (2000), second (2001), third (2002) and reproductive variables only in the fourth (2003) growing season. To assess differences in within-season growth rates, we also measured the growth variables during the second and the third growing season in late May (before any growth had started), late June and late July. However, to enable possible remaining legacy effects caused by the removal treatment to decline, only the 2002 and 2003 measurements were used in the statistical analyses, with the 2000 measurements as co-variables.

Sexually reproducing *Carex* tillers normally die the year after flowering, with new tillers growing out from the old (*Carex vaginata*; personal observation, *C. bigelowii*; see Brooker *et al.* 2001). To simplify interpretation of growth and sexual reproduction of *Carex*, we obtained target tillers at similar developmental stages by selecting flowering *Carex* tillers at the start of the experiment. Thus, we measured the new daughter tillers if the mother tiller died. Daughter tillers may also grow out from living target tillers of both *Thalictrum* and *Carex*, and to obtain an estimate of vegetative growth of the two species, we counted the number of green leaves on each target tiller with daughter tillers if present. The data from the target and daughter tillers are pooled in the statistical analyses. As the number of leaves is not reported per tiller, possible changes may be due either to increased tillering or increased size of the individual tillers. Furthermore, we measured the length and the width of the largest and the smallest leaf and the length of their leaf stalks (*Thalictrum*), and the length of the longest leaf (*Carex*), using a digital caliper. We calculated an approximate leaf area for *Thalictrum* leaves by multiplying the width by the length and used the mean of the values for the largest and smallest leaf to represent average area for that tiller. Number of leaves, average leaf area, and the length of leaf stalks are parameters commonly used to obtain non-destructive measures of vegetative growth for herbs, whereas number of leaves and the length of the longest leaf are commonly used for sedges (Molau & Edlund 1996; Arft *et al.* 1999). We recorded dead target tillers to estimate mortality. Measuring mortality on clonal plants is, however, not easily applied because individuals usually persist, and only parts of the plants die. The data for *Carex* were not analysed since mortality here coincided with sexual reproduction.

Vegetative regeneration is common for alpine plants. *Thalictrum* and *Carex* grow clonally by producing new tillers from below ground rhizomes, and seedlings of these species are rarely found on Sandalsnuten. Therefore, our assessment of population dynamic responses relates to effects on mature individuals rather than seedling responses.

SEXUAL REPRODUCTION MEASUREMENTS

To estimate the sexual reproductive effort of *Thalictrum* and *Carex,* we measured the height of flowering stems and collected mature infructescences at the end of each season and recorded the number of flowers and number and weight of dried seeds. Alpine and arctic plants normally do not produce flowers every year (Sonesson & Callaghan 1991), and the same tiller did not reproduce more than once during the experiment for either of the two species. To increase the sample size, we therefore pooled measurements of all flowering tillers from 2002-2003 to conduct statistical tests on height of flowering stem, number of flowers and seeds, and flowering frequency of *Thalictrum.* There were too few mature seeds to conduct statistical tests on seed weight. In *Carex,* there were not enough flowering tillers to test for any of the sexual reproduction parameters.

STATISTICAL ANALYSES

To examine if warming, nutrient addition and removal of neighbour vegetation had any impact on the growth of *Thalictrum* and *Carex*, and if possible species interactions were affected by the environmental factors, we used general linear models (GLM, SYSTAT 10) with the temperature treatment (main-plot factor), nutrient addition, vegetation removal and their interactions (sub-plot factors) as fixed factors, and plot nested within temperature as a random factor in a split-plot ANCOVA. We used the first year (2000) measurements as co-variables in the analyses to increase the model's ability to detect treatment effects, although this may decrease the ability to detect any responses if these actually occurred during the first year. The effect of temperature was tested over the plot error (main-plot term), whereas all other effects were tested over the model error (sub-plot term) as described in e.g. Underwood (2001). Analyses were conducted separately for the two species. Data on leaf number, leaf area (*Thalictrum*), and leaf length (*Carex*) were log-transformed to fulfil the ANCOVA assumptions of normality and equal variances. All graphs are shown with untransformed data.

To examine if the removal of neighbour vegetation or the environmental factors had any impact on the growth phenology of *Carex* and *Thalictrum* during the third (2002) growing season, we used repeated-measures ANOVA with the same factors as above, and with tiller identity during three measurements throughout the season (time) as the repeated measures factor. A significant interaction between time and treatment may then indicate that treatments differ in the pattern of growth during the season.

Because of low sample sizes for sexual reproduction, we used Mann-Whitney U-tests to assess if the height of flower stems, number of flowers per tiller and number of seeds per flower were affected by the treatments. Analyses were done within each treatment separately (temperature vs. ambient, nutrient addition vs. natural, removal vs. undisturbed). We used Pearson's chi-square to examine if flowering frequency and mortality for *Thalictrum* differed between treatments.

Results

VEGETATIVE GROWTH

Removal of neighbour vegetation increased the number of leaves of *Thalictrum alpinum* by 79.2 % (Fig. 1a) and of *Carex vaginata* by 54.5 % (Fig. 2a) across all treatments. The *Thalictrum* leaves became 31.3 % smaller and the *Carex* leaves became 10.2 % shorter after vegetation removal, although this effect was not significant for *Thalictrum* and only close to significant for *Carex* (Table 1, Figs 1b and 2b). Furthermore, vegetation removal decreased the length of *Thalictrum* leaf stalks by 22.6 %, although a significant three-way interaction indicated that temperature, nutrient and removal treatments modified each other's impacts on the leaf stalk lengths (Table 1, Fig. 1c). Two-way ANCOVAs performed on tillers inside and outside OTCs separately, suggested that the removal treatment significantly decreased the length of *Thalictrum* leaf stalks outside the OTCs ($F_{1,34} = 10.07$, $P = 0.003$) but not inside ($F_{1,32}= 0.12$, $P = 0.728$) (Fig. 1c). Moreover, close to significant and significant interactions between nutrient addition and vegetation removal outside ($F_{1,34} = 3.87$, $P = 0.057$) and inside ($F_{1,32} = 5.15$, $P = 0.03$) the OTCs (Fig. 1c), suggested that the responses to the combined effect of these factors were less than the sum of the separate effects. Thus, warming increased the length of *Thalictrum* leaf stalks, but only in combination with added nutrients or after vegetation removal (Table 1, Fig. 1c).

Warming or nutrient addition had no effects on the number of *Thalictrum* leaves (Table 1, Fig. 1a). For *Carex*, on the other hand, an interaction between warming and nutrient addition suggests that the responses to the combined effect of these factors were less than the sum of the separate effects (Table 1, Fig. 2a). Overall, warming and nutrient addition increased leaf area of *Thalictrum* by 43.5 % and 30.3 %, respectively. The warming effect had already occurred by the end of the first growing season (significant 2000 measure Table 1, Fig. 1b), which may explain why no such response was detected by the ANCOVA. An interaction between warming and nutrient addition suggests that the combined effect of these treatments was larger than the effect of each treatment alone (Table 1, Fig. 1b). Nutrient addition increased the length of *Carex* leaves by 28.8 %, and warming had no effect on the length of *Carex* leaves (Table 1, Fig. 2b).

There were no significant treatment effects on growth phenology of *Thalictrum* or *Carex* (non-significant interactions between time and treatment in the repeated-measures ANOVA).

SEXUAL REPRODUCTION AND MORTALITY

17.5 %, 18.8 %, 46.3 %, and 10 % of the *Thalictrum* tillers reproduced sexually in 2000, 2001, 2002, and 2003 respectively. Removal of neighbours or nutrient addition had no effect on its flowering frequency of (Pearson's $\chi^2 < 0.001$, $P > 0.10$ in both cases). The height of the flower stems of *Thalictrum* were increased by 55.8 % by warming (Mann-Whitney U = 198, $P = 0.002$) and reduced, across all treatments, by 22.4 % following neighbour removal (Mann-Whitney U = 165, $P = 0.039$, Fig. 3a). None of the treatments had any significant effects on the number of flowers and seeds (Table 2, Fig. 3b, c), although the combination of warming and nutrient addition appeared to increase the number of flowers per tiller (Fig. 3b).

For *Carex*, 98.8 %, 0 %, 5 %, and 8.8 % of the target tillers reproduced sexually in 2000, 2001, 2002, and 2003, respectively.

None of the treatments had any significant effects on *Thalictrum* mortality (Pearson's $\chi^2 < 0.001$, $P > 0.98$ in all cases).

Discussion

Neighbour vegetation clearly affected plant growth and, potentially, population dynamics of *Thalictrum alpinum* and *Carex vaginata* at alpine Finse. The responses of the two species to the removal of neighbours in this study were, however, not as pronounced as their responses to the removal of the dominant dwarf shrub *Dryas octopetala* in the same system (Klanderud 2005). This result may suggest that the role of one dominant species in affecting population dynamics of plant species may be more important than the net effect of all the other species in this community.

EFFECTS OF VEGETATION REMOVAL

Flower stems and leaf stalks of *Thalictrum*, and leaves of *Carex* became shorter (although only marginally significant for *Carex*), whereas leaf number of *Thalictrum* and *Carex* increased after removal of neighbour vegetation (Table 2). These opposing responses, which occur in both species, are in line with the responses to *Dryas* removal (Klanderud 2005), and suggest that individual tillers change their internal resource allocation after vegetation removal. The results are, however, in contrast to removal treatments in other arctic sites, where there have been few detected effects of neighbours (Hobbie *et al.* 1999; Jonasson 1992; Bret-Harte *et al.* 2004), and thus no evidence for species interactions (but see Dormann *et al.* 2004). The increased number of leaves of *Thalictrum* and *Carex* after vegetation removal, suggests competitive rather than facilitative impacts of other species at Finse, which is in line with Klanderud (2005) and some other removal experiments in alpine or sub-arctic sites (Aarssen & Epp 1990; Shevtsova *et al*. 1995). However, plants can be suppressed by some neighbours, and at the same time, benefit from the presence of others (Aarssen & Epp 1990; Dormann *et al*. 2004), and the shorter leaf stalks, flower stems, and leaves after removal treatment may be caused by a loss of facilitative shelter against low temperature and strong winds. The positive effects of warming on flower stems and leaf stalks of *Thalictrum* further suggests a possible benefit from protective neighbours, which is regarded as an important factor in extreme environments (e.g. Carlsson & Callaghan 1991; Callaway *et al*. 2002). Bret-Harte *et al.* (2004) found possible facilitation effects from one shrub (*Ledum palustre*) on forb species (*Pedicularis* spp.) in the Alaskan tundra, and Shevtsova *et al*. (1997) found negative effects on *Vaccinium vitis-idaea* after removal of *Empetrum nigrum.* Moreover, Shevtsova *et* *al*. (1995) found decreased shoot length in various species after neighbour removal, which they suggested to be due to either a loss of facilitative protection or a release from negative shading effects. The latter explanation assumes that plants may produce larger leaves (e.g. Dormann & Woodin 2002; Totland & Esaete 2002) or longer shoots to compensate for shading and to position flowers, seeds or photosynthetically active tissue above neighbour plants (Grime 1979). However, the positive growth responses to warming, and the negative effect of removal on leaf stalks outside but not inside the OTCs (Fig. 1c), suggest that, at Finse, at least part of the effect is due to facilitation. Furthermore, a larger relative decrease of *Carex* leaf lengths after *Dryas* removal (Klanderud 2005) than after removal of other species (this study), may suggest a greater facilitative effect of *Dryas* than of other species on the vegetative growth of *Carex.*

EFFECTS OF CLIMATE CHANGE SIMULATION

Both warming and nutrient availability limited the growth of *Thalictrum* and *Carex* at Finse, with the two factors often showing synergistic effects. Warming alone had only minor effects on vegetative growth of either species, but increased the height of flowering stems of *Thalictrum* (Table 2). Nutrient addition on the other hand, had only minor effects on the sexual reproduction of *Thalictrum*, but increased the vegetative growth of both species (Table 2). Other climate change experiments have also found that nutrients limit plant growth in alpine and arctic environments and that enhanced temperature alone has only minor effects (Dormann & Woodin 2002). Often, however, studies have found synergistic effects of warming and nutrients together, suggesting that the conditions of one factor may affect responses to another factor (e.g. Chapin & Shaver 1985; Robinson *et al*. 1998; Klanderud & Totland in press).

EFFECTS OF WHOLE VEGETATION VERSUS ONE DOMINANT SPECIES

Although the vegetation removal in this study had generally similar effects on the population dynamic parameters of *Thalictrum alpinum* and *Carex vaginata* as the removal of the dominant *Dryas octopetala* had in a previous study of Klanderud (2005), the overall effects of *Dryas* appeared to be larger. For example, vegetation removal (this study) had no significant effects on the combination of seasonal growth and effect sizes of *Thalictrum* and *Carex*, whereas *Dryas* removal had (Klanderud 2005). Furthermore, nutrient addition increased leaf sizes of *Thalictrum* and *Carex* tillers surrounded by general vegetation (this study), but had no effect on leaf sizes of tillers surrounded by *Dryas* (Klanderud 2005). Moreover, flowering frequency of *Thalictrum* was considerably higher when surrounded by general vegetation than inside *Dryas* mats. All these results may suggest that *Dryas* controls more of the population dynamics of the two target species than the sum of all other species in the community in concert. Moreover, the role of *Dryas*, both as a facilitator and a competitor, appears to be greater than the net effect of the general vegetation. Although individual species may have imposed equally large effects on the target species as did *Dryas*, the effects of species acting in opposite directions could have cancelled out, leading to a smaller net effect compared to that of *Dryas*. Moreover, the larger *Dryas* effect may have been due to the *Dryas* biomass removed in the previous experiment being more than the biomass of surrounding vegetation removed here. Indeed, it may be important to distinguish between the roles of the amount versus the identity of the biomass removed to understand ecosystem functioning (Díaz et al. 2003). Unfortunately, our data are not suitable for testing these potentially opposing effects.

Our results are in contrast to our predictions, where we anticipated a larger effect of vegetation removal because numerous species and functional groups are expected to utilize more resource niches than only one species (e.g. Tilman 1996). The weaker effects of vegetation removal than *Dryas* removal are, however, partly in line with Bret-Harte *et al.*

(2004), who did not find any effects of neighbour removal in the Alaskan tussock tundra, even though nutrient release increased by up to two orders of magnitude. They suggested that rigid niche differentiation and complementarities of nutrient uptake of tundra plants make species unable to utilize additional resources released by neighbour removal (Bret-Harte *et al.* 2004). Nevertheless, *Dryas,* which already dominated the resource use in our site, apparently strengthened its dominance position when resources increased after nutrient addition. Moreover, warming decreased flowering frequency and nutrient addition decreased seed number of *Thalictrum* tillers associated with *Dryas* (Klanderud 2005), whereas these treatments had no effects on individuals surrounded by other species (this study). This may suggest that possible negative effects of *Dryas* may be larger when resources increase, most likely because *Dryas* benefits more from increased temperature and nutrient availability than the majority of other species.

EFFECTS OF ENVIRONMENTAL CONDITIONS ON SPECIES INTERACTIONS

Warming and nutrient addition significantly influenced the effect of vegetation removal on population dynamic parameters of *Thalictrum*, suggesting that climate change may modify species interactions at alpine Finse. In particular, the negative effect of removal on *Thalictrum* leaf stalks outside the OTCs but not inside, may suggest a benefit of protective neighbours that could become redundant under global warming. Similarly, the interaction between nutrient addition and vegetation removal on *Thalictrum* leaf stalks may suggest that, after removal of potential competitors, there is no benefit of the added nutrients, i.e. the plants are no longer nutrient limited.

The results of this study, combined with those of Klanderud (2005), highlight the role of both positive (e.g. Callaghan & Emanuelson 1985; Bertness & Callaway 1994) and negative (e.g. Chapin & Shaver 1985; Tilman 1988; Körner 1999; Dormann *et al.* 2004) species interactions in structuring alpine plant communities of high abiotic stress. Global warming may cause a shift towards an increased role of competition in cold environments, because the role of facilitation appears to decrease under warming (this study; Callaway et al. 2002). Moreover, increased nutrient availability, due to higher decomposition and mobilization of resources in warmer soils, may change competition hierarchies resulting in an increased role of competition for light and space. Significant interactions between removal manipulations and climatic factors in this study and that of Klanderud (2005) highlight the importance of understanding how climate change modifies species interactions, in order to predict future plant community responses to global warming with greater precision.

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Table 1 $F_{\text{d.f.}}$ and P values (significant at ≤ 0.05 in bold, < 0.1 in bold italics) of treatments performed in alpine *Dryas* heath vegetation; T = temperature (OTC vs. ambient, main-plot fixed factor), N = nutrient addition (increased vs. ambient, sub-plot fixed factor), R = removal of vegetation (yes vs. no, sub-plot fixed factor), their interactions, plot nested within T (random factor), and measurements from 2000 as co-variables in a split-plot design ANCOVA on number of leaves of *Thalictrum alpinum* and *Carex vaginata,* average leaf area and length of leaf stalk of the biggest and the smallest leaf of *Thalictrum*, and length of the longest leaf of *Carex*. $N = 10$ for each treatment

Sources of Variation	No of leaves		Leaf area or length		Leaf stalk	
	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P	$F_{\text{d.f.}}$	P
Thalictrum alpinum						
T	$0.60_{1,18}$	0.448	$0.15_{1,18}$	0.705	**$7.39_{1,18}$**	**0.014**
N	$1.04_{1,46}$	0.313	**5.95**$_{1,46}$	**0.018**	$1.95_{1,46}$	0.169
R	**17.75**$_{1,46}$	**<0.001**	$0.04_{1,46}$	0.841	**7.71**$_{1,46}$	**0.008**
T × N	$0.71_{1,46}$	0.402	**6.83**$_{1,46}$	**0.012**	**6.44**$_{1,46}$	**0.014**
T × R	$0.00_{1,46}$	0.966	$0.09_{1,46}$	0.767	**5.44**$_{1,46}$	**0.024**
N × R	$1.38_{1,46}$	0.246	$0.92_{1,46}$	0.342	$0.03_{1,46}$	0.864
T × N × R	$1.78_{1,46}$	0.189	$0.55_{1,46}$	0.462	**7.45**$_{1,46}$	**0.009**
Plot (T)	$1.12_{1,46}$	0.360	**2.28**$_{1,46}$	**0.011**	$1.28_{1,46}$	0.243
2000 measure	$0.08_{1,46}$	0.773	**18.99**$_{1,46}$	**<0.001**	$1.58_{1,46}$	0.215
Carex vaginata						
T	$0.84_{1,18}$	0.373	$0.15_{1,18}$	0.704		
N	**22.98**$_{1,44}$	**<0.001**	**13.67**$_{1,43}$	**0.001**		
R	**5.05**$_{1,44}$	**0.030**	***2.94***$_{1,43}$	***0.094***		
T × N	**3.97**$_{1,44}$	**0.053**	$0.25_{1,43}$	0.620		
T × R	$0.06_{1,44}$	0.812	$0.90_{1,43}$	0.347		
N × R	$0.23_{1,44}$	0.633	$0.003_{1,43}$	0.959		
T × N × R	$2.38_{1,44}$	0.130	$0.006_{1,43}$	0.938		
Plot (T)	***1.78***$_{1,44}$	***0.060***	$1.30_{1,43}$	0.234		
2000 measure	$0.21_{1,44}$	0.647	$0.69_{1,43}$	0.410		

Table 2 Summary of treatment responses with significant effects ($P < 0.05$, $P < 0.1 > 0.05$ in parentheses) on growth and reproductive parameters of *Thalictrum alpinum* and *Carex vaginata* growing in alpine *Dryas* heaths*,* as tested by different methods (see text). +: positive response; -: negative response; empty cells indicate no response ($P \geq 0.1$), and dots (.) indicate that no tests are done. Treatment abbreviations as in Table 2.

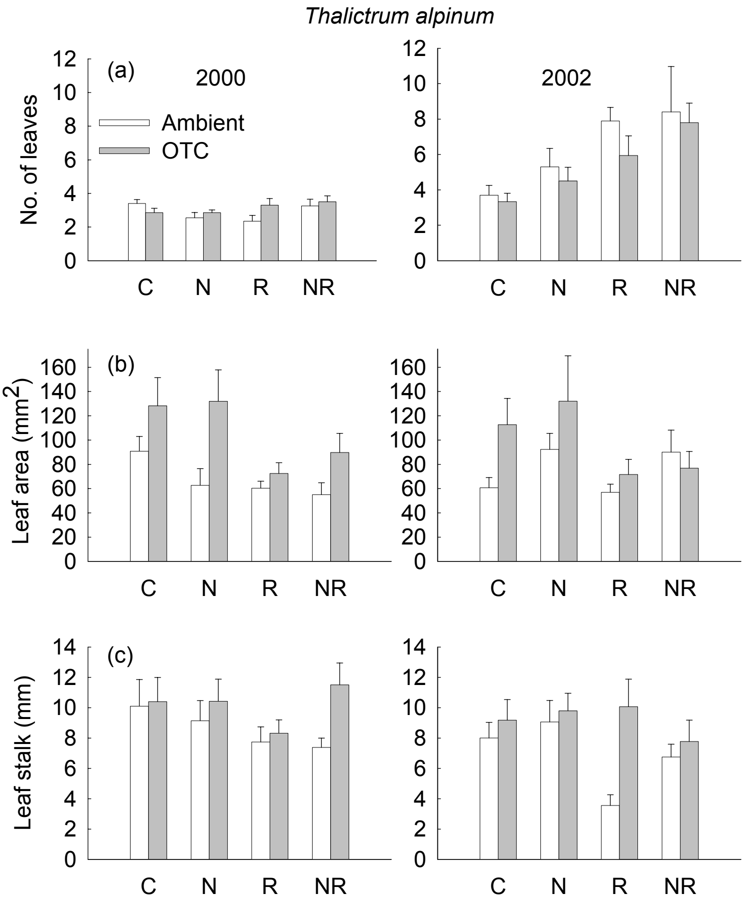
Species and parameters	Treatments and responses +T	+N	+R	+T+N	+N+R	+T+R	+T+N+R
Thalictrum alpinum							
No. of leaves			+				
Leaf area				+			
Length of leaf stalk		-	-	+	(-)		-
Height of flower stem	+		-	.	.	.	.
No. of flowers				.	.	.	.
No. of seeds				.	.	.	.
Flowering frequency				.	.	.	.
Mortality				.	.	.	.
Carex vaginata							
No. of leaves		+	+	+			
Leaf length		+	(-)				

Figure legends

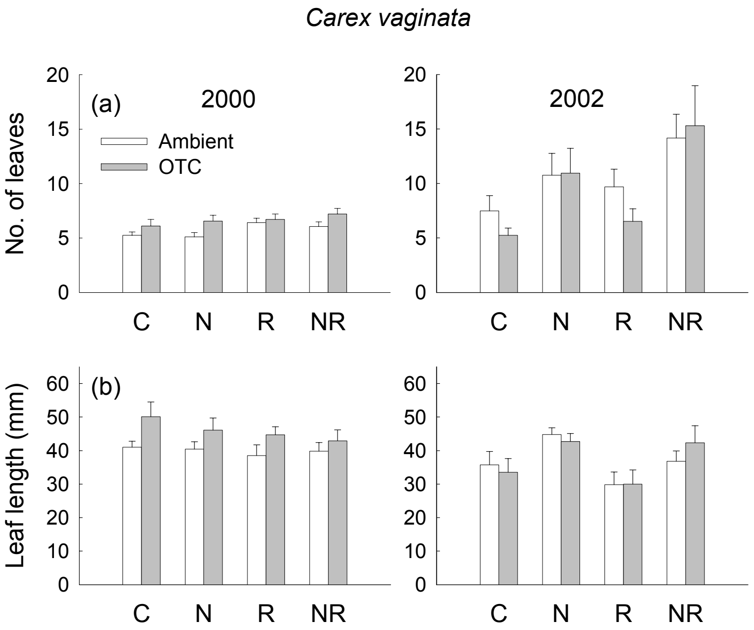
Fig. 1 Means and standard errors of (a) the number of leaves, (b) leaf area, and (c) length of leaf stalks of *Thalictrum alpinum* measured at the start of the experiment in 2000 (ANCOVA pre-treatment values) and by the end of the 2002 growing season in alpine *Dryas* heath vegetation outside (ambient) and inside OTCs, on tillers receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway. $N = 10$ for each treatment.

Fig. 2 Means and standard errors of (a) the number of leaves and (b) leaf length of *Carex vaginata* measured in alpine *Dryas* heath vegetation by the start of the experiment in 2000 (ANCOVA pre-treatment values) and by the end of the 2002 growing season outside (ambient) and inside OTCs, on tillers receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatments (C), at Finse, alpine south Norway. $N = 10$ for each treatment.

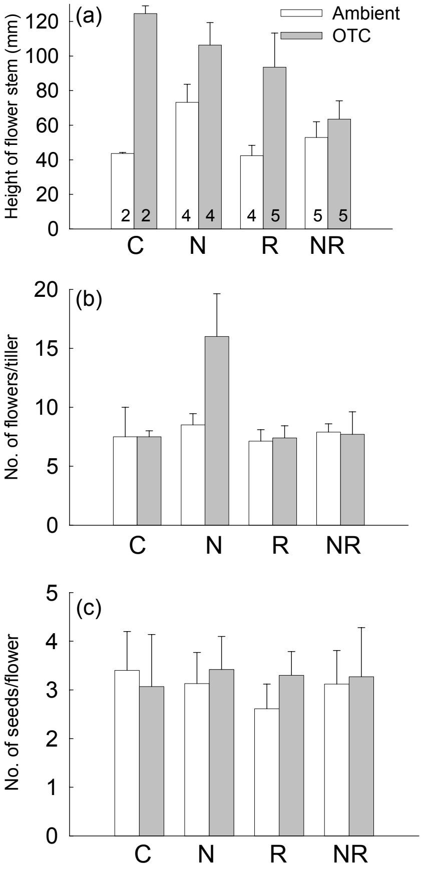
Fig. 3 Means and standard errors of (a) the height of flower stems, (b) number of flowers per tiller, and (c) number of seeds per flower of *Thalictrum alpinum* measured in alpine *Dryas* heath vegetation by the end of the 2002 and 2003 growing season outside (ambient) and inside OTCs, on tillers receiving nutrients (N), removal (R), nutrients and removal (NR), or no treatment (C), at Finse, alpine south Norway. Numbers in the columns in (a) are sample sizes for each treatment in (a), (b), and (c).



Klanderud & Totland, Figure 1



Klanderud & Totland Figure 2



Klanderud & Totland Figure 3

Paper IV

Running head: CLIMATE CHANGE EFFECTS IN THE ALPINE

SIMULATED CLIMATE CHANGE ALTERED DOMINANCE HIERARCHIES AND DIVERSITY OF AN ALPINE BIODIVERSITY-HOTSPOT

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Abstract. Alpine and arctic ecosystems may be particularly vulnerable to climate change. We know little about alpine plant community responses to the predicted abiotic changes, or to possible changes in the biotic environment caused by climate change. Four years of experimental warming and nutrient addition altered dominance hierarchies, community structure and diversity of an alpine biodiversity-hotspot in south Norway. The previously dominant dwarf shrub *Dryas octopetala* was replaced by graminoids and forbs under nutrient addition and warming with nutrients. Community diversity declined due to decreased bryophyte and lichen richness and abundances, and dwarf shrub abundances. In controls and in plots with only warming, where *Dryas* maintained dominance, the relationships between changes in *Dryas* cover and changes in community parameters were negative, suggesting that *Dryas* control community processes. Under nutrient addition, bryophyte and lichen diversity decreased with decreasing *Dryas* cover, probably due to increased competition from graminoids and forbs. The shift in dominance hierarchies changed community structure and dynamics through increased biomass, vegetation height, and competition for light. Community diversity dropped primarily because changes in the abiotic environment modified biotic interactions, highlighting that species interaction must be considered in climate change experiments and in models predicting climate change effects.

Key words: alpine tundra; plant community diversity; competition; dominant species; Dryas octopetala*; functional groups; nutrient addition; open top chambers; south Norway; species interactions; warming*

INTRODUCTION

Changes in the abiotic environment caused by global warming, such as increased growing season length, permafrost melting, and nutrient availability due to higher mobilization of resources in warmer soils (IPCC 2001), are predicted to impose large effects on alpine and arctic plant species (e.g. Callaghan and Jonasson 1995, Körner 1999). However, associated changes in the biotic environment may have even greater effects on plant community composition and diversity (Mooney 1991, Kingsolver 1993). Alpine and arctic climate change experiments show that most plants increase their vegetative growth and reproductive effort and success after short-term increases in temperature (e.g. Arft et al. 1999) and/or nutrient availability (e.g. Dormann and Woodin 2002). However, the speed and amplitude of responses to abiotic environmental change may differ substantially between species and functional groups (e.g. Arft et al. 1999, Dormann and Woodin 2002). Thus, longer-term changes in the biotic environment (e.g. biomass, canopy height) experienced by individual species may occur within a community. Furthermore, individual species or functional groups may vary in their competitive abilities and may respond differently to the presence of other species (Wilson and Whittaker 1995), which may again affect plant community dynamics and diversity.

Dominant species, i.e. the most prevalent species in a community, may strongly influence the biotic conditions experienced by other species and are often important drivers of ecosystem function and community dynamics (Grime 1998). A dominant species may have negative (competition) or positive (facilitation) impacts on other species (e.g. Callaway 1995, Baer et al. 2004, Klanderud and Totland 2004). Thus, the changes in abundance of a dominant species may influence community dynamics and diversity because of altered interactions (both direction and magnitude) between this species and others.

Few studies have examined climate change effects at the community level (but see e.g. Chapin et al. 1995, Molau and Alatalo 1998, Press et al. 1998, Robinson et al. 1998, Shaver and Jonasson 1999, Gough et al. 2002). Furthermore, although both alpine and arctic ecosystems are predicted to be particularly vulnerable to climate change (e.g. Callaghan and Jonasson 1995, Körner 1999), we know of only one experimental study on alpine plant community responses to increased nutrient availability (Theodose and Bowman 1997) and one on the possible effects of warming and grazing (Klein et al. 2004). Furthermore, the relationship between possible changes in the cover of a dominant species and changes in community diversity has received little attention. Climate change effects on the interactions among species may modify direct responses of abiotic environmental change (Shevtsova et al. 1997, Dormann et al. 2004, Klanderud 2005), but biotic interactions are still mostly ignored in experiments and in models predicting climate change effects (Mooney 1991, Davies et al. 1998, Dormann and Woodin 2002).

The dwarf shrub *Dryas octopetala* L. is a circumpolar ‘wintergreen’ species (Welker et. al 1997) that may dominate plant communities in alpine, subarctic, and arctic habitats (Hultén 1959). The northern European *Dryas* heaths may be characterised as biodiversity-hotspots relative to other alpine plant communities in this region. *Dryas* may be a key species with both negative and positive impacts on ecosystem carbon gain (Welker et al. 1997), population dynamics of other species (Klanderud 2005), community diversity (Klanderud and Totland 2004), and establishment of other species (*Dryas drummondii* Richard: Chapin et al. 1994). Previous studies have found both increased (Welker et al. 1997) and decreased (Henry et al. 1986, Robinson et al. 1998) abundance of *Dryas* after climate change simulations.

Dryas covers ca 35 % of the ground of our study site in alpine Norway, and had primarily a competitive role on the performance of other plant species here (Klanderud and Totland 2004, Klanderud 2005). Thus, with continued global warming (IPCC 2001), three possible scenarios may occur: A) If *Dryas* cover increases as a result of environmental changes (Welker et al. 1997), community diversity may decrease because of increased competition from *Dryas*. B) If *Dryas* cover decreases (Henry et al. 1986, Robinson et al. 1998), *Dryas* heath diversity might increase due to competitive release experienced by other species. C) Other species than *Dryas* may become dominant as a result of environmental changes and thereby affect community diversity. To better understand how biotic interactions influence community response to climate change, we experimentally manipulated the environmental conditions in an alpine *Dryas* heath. The specific objectives of our study were to determine: 1. How warming and increased nutrient availability affect the cover of the dominant *Dryas octopetala* and the diversity of different functional groups (graminoids, forbs, dwarf shrubs, bryophytes, lichens). 2. If there are any effects of changes in *Dryas* cover on community diversity. 3. If dominance hierarchies change as a result of environmental change, and if so, what the consequences are for community structure.

STUDY SYSTEM AND METHODS

This study was conducted on a southwest exposed slope of a *Dryas octopetala* heath at ca 1500 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (ca 60° N, 7° E), the alpine region of southwest Norway. Mean monthly temperature during June, July, and August at 1200 m elevation at Finse is 6.3 °C (Aune 1993), and mean monthly precipitation during the same months is 89 mm (Førland 1993). See Klanderud and Totland (2004) for species composition on Sandalsnuten, and Welker et al. (1997) for growth characteristics of *Dryas octopetala*. The experiment started in early July 2000 and lasted until the end of the growing season (late August) in 2003. To examine if environmental changes may affect *Dryas* cover and plant community diversity, we randomly positioned ten blocks in the *Dryas* heath. Temperature treatment (T), nutrient addition (N), temperature and nutrient addition

(TN), and controls (C, no treatment) were randomly allocated to four randomly positioned 1 × 1 m plots (ca 1 m apart from each other) within each block. We used open top chambers (OTCs) with an inside diameter of ca 1 m, and with qualities as described in Marion et al. (1997) to increase temperature. OTCs are commonly used in climate change experiments to raise the temperature while minimizing secondary experimental effects, such as changes in atmospheric gas concentrations and ambient precipitation (e.g. Marion et al. 1997, Hollister and Webber 2000). The chambers did not affect the duration of snow cover and we therefore left them in place during the whole experimental period. To increase nutrient availability, we added slow-released granular NPK (ca 10 g N, 2 g P, and 8 g K per m^2/growing season) fertilizer immediately after snowmelt in the beginning of each growing season. These amounts are in line with other climate change experiments (e.g. Chapin et al. 1995, Press et al. 1998, Shaver and Jonasson 1999).

To determine changes in *Dryas* cover and plant species diversity, we established two 60 × 30 cm permanent squares in the centre of each plot separated by a 10 cm wide row. Furthermore, we divided each square into eighteen 10 × 10 cm sub-plots and recorded percent cover of live and dead *Dryas,* and presence of species (graminoids, forbs, dwarf shrubs, bryophytes, lichens) in all the sub-plots during two weeks of the approximate peak of the growing season in August 2000 and 2003. We used sub-plot frequencies averaged over the two squares in each plot as a measure of abundance of each species in the analyses. To assess possible changes in community structure, we measured the height of the vegetation in the centre of five randomly selected sub-plots per square, and sampled aboveground biomass (only green parts of the woody plants) in two randomly chosen sub-plots in each square during one day at the end of the last growing season (late August 2003). We dried the biomass at 75 °C for 48 hours and weighted them immediately thereafter. Average values per plot are used for all parameters in all analyses.

We measured mean air (ca 5 cm above ground) and soil (ca 5 cm below ground) temperature with Tinytag 12 Plus G data loggers (Intab Interface-Teknik AB, Stenkullen, Sweden) inside and outside four of the OTCs from early June to early September 2003. We measured leaf surface temperature of *Dryas* inside and outside ten OTCs by using an infrared thermometer (FLUKE 65, Fluke Corporation, Everett, USA). To assess the effect of community structure on light levels, we measured the photosynthetically active radiation (PAR) with a Li-Cor Quantum Sensor on the ground at five randomly chosen positions in each 30 × 60 cm square (ten measurements per plot) on a clear day in August 2003.

To separate natural changes in *Dryas* cover and community diversity parameters from treatment-induced changes when comparing treatment effects with controls, we used the changes in the vegetation data (i.e. sampling in 2003 minus sampling in 2000) as response variables in the analyses (see Robinson et al. 1998). All measured variables had equal variances. To assess the effects of warming, nutrient addition, and the combined effects of these manipulations on *Dryas* cover, total biomass, height of vegetation, species richness, abundances, and diversity (Shannon's index; $H = - \Sigma\ p_i \ln p_i$, where p_i is the proportion of a particular species in the sample, Ludwig and Reynolds 1988) of each of the functional groups (graminoids, forbs, dwarf shrubs, bryophytes, lichens), we used a randomised block design, with treatment as the fixed factor and block as the random factor in multifactorial General Linear Models (GLMs). To examine significant differences between treatment means, we used Tukey HSD post-hoc test. To separate possible diversity changes in changes in species richness from changes in abundances, we used both Shannon's diversity index, species richness, and abundances as response variables in the analyses.

To assess if there was a relationship between the changes in *Dryas* cover and the changes in community parameters, we used the change in *Dryas* cover as a predictor in simple linear regressions, with diversity, richness, and abundances of all species, graminoids, forbs, dwarf shrubs, bryophytes, and lichens as dependent factors. Because of heterogeneity of slopes, the regressions were done separately within each treatment. Simple linear regressions were also used to assess possible relationships between biomass (predictor) and PAR (dependent factor). All analyses were done in SYSTAT 10.

RESULTS

Environmental factors

The OTCs increased mean *Dryas* leaf surface temperature from 12.1 ± 0.1 (SE) °C (controls) to 13.6 ± 0.2 (SE) °C, air temperature from 9.8 ± 0.1 (SE) °C (controls) to 11.3 ± 0.1 (SE) °C, and soil temperature from 9.0 ± 0.1 (SE) °C (controls) to 10.0 ± 0.1 (SE) °C. Photosynthetically active radiation (PAR) measured on the ground at the end of the experiment differed significantly between all treatments (Tukey HSD, GLM treatment effect; $F_{3,27} = 126.01$, $P < 0.001$, block effect; $F_{9,27} = 3.17$, $P = 0.001$), with 1653.2 ± 43.5 (SE), 1457.2 ± 53.3 (SE), 797.0 ± 97.5 (SE), and 394.0 ± 49.4 (SE) μmol $m^{-2}s^{-1}$ measured in the control-, warming-, nutrient addition-, and warming combined with nutrient addition-plots, respectively.

Dryas *cover and community structure*

Four years of experimental warming alone had no effect on the cover of *Dryas octopetala.* On the other hand, the cover of both live and dead *Dryas* leaves decreased in plots with nutrient addition and in plots with warming combined with nutrient addition from 2000 to 2003 (change significantly different from zero), although only the decrease of dead leaves differed significantly from the control plots (Tukey HSD, Figs. 1A-B, Appendix A).

Community biomass measured at the end of the experiment was 56.3 % higher in plots with nutrient addition and 77.4 % higher in plots with warming combined with nutrient addition compared to the control plots (Fig. 1C, GLM treatment effect $F_{3,27} = 7.13$, $P = 0.001$, block effect $F_{9,27} = 0.64$, $P = 0.756$). Biomass in plots with only warming did not differ significantly from the controls (Tukey HSD, Fig. 1C). Compared to controls, the vegetation was 393.2 % taller in plots with only nutrient addition and 835.0 % taller in plots with warming combined with nutrient addition. Vegetation height in plots with only warming did not differ significantly from the controls (Fig. 1D, GLM treatment effect $F_{3,27} = 57.25$, $P = < 0.001$, block effect $F_{9,27} = 1.46$, $P = 0.213$). PAR measured on the ground decreased significantly with increasing biomass (linear regression, Std. Coef. = -0.58, $P < 0.001$).

Community diversity

Community diversity index (Shannon) decreased from 2000 to 2003 due to species loss and decreased species abundances, in particular in plots with nutrient addition combined with warming (Figs. 2A-C, Appendix A). Graminoid diversity increased in plots with only nutrient addition and in plots with warming combined with nutrient addition due to increases in species richness and abundances (change significantly different from zero, Figs. 2D-F, Appendix A), although these changes did not differ significantly from the changes in the control plots due to large variation in the changes among plots within each of the treatments (Tukey HSD, Figs. 2D-F). Forb diversity increased in plots with only nutrient addition, primarily due to increased species abundances (Figs. 2G-I, Appendix A). Dwarf shrub diversity decreased in plots with only nutrient addition and warming combined with nutrient addition, primarily due to decreased species abundances, although these decreases did not differ significantly from the controls due to large variation in the changes among plots within each of the treatments (Tukey HSD, Figs. 2J-L, Appendix A). Bryophyte and lichen diversity decreased significantly in plots with warming combined with nutrient addition due to significant species loss and decreased species abundances (Figs. 2M-R). Moreover, abundances of bryophytes decreased significantly in plots with only warming and only nutrient addition, whereas the number and abundances of lichen species decreased significantly in plots with only nutrient addition (Tukey HSD, Figs. 2M, O, P, R, Appendix A).

Relationship between Dryas cover and changes in community diversity

The percent cover of *Dryas* decreased over the four years, both in the control plots and in plots with only nutrient addition and warming combined with nutrient addition (Fig. 1A, Appendix A). However, the persisting high *Dryas* cover (Appendix A) and the lack of increased diversity or abundance in functional groups in the controls and in plots with only warming (Figs. 1C-D, 2A-R) suggests that *Dryas* maintained dominance here. On the other hand, in plots with only nutrient addition and warming combined with nutrient addition, *Dryas* cover decreased (Fig. 1A, Appendix A), biomass and vegetation height increased due to increased richness and abundances of graminoids and forbs (Figs. 1C-D, 2D-I), and diversity of all other functional groups decreased (Figs. 2J-R). These changes suggest that *Dryas* was replaced as the dominant species by graminoids and forbs in plots with only nutrient addition and mainly by graminoids in plots with warming combined with nutrient addition.

There were few significant relationships between the changes in *Dryas* cover and changes in community parameters, which may be due to small variations in the changes within treatments. However, the sign of the relationship between *Dryas* cover and community parameters differed between the treatments. In plots where *Dryas* maintained dominance (control plots and plots with only warming), significant or close to significant relationships between changes in *Dryas* cover and changes in community parameters were negative (Appendix B, C). When *Dryas* cover decreased, lichen diversity increased in the controls, and total diversity, forb diversity, total species richness, bryophyte richness, and forb abundances increased in plots with only warming (Appendix B, C). In plots with only nutrient addition on the other hand, where graminoids and forbs had increased in abundances at the expense of *Dryas*, the significant or close to significant relationships were always positive. Lichen diversity, total, bryophyte and lichen richness, and bryophyte abundances decreased with decreasing *Dryas* cover (Appendix B, C). In plots with warming combined with nutrient addition, forb abundances increased with decreased *Dryas* cover (Appendix B, C).

DISCUSSION

Four years of environmental manipulations altered dominance hierarchies and community structure of an alpine *Dryas* heath community. In particular, graminoids and forbs increased in abundances in plots previously dominated by the dwarf shrub *Dryas octopetala* and community diversity decreased, primarily because of a sharp decline in the number and abundances of bryophyte and lichen species.

The decreased cover of the key species *Dryas* after nutrient addition and warming combined with nutrient addition was unexpected based on the results of Welker et al. (1997). They found increased *Dryas* cover after 1-3 years of climate change simulations (warming, watering, fertilizing, or combinations of these) in one alpine and three arctic sites. On the other hand, negative effects of nutrient addition on *Dryas* abundance was found in some arctic sites, but these decreases were most likely caused by delayed winter hardening (Robinson et al. 1998) or direct damage on *Dryas* leaves caused by the fertilizer (Henry et al. 1986). One important difference between alpine and arctic habitats is that vegetation cover in the alpine is more closed and consists of more species (e.g. Klanderud and Totland 2004). In the arctic, graminoid species are very rare in *Dryas* heaths (Wookey et al. 1993), suggesting limited possibilities for competitive interactions here, at least in the short-term (Wookey et al. 1995).

This is in sharp contrast to alpine Finse, where the faster and greater amplitude of the responses of graminoids and forbs to the increased nutrient availability and warming combined with nutrients altered the dominance relationship. *Dryas* commonly dominates severe habitats with low soil nitrogen levels, and may be a stress tolerator more than a competitor (Chapin et al. 1994). The increased dominance of nutrient-demanding competitors, such as graminoids and some forbs, at the expense of *Dryas* when nutrient availability increased at Finse, supports this. Our results are in line with studies from Alaskan fell fields, where *Dryas* cover decreased due to increased competition from graminoids after fertilization (McGraw 1985, Fox 1992). Our results are also in line with studies in the Alaskan moist tussock tundra where three years of warming and fertilizing increased biomass of graminoids and decreased evergreen shrubs and forbs (Chapin et al. 1995), and in the dry Alaskan tundra where long term fertilizing (Gough et al. 2002) resulted in a shift from an evergreen to a graminoid dominated system. After nine years in the moist tundra, however, deciduous shrubs dominated the plots, which may indicate that we still know little about the long-term responses of arctic and alpine plant communities to climate change (Chapin et al. 1995). The warming induced by the OTCs corresponded with the predicted increase in summer temperature of ca 1.5 °C over the next 75 years in southern Norway (IPCC 2001). However, four years of warming alone had only minor effect on community parameters at Finse. This is in line with climate change experiments from the arctic, where nutrients appear to limit plant growth more than temperature, but that synergistic effect of warming and nutrients may occur (e.g. Robinson et al. 1998, Dormann and Woodin 2002).

The *Dryas* heath diversity decreased due to decreased abundances of dwarf shrubs, bryophytes, and lichens, and a significant loss of bryophyte and lichen species. These results are in line with arctic and sub arctic climate change experiments, which have found decreased community diversity, most likely due to increased cover of vascular at the expense of the number of non-vascular species (e.g. Chapin et al. 1995, Molau and Alatalo 1998, Press et al. 1998). Although the decrease of some species may be due to direct effects of warming and nutrient addition at alpine Finse, the main causes to the decreased community diversity was most likely caused by the change in community structure caused by the shift in dominance hierarchies. When the community changed from heaths dominated by the low-stature *Dryas*, to meadows of tall graminoids and forbs, community biomass and height of vegetation increased significantly. Moreover, the role of biotic interactions, such as competition for light, likely increased considerably. The most dramatic diversity decrease occurred when warming was combined with nutrient addition. In these plots, graminoid diversity increased at the expense of all other functional groups, attaining higher biomass and taller vegetation compared to the other plots. Graminoids are expected to respond faster to environmental changes than other functional groups because of their modular organisation and high tissue turnover (Shaver et al. 1997). The role of competition in alpine and arctic habitats is still debated, but changes in nutrient regimes caused by higher soil temperature and increased nitrogen mineralization is predicted to increase the role of species interactions, and alter the competition hierarchies in alpine and arctic plant communities (Chapin et al. 1995, Shaver and Jonassen 1999, Dormann and Woodin 2002), as we have found here. Moreover, decreased diversity after nutrient addition is commonly observed, and is often explained by competitive displacements of species of low stature because of light limitation (Shevtsova et al. 1997, Theodose and Bowman 1997, Baer et al. 2004).

The negative relationship between changes in *Dryas* cover and changes in forb, bryophyte, and lichen community parameters in the control plots and in plots with only warming, where *Dryas* maintained dominance, may suggest that competition from *Dryas* control community processes of these groups. This is in line with previous studies predicting negative impacts of *Dryas* on community diversity at Finse (Klanderud and Totland 2004).

The positive relationship between *Dryas* cover and bryophyte and lichen community parameters in plots with only nutrient addition, on the other hand, is most likely explained by the increased diversity of graminoids and forbs here. Because these functional groups may be stronger competitors than *Dryas* when nutrient availability increases, they may have negative effects on both *Dryas* and bryophytes and lichens. Thus, this may result in a negative relationship between changes in *Dryas* cover and changes in bryophyte and lichen community parameters. Furthermore, the increased abundances of forbs with decreasing *Dryas* cover in plots with warming combined with nutrient addition, may also suggest a shift in the competitive hierarchies, with forbs becoming more competitive than *Dryas* when resources increase.

Environmental manipulations led to considerable community changes in the alpine *Dryas* heath at Finse. From being a diversity-hotspot, it became a graminoid and forb meadow, with substantially lower diversity. The drop in diversity was primarily caused by changes in the community structure. Thus, this study highlights that the complexity of biotic interactions and their responses to environmental changes may modify the direct effects of changes in the abiotic conditions, and that species interactions must be considered in climate change experiments and in models predicting climate change effects.

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Figure legends

FIG.1 Mean changes in percent live (A) and dead (B) cover of *Dryas octopetala* from 2000 to 2003 with 95% confidence intervals, and mean total biomass (C) and height of vegetation (D) with standard errors measured in 2003, in control plots (C), plots with warming (T), nutrient addition (N), and warming combined with nutrient addition (NT). Bars not sharing a common letter differ significantly (Tukey HSD, $P < 0.05$).

FIG. 2. Changes in all species, graminoid, forb, dwarf shrub, bryophyte, and lichen species diversity index (Shannon), species richness, and abundances from 2000 to 2003 with 95 % confidence intervals in the treatments C, T, N, and TN (abbreviations explained in Figure 1). Bars not sharing a common letter differ significantly (Tukey HSD, $P < 0.05$).

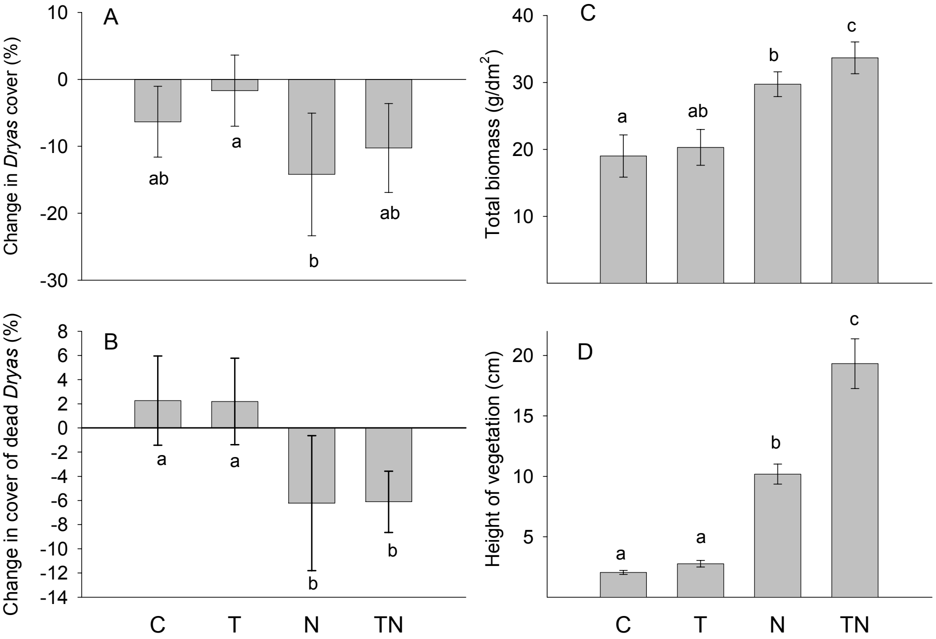

A
Change in *Dryas* cover (%)
10
0
-10
-20
-30
ab
a
b
ab
B
Change in cover of dead *Dryas* (%)
8
6
4
2
0
-2
-4
-6
-8
-10
-12
-14
a
a
b
b
C
T
N
TN
C
Total biomass (g/dm²)
40
30
20
10
a
ab
b
c
D
Height of vegetation (cm)
20
15
10
5
a
a
b
c
C
T
N
TN

Figure 1

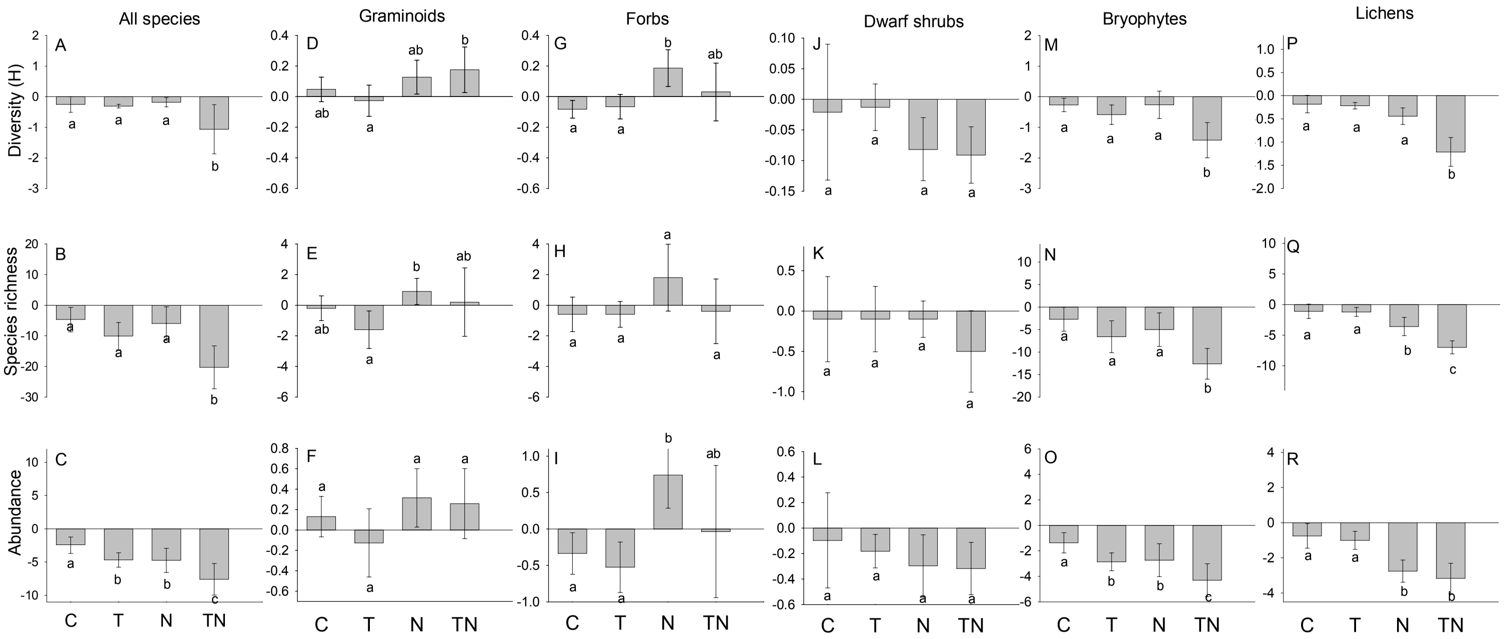

All species
Graminoids
Forbs
Dwarf shrubs
Bryophytes
Lichens
Diversity (H)
Species richness
Abundance
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
C
T
N
TN
a
b
ab
c

Figure 2

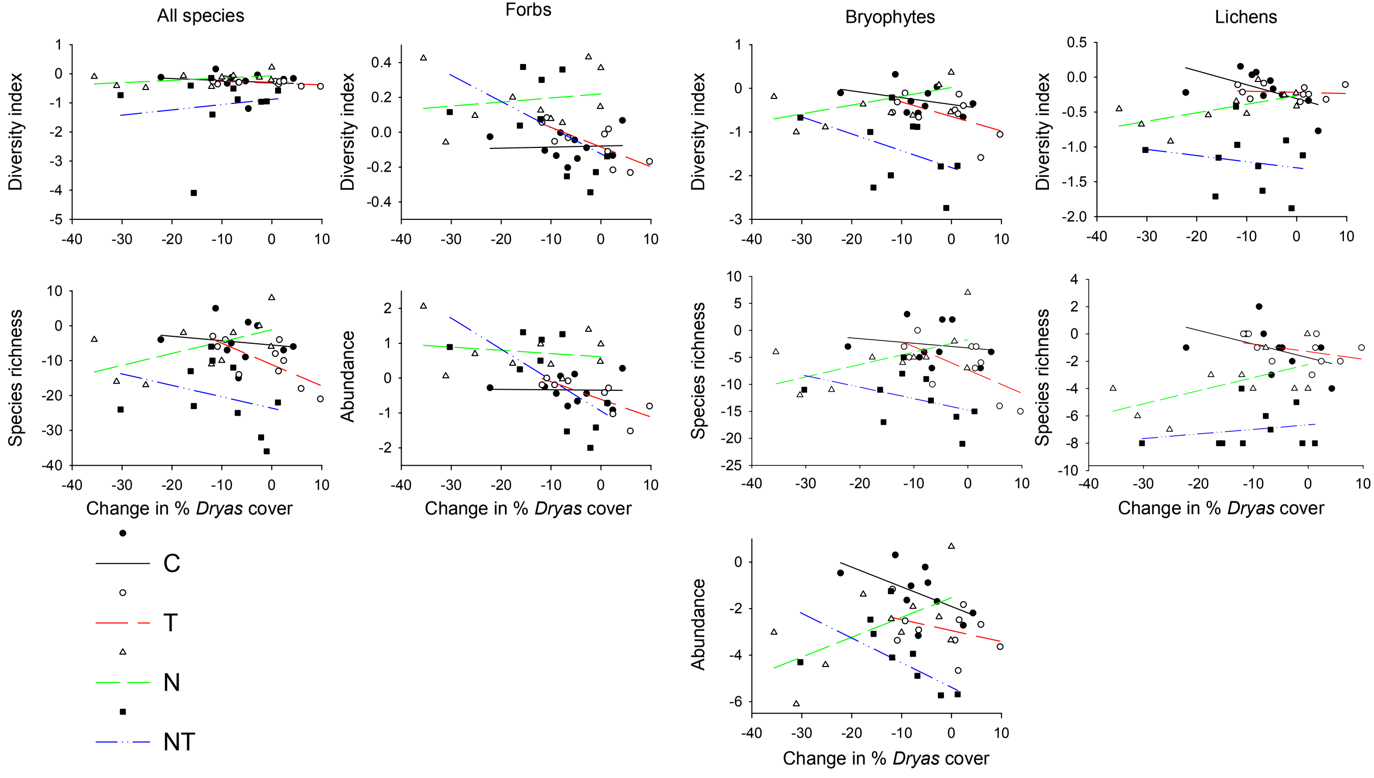
APPENDIX A. Mean values with standard errors (in parentheses) in 2000 (upper value) and 2003 (lower value) of community parameters in control plots (C), plots with warming (T), nutrient addition (N), and warming combined with nutrient addition (TN) at Finse, alpine south Norway. GLM *F*- and *P*-values are shown for tests of significance of treatment and block effects on the change in community parameters from 2000 to 2003. Degrees of freedom are 3,27 and 9,27 for treatment and block effects respectively. N = 10 blocks.

Community response	Year	Treatment				Treat effect	Block effect
		C	T	N	TN	*F/P*	*F/P*
Live *Dryas* (%)	2000	33.5 (5.3)	44.1 (5.0)	36.3 (6.6)	27.6 (6.2)	**3.16/0.041**	0.97/0.489
	2003	27.2 (4.2)	42.4 (5.3)	22.1 (5.1)	17.3 (4.1)		
Dead *Dryas* (%)	2000	16.0 (3.1)	13.9 (2.0)	12.5 (2.9)	11.6 (1.6)	**6.45/0.002**	0.44/0.903
	2003	18.3 (3.6)	16.1 (2.3)	6.3 (1.4)	5.4 (1.4)		
Total diversity	2000	3.25 (0.10)	3.34 (0.06)	3.30 (0.09)	3.68 (0.35)	**4.60/0.010**	0.91/0.528
	2003	2.99 (0.14)	3.03 (0.06)	3.12 (0.07)	2.61 (0.10)		
- species richness	2000	40.7 (3.3)	44.2 (2.7)	43.3 (3.3)	44.5 (2.8)	**15.44/< 0.001**	**3.97/0.003**
	2003	36.0 (2.6)	34.1 (1.7)	37.3 (2.2)	24.2 (0.8)		
- abundance	2000	13.33 (1.58)	14.68 (1.11)	14.25 (1.28)	14.38 (1.11)	**14.92/< 0.001**	**4.60/0.001**
	2003	10.91 (1.10)	10.00 (0.73)	9.5 (0.62)	6.79 (0.23)		

Graminoid diversity	2000	0.54 (0.03)	0.59 (0.05)	0.54 (0.04)	0.56 (0.04)	**3.70/0.024**	1.66/0.150
	2003	0.59 (0.05)	0.56 (0.04)	0.67 (0.05)	0.74 (0.04)		
- richness	2000	4.8 (0.7)	5.2 (0.7)	4.8 (0.6)	5.1 (0.8)	**3.10/0.043**	1.31/0.279
	2003	4.6 (0.7)	3.6 (0.4)	5.7 (0.7)	5.3 (0.6)		
- abundance	2000	1.44 (0.18)	1.62 (0.19)	1.39 (0.12)	1.54 (0.16)	***2.57/0.075***	1.57/ 0.174
	2003	1.57 (0.22)	1.49 (0.12)	1.71 (0.19)	1.80 (0.12)		
Forb diversity	2000	1.35 (0.08)	1.34 (0.12)	1.33 (0.08)	1.37 (0.09)	**6.43/0.002**	***1.91/0.094***
	2003	1.27 (0.07)	1.28 (0.10)	1.51 (0.06)	1.40 (0.04)		
- richness	2000	10.1 (0.1)	10.1 (1.2)	11.0 (1.0)	11.2 (1.1)	***2.72/0.064***	1.34/0.261
	2003	9.5 (0.8)	9.5 (1.0)	12.8 (0.9)	10.8 (0.4)		
-abundance	2000	3.49 (0.51)	3.64 (0.53)	3.31 (0.41)	3.52 (0.48)	**7.10/0.001**	**2.51/0.031**
	2003	3.15 (0.44)	3.12 (0.45)	4.04 (0.19)	3.48 (0.22)		
Dwarf shrub diversity	2000	0.30 (0.05)	0.25 (0.05)	0.32 (0.05)	0.27 (0.04)	1.95/0.145	1.30/0.284
	2003	0.28 (0.05)	0.24 (0.05)	0.24 (0.05)	0.18 (0.03)		
- richness	2000	1.8 (0.3)	1.7 (0.4)	1.9 (0.2)	1.7 (0.3)	1.10/0.365	1.04/0.435
	2003	1.7 (0.3)	1.6 (0.4)	1.8 (0.2)	1.2 (0.2)		

- abundance	2000	0.82 (0.17)	0.72 (0.16)	0.95 (0.22)	0.74 (0.17)	0.91/0.452	1.28/0.291
	2003	0.72 (0.16)	0.54 (0.14)	0.66 (0.17)	0.42 (0.10)		
Bryophyte diversity	2000	2.3 (0.1)	2.4 (0.1)	2.2 (0.1)	2.4 (0.1)	**8.63/< 0.001**	0.89/0.548
	2003	2.0 (0.1)	1.8 (0.1)	1.9 (0.1)	1.0 (0.3)		
- richness	2000	15.0 (1.3)	16.9 (1.1)	15.8 (1.3)	16.6 (1.2)	**12.71/< 0.001**	**3.27/0.008**
	2003	12.3 (1.1)	10.3 (1.0)	10.8 (0.9)	4.0 (0.9)		
- abundance	2000	3.61 (0.58)	4.49 (0.46)	4.46 (0.49)	4.57 (0.56)	**15.75/< 0.001**	**6.53/< 0.001**
	2003	2.24 (0.32)	1.62 (0.27)	1.72 (0.24)	0.27 (0.09)		
Lichen diversity	2000	1.6 (0.1)	1.8 (0.1)	1.7 (0.1)	1.7 (0.1)	**29.95/< 0.001**	1.27/0.300
	2003	1.5 (0.1)	1.6 (0.1)	1.3 (0.1)	0.5 (0.1)		
- richness	2000	8.0 (0.8)	9.3 (0.6)	8.8 (0.7)	8.9 (0.7)	**32.78/< 0.001**	1.41/0.232
	2003	6.9 (0.8)	8.1 (0.6)	5.2 (0.7)	1.9 (0.5)		
- abundance	2000	3.15 (0.47)	3.23 (0.43)	3.34 (0.34)	3.27 (0.40)	**23.89/<0.001**	**2.92/0.015**
	2003	2.40 (0.32)	2.33 (0.22)	0.59 (0.12)	0.10 (0.04)		

Appendix B. Simple linear regressions of the relationship between change in % *Dryas octopetala* cover and changes in community parameters from 2000 to 2003 for each of the treatments C (control), T (temperature), N (nutrient addition), TN (temperature and nutrient addition) at Finse, alpine Norway. See Appendix C for standardised regression coefficients and *P*- values.



Appendix C. Standardised regression coefficients and significance values (in parentheses) of simple linear regressions between change in *Dryas octopetala* cover and change in community diversity parameters from 2000 to 2003, in control plots (C), plots with warming (T), nutrient addition (N), and warming combined with nutrient addition (TN).

Community response	Treatments			
	C	T	N	TN
Total diversity	-0.14 (0.696)	***-0.56 (0.091)***	0.46 (0.180)	0.15 (0.678)
- richness	-0.17 (0.649)	**-0.73 (0.017)**	***0.57 (0.088)***	-0.31 (0.383)
- abundance	-0.49(0.149)	-0.45 (0.187)	0.33 (0.348)	-0.54 (0.110)
Graminoid diversity	0.07 (0.850)	0.35 (0.319)	-0.08 (0.818)	0.09 (0.797)
- richness	-0.08 (0.818)	-0.17 (0.646)	0.28 (0.427)	-0.16 (0.665)
- abundance	0.06 (0.876)	0.07 (0.847)	-0.37 (0.292)	-0.10 (0.780)
Forb diversity	0.06 (0.874)	**-0.76 (0.011)**	0.18 (0.622)	-0.53 (0.116)
- richness	0.19 (0.594)	-0.55 (0.100)	-0.03 (0.931)	-0.28 (0.433)
- abundance	-0.02 (0.954)	**-0.78 (0.008)**	-0.19 (0.603)	**-0.65 (0.042)**
Dwarf shrub diversity	0.41 (0.244)	0.25 (0.480)	0.24 (0.511)	0.24 (0.507)
- richness	0.32 (0.362)	0.01 (0.985)	-0.18 (0.623)	-0.08 (0.817)
- abundance	0.38 (0.283)	0.23 (0.525)	-0.11 (0.770)	-0.27 (0.449)
Bryophyte diversity	-0.38 (0.278)	***-0.56 (0.094)***	0.41 (0.235)	-0.45 (0.197)
- richness	-0.17 (0.636)	**-0.65 (0.043)**	***0.56 (0.090)***	-0.41 (0.236)
- abundance	***-0.56 (0.093)***	-0.36 (0.306)	***0.61 (0.063)***	-0.55 (0.102)
Lichen diversity	***-0.56 (0.095)***	-0.13 (0.715)	**0.63 (0.052)**	-0.19 (0.602)
- richness	-0.45 (0.197)	-0.40 (0.253)	***0.59 (0.070)***	0.21 (0.571)
- abundance	-0.47 (0.169)	-0.05 (0.894)	0.02 (0.948)	0.13 (0.712)

Notes: Bold and bold italic *P*-values are significant at the 0.05 and 0.1 levels, respectively. Sample sizes are 10.

Paper V

Invasibility, propagule availability, and diversity of an alpine plant community under simulated climate warming

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Abstract

Climate change is predicted to be the most important driver of alpine biodiversity change. However, little is known about which factors that control alpine plant community invasibility and diversity under natural conditions, and in particular how climate change may affect colonization processes and diversity. We examine the relative role of propagule availability and community-level interactions for the invasibility and diversity of a *Dryas* heath at Finse, alpine Norway, under natural and elevated temperature conditions, by adding propagules from 27 regionally occurring species into natural *Dryas* heath and into *Dryas* heath vegetation exposed to experimental warming (open top chambers). Invasibility increased with the number of species added as propagules and with the soil moisture, and decreased with the resident vascular species richness, the cover of the dominant *Dryas,* and the soil nutrient content. The amount of bare soil increased invasibility only under experimental warming. Thus, propagule availability and competitive exclusion had a greater role on community invasibility and diversity at alpine Finse than the availability of safe germination sites and the experimental temperature increase. Most of the added species established more frequently and had a larger increase in abundance under elevated than under natural temperature conditions. Moreover, the significance of the amount of bare soil for invasibility under experimental warming suggests that if dispersal limitations are overcome, vacant patches in the *Dryas* heath may be colonized, resulting in a denser vegetation cover. Moreover, the increased role of competition from established plants on emerging seedlings under experimental warming, suggests that climate change effects on biotic interactions may affect long-term colonization processes and diversity of alpine plant communities.

INTRODUCTION

The dramatic species loss caused by anthropogenic impacts during the last decades has increased the interest in the structure and function of local species diversity (Levine et al. 2002). However, it is still unclear how local and regional processes influence small-scale diversity. The traditional view is that biotic interactions (e.g. competition, facilitation, herbivory, predation) determine local diversity by controlling the invasion and persistence of new species, and dynamics of present species (Hutchinson et al. 1959, Sih et al. 1986). An alternative school propose that the dispersal of species among sites and the species composition of the regional species pool is the prime constraint on community diversity (e.g. Taylor et al. 1990, Cornell & Lawton 1992, Eriksson 1993). However, recent studies have demonstrated that there is not necessary a dichotomy between community-level interactions and dispersal-based processes in determining local species diversity (Tilman 1997, Zobel 1997, Turnbull et al. 2000, Mouquet et al. 2004). Moreover, the relative importance of these groups of factors on community diversity may change along productivity gradients (Zobel et al. 2000, Foster 2001). Competition from resident species may prevent colonization and diversity when productivity is high (Grime 1979, Huston 1999, Zobel et al. 2000, Foster 2001), whereas propagule availability may limit diversity in relatively low productive communities that are unsaturated with species (Eriksson 1993, Tilman 1997, Cantero et al. 1999, Turnbull et al. 2000, Zobel et al. 2000). On the other hand, in climatically extreme habitats of low biomass, the availability of safe sites (census Harper 1977) and facilitation from resident species may control colonization and diversity because high abiotic stress may inhibit germination and establishment of new invaders (Eriksson & Fröborg 1996, Cooper et al. 2004).

The relative role of various vegetation properties, such as the number of resident species, species richness of different functional groups, and the presence of a dominant species, on community invasibility is also unclear (e.g. Tilman 1997, Symstad 2000, Levine et al. 2002). Moreover, most studies on the significance of different local and regional processes on community invasibility and diversity are from temperate grasslands, whereas little is known from other habitats, such as alpine plant communities (but see Cantero et al. 1999). In alpine communities, characterized by harsh environmental conditions and low productivity, abiotic factors may be more important for community dynamics than biotic factors (e.g. Billings and Mooney 1968, Grime 1977), and facilitation among species is predicted to be more common than interspecific competition (e.g. Callaghan and Emanuelson 1985, Bertness and Callaway 1994).

Climate change is expected to be the most important driver of biodiversity change in alpine regions (Sala et al. 2000). Moreover, warmer summers the last 100 years have been proposed to be a driving factor on recent up shift of plant species along altitudinal gradients of European mountains (Grabherr et al. 1994, Kullmann 2002, Klanderud and Birks 2003). Although species richness has increased in these mountains during the same period, a number of alpine plant species decreased in abundances, possibly due to competitive exclusion by recently invading species (Grabherr et al. 1995, Klanderud and Birks 2003). Thus, if colonization occurs faster than resident alpine species are able to disperse to new sites, locally rare and competitively weak species might disappear on some mountains due to an increased role of competition under climate change (Grabherr et al. 1995, Gottfried et al. 1999, Klanderud and Birks 2003). These predictions highlight the need for a greater understanding of the relationships between alpine species’ dispersal abilities, community-level interactions, and alpine plant community invasibility and diversity, to be better able to forecast possible climate-change effects on alpine ecosystems.

Here, we aim at assessing the relative significance of propagule availability and local interactions for the invasibility and diversity of an alpine *Dryas* heath community in south Norway. *Dryas* heaths are particularly species-rich communities compared to other alpine plant communities in northern Europe, with the dwarf shrub *Dryas octopetala* L. as a high-abundant species that may have both positive and negative impacts on the establishment and population dynamics of other species (Cooper et al. 2004, Klanderud and Totland 2004, Klanderud 2005). We added propagules of 0 to 27 species from the regional species pool into control plots and plots exposed to experimental warming (open top chambers). The following questions are addressed: (1) What are the relative importance of propagule availability and different biotic (species richness, richness of different functional groups, cover of the dominant *Dryas*) and abiotic (soil parameters) community properties on the invasibility and diversity of an alpine *Dryas* heath community? (2) Will the relative importance of these factors on invasibility and diversity change under global warming?

METHODS

Study area and experimental design

The study was conducted in a *Dryas octopetala* heath at ca 1550 m elevation on Sandalsnuten, Finse, northern part of Hardangervidda (60° 36’ N, 7° 31’ E) in alpine southwest Norway. Mean summer (June, July, August) temperature at 1222 m elevation at Finse is 6.3 °C (Aune 1993), and mean summer precipitation is 89 mm (Førland 1993). The experiment was initiated in early July 2000 and lasted until the end of the growing season (late August) in 2004. On average, the dwarf shrub *Dryas octopetala* covers *c.* 35 % of the ground of the study site. Klanderud and Totland (2004) present the abundances of other species within the study site.

We established eighty 1 × 1 m plots in a completely randomised design to determine how invasibility is affected by propagule availability and different biotic and abiotic community parameters. Each plot was divided into two 30 × 60 cm plots separated by a *c.* 10 cm wide row. One of these plots was randomly selected to receive propagule addition whereas the other was a control for the natural background germination. To measure the resident community properties in 2000, before propagule addition, and the possible changes in vascular species richness from 2000 to 2004, we divided each plot into eighteen 10 × 10 cm sub-plots. We recorded the percent cover of *Dryas,* total plant cover, plant litter, and bare soil, within each sub-plot, and used plot averages in the analyses. We estimated the abundances of vascular, bryophyte, and lichen species by calculating the frequency of sub-plots each species was present within each plot.

Propagules of 27 species were collected from *c*. 1440 - 1550 m of Sandalsnuten during August-September 2000. Some of these species were already present in our study plots, whereas others were absent (Table 1). To examine if the number of new species added as propagules had any impact on the community invasibility and diversity, we varied the number species added randomly among plots. We added 0 (control), 3, 6, 9, 12, 15, 18, 21, 24, and 27 species as propagules, and used eight replicates per propagule-addition treatment. Each of the treatments received separate identities of the added species by randomly drawing species with replacement from the 27-species addition pool. Because propagule size normally is positively correlated with seedling survival (Moles & Westoby 2004), we added propagules of each species at equal volume (*c*. 1 ml/plot) rather than equal numbers. We mixed all propagules designated for one plot before they were added into the appropriate plot on 5 September 2000. To ensure that the propagules arrived onto the surface inside the plots, we placed a 30 cm high bottomless box fitting the plot-size upon the plot before dispersing the seeds and carefully brushed the vegetation without disturbing the soil (see Tilman 1997).

To assess if climate warming will affect the relative importance of propagule availability and community-level interactions on community invasibility and diversity, we placed open top chambers (OTCs) upon half of the eighty plots. This resulted in four replicates of each of the species addition treatments inside OTCs and four replicates outside OTCs (controls for the warming treatment). The OTCs are hexagonally shaped polycarbonate chambers with an inside diagonal of ca 1 m, and with qualities as described in Marion et al. (1997). OTCs are commonly used to raise the temperature in climate change experiments (e.g. Marion et al. 1997; Hollister and Webber 2000). It is conceivable that OTCs may inhibit natural propagule dispersal into the plots, but equal mean numbers of seedlings inside (5.2 ± 1.4 [SE]) and outside (5.2 ± 1.5 [SE]) the OTCs (*t*-test, $P = 1.00$) in the control plots that had no propagule addition, suggests that this is not a problem in this study. The chambers were left in place during winters throughout the experiment.

We measured seedling establishment by identifying and counting the seedlings of each species inside each sub-plot in August 2001, 2002, and 2003. We recorded the number of established vascular species in each plot in August 2004, and used vascular richness in 2004 minus vascular richness in 2000 as a measure of invasibility (see Tilman 1997). To obtain soil parameters, we collected two soil samples from *c*. 5 cm below ground in each plot by the end of August 2004 and mixed the samples from each plot properly before analyses. The soil was dried at 105 °C for 24 hours to estimate water content, and then warmed at 550 °C for 12 hours to measure the organic content. Extractable soil nitrogen ($NH_4 + N0_3$) was measured by extraction with KCl and analysed by Flow Injection Analysis at the Department of Plant and Environmental Sciences, Norwegian University of Life Sciences, Ås. We measured mean air (*c*. 5 cm above ground) and soil (*c*. 5 cm below ground) temperature with Tinytag 12 Plus G data loggers (Intab, Sweden) inside and outside four of the OTCs from early June to mid August 2004. The OTCs increased summer air temperature from 8.5 ± 0.1 °C (controls; range: -4.9 - 43.4 °C) to 10.1 ± 0.1 °C (OTCs; range: -4.3 - 47.9 °C), and soil temperature from 6.6 ± 0.1 °C (controls range: 1.1 - 13.7 °C) to 8.6 ± 0.1 °C (OTCs; range: 1.1 - 21.5 °C).

Statistical analyses

Simple linear regressions were used to examine the relationships between the number of species added to the plots and seedling species richness and density (total number of seedlings) in each of 2001, 2002, and 2003, and vascular species richness in 2004, separately inside and outside the OTCs. Repeated-measures GLMs with the OTC treatment (fixed factor) and seedling species richness and seedling density of individual species in each year as the repeated measures, were used to assess possible effects of warming on seedling species richness and on seedling density of individual species. We used multiple linear regressions were used to examine the relationship between community invasibility (response) and the predictor variables; number of species added as propagules, resident vascular species richness, *Dryas* cover (biotic variables), and amount of bare soil, soil moisture, and extractable soil nitrogen ($NH_4 + NO_3$) (abiotic variables) separately inside and outside the OTCs. Another set of multiple linear regressions with the same variables as above, but with resident vascular species richness divided into the resident richness of graminoids, forbs, and woody species, were used inside and outside the OTCs separately to examine if the control on invasibility differed among functional groups. Variance inflation factor (VIF; all < 2.6), eigenvalues, and condition index criteria indicated that there were no multicollinearity problems in any of these regression models. Total plant cover and diversity (Shannon's index), litter, and soil organic content were not included in the regressions due to high collinearity with other variables. We used ANCOVAs (GLM-procedure) to examine if there were any interactions between the OTC treatment (factor) and each of the biotic and abiotic community variables (co-variables) on invasibility. Total seedling density and soil nutrient content was log-transformed in all analyses, whereas all other variables were within the criteria for normality- and variance-assumptions for regressions and ANCOVAs. SYSTAT 10 for Windows was used in all the statistical analyses, except for the VIF diagnostics that were obtained from SPSS version 12.0.

RESULTS

Seedling establishment and dynamics

Eleven of the 27 species added as propagules were not present in the plots before propagule addition (Table 1). Ten of these species had established in the plots in 2004 (Table 1), with no significant abundance differences inside and outside the OTCs (*t*-test, $P > 0.12$ for all species). Overall, the added species established more often in warmed plots, i.e. the species were present in 174 new plots inside the OTCs and in 131 new plots outside the OTCs in 2004 compared to 2000 (Table 1). Fifteen of the 27 added species increased significantly in abundances after the propagule addition (Table 1). Eleven of these species increased in abundance both inside and outside OTCs, and two species increased in each of the OTC-treatment and control (Table 1). All of these increases, except the two outside the OTCs, were significantly higher than the abundance increases in control plots not receiving any propagules, showing that these increases were caused by the propagule addition treatment and not by natural seasonal variations in species abundances (Table 1).

There were significant positive relationships between the number of species added as propagules and seedling richness and density in 2001, 2002, and 2003, both inside and outside the OTCs (Figs.1a-f). On average, total seedling density per plot was 9.7 %, 9.4 %, and 26.2 % higher inside than outside the OTCs in 2001, 2002, and 2003, respectively. However, there were no effects of the OTC treatment on total seedling density across years (between subject effect in repeated-measures ANOVA: $F_{1, 78} = 0.30$, $P = 0.587$) or of the interaction between year and OTC ($F_{2, 156} = 0.10$, $P = 0.903$). Total seedling density differed significantly between years (within subject effect in repeated-measures ANOVA: $F_{2, 156} = 33.0$, $P < 0.001$).

Comparisons of seedling density inside and outside the OTCs for each species separately, showed that the OTC treatment only had significant effect on two of the 27 species added as seeds. The density of *Taraxacum* seedlings was 70.7 %, 95.2 %, and 124 % higher inside than outside the OTCs in 2001, 2002, and 2003, respectively, with a marginally significant OTC effect across years (repeated-measures between subject effect; $F_{1, 78} = 3.57$, $P = 0.063$) and a significant year effect ($F_{2, 156} = 8.99$, $P < 0.001$), but no interaction between year and OTCs ($F_{2, 156} = 1.54$, $P = 0.217$). The density of *Thalictrum* seedlings was 70.0 % and 66.7 % higher inside than outside the OTCs in 2001 and 2002, respectively, and 66.9 % lower inside the OTCs in 2003. There was no OTC effect across years (repeated-measures between subject effect; $F_{1, 78} = 2.18$, $P = 0.144$), but a significant effect of year ($F_{2, 156} = 14.83$, $P < 0.001$), and a significant interaction between year and OTCs ($F_{2, 156} = 8.89$, $P = 0.002$).

Community invasibility

Vascular species richness measured in 2004 was positively related to the number of species added to the plots in 2000, both inside and outside the OTCs (Fig. 2). Furthermore, multiple regressions showed significant increase in the number of vascular species from 2000 to 2004 (invasibility) with the number of species added as propagules, inside and outside the OTCs (Table 2). Invasibility was negatively related to resident vascular species richness and with the cover of *Dryas octopetala* both inside and outside the OTCs. However, vascular richness appeared to have a stronger negative impact on invasibility under warming (Table 2), as also indicated by a close to significant interaction between the OTC factor and resident vascular richness on invasibility (ANCOVA; $F_{1,76} = 3.26$, $P = 0.075$). Community invasibility increased with soil moisture inside and outside the OTCs, and with the amount of bare soil inside the OTCs (Table 2). There was a negative relationship between soil nitrogen content ($NH_4 + NO_3$) and community invasibility, although only marginally significant inside the OTCs (Table 2). Furthermore, a significant interaction between the OTC factor and soil nutrients (ANCOVA; $F_{1,76} = 5.28$, $P = 0.024$) showed that the relationship between soil nitrogen content and invasibility differed between the OTCs and controls. There were no significant interactions between the OTC treatment and any of the other community variables (ANCOVA; $F_{1,76} < 1.53$, $P > 0.22$ for all variables). The multiple regressions explained a larger portion of the variance in invasibility inside than outside the OTCs (Table 2).

Multiple regressions where species richness of functional groups replaced vascular species richness showed that there were significant negative relationships between the species richness of graminoids and invasibility outside ($\beta = -0.39$, $P = 0.015$) and inside ($\beta = -0.54$, $P < 0.001$) the OTCs, and between the species richness of forbs and invasibility outside the OTCs ($\beta = -0.31$, $P = 0.025$). There were no significant relationships between forb species richness and invasibility inside the OTCs, or woody species richness and invasibility inside or outside the OTCs ($P > 0.12$ in all cases). There was a significant interaction between the treatment factor and graminoid species richness on invasibility (ANCOVA; $F_{1,76} = 5.35$, $P = 0.023$), and no significant interactions between the treatment factor and species richness of forbs or woody species ($P > 0.46$ in both cases). The results of those variables included in these regressions and in the regressions with total vascular species richness were similar. The regressions that included functional groups were highly significant and had a high explanatory power (outside OTCs: $F_{8,31} = 5.87$, $P < 0.001$, $R^2 = 0.602$; inside OTCs: $F_{8,31} = 13.15$, $P < 0.001$, $R^2 = 0.772$).

DISCUSSION

Dispersal processes and local competition limit colonization and diversity

The significant increase in vascular species richness and community invasibility when species were added as propagules to the *Dryas* heath shows that the local dispersal of species limits community diversity at alpine Finse. It also shows that the *Dryas* heaths, despite their relatively high diversity, are unsaturated with species, and that vacant sites occur that may be colonized if dispersal limitations of species are overcome. Furthermore, our results show that species that are locally abundant at lower elevations are able to germinate, survive, and establish in environmentally more severe habitats at higher elevations. Our results from an alpine plant community are in line with studies from grasslands and from various temperate terrestrial and aquatic ecosystems (see Tilman 1997 and references therein) supporting the view that propagule availability limits local diversity (e.g. Taylor et al. 1990, Cornell & Lawton 1992, Eriksson 1993). Moreover, our study is the first to show that site-to-site dispersal of species limits diversity in alpine communities, where the abiotic stress likely is higher and productivity lower than in most previously studied systems (see Turnbull et al. 2000, Zobel et al. 2000, Foster 2001).

Our results also suggest that community-level interactions limited invasibility of the *Dryas* heaths at Finse. Indeed, the reduced community invasibility when resident species richness and *Dryas* cover increased, and the lower significance of bare soil and soil moisture, suggest that competition from established species overrule possible facilitative effects of the resident vegetation on emerging seedlings and the availability of recruitment microsites. This suggests that the role of competition in structuring environmentally harsh and low-productive communities unsaturated with species is more important than previously thought (Grime 1979, Huston 1999, Zobel et al. 2000, Foster 2001). Furthermore, our results from the alpine and the study of Cooper et al. (2004) from the high arctic, suggest that even among low productive systems, the processes that control community invasibility and diversity may vary. At alpine Finse, propagule availability and competition from established species controlled invasibility and diversity. In the high arctic Svalbard on the other hand, safe sites in the term of protecting vegetation on emerging seedlings were more important for colonization processes than the lack of seeds (Cooper et al. 2004). Thus, safe microsites and facilitation may determine species establishment under more extreme abiotic environmental conditions (Coulson et al. 1993, Eriksson & Fröborg 1996) than in the alpine.

The negative relationship between resident vascular species richness and invasibility is in line with Tilman (1997) and other studies (see Levine et al. 2002), suggesting that diversity may enhance invasion resistance at a local neighborhood scale (Levine et al. 2002). A relatively high number of species present in a community could exploit more of the resources in a more complete way, resulting in less available resources for new species (e.g. Tilman et al. 2001, Symstad 2000). However, the reduced invasibility with increasing soil nitrogen found in our study and by Tilman (1997) suggests that nitrogen constraints cannot explain the higher invasion resistance here. A high number of species present in a community increases the probability that highly competitive species are already present (Tilman et al. 2001). In our study, invasibility decreased with increased graminoid and forb species richness. This is in line with a previous study in the *Dryas* heaths at Finse, where community diversity decreased with increasing graminoid and forb diversity, most likely due to a simultaneous decrease in light penetration to the ground (Klanderud and Totland in press). Indeed, light limitation is suggested to constrain species richness in productive grasslands (e.g. Cantero et al. 1999, Foster 2001). Our results, and shading effects from neighbours found in other studies at alpine Finse (Totland and Esaete 2002, Klanderud 2005, Klanderud and Totland 2005, Klanderud and Totland in press) and in the sub-arctic Finland (Shevtsova et al.1995) may suggest that light is a limiting factor for recruitment and diversity also in relatively low-productive communities.

High cover of *Dryas* reduced invasibility at Finse, which is in contrast to Chapin et al. (1994) who found positive impacts of *Dryas drumondii* on species establishment on an early succession site in Glacier Bay, Alaska, and to Cooper et al. (2004), who found increased seedling density with higher *Dryas* cover in the high-arctic Svalbard. On the other hand, the results of all these studies are in line with Klanderud and Totland (2004), who predicted negative impacts of *Dryas* on community diversity at Finse but not in Svalbard, because the role of *Dryas* as a competitor or a facilitator may shift along gradients of abiotic severity.

The amount of bare soil increased invasibility under experimental warming but not under ambient temperature conditions. This corresponds with the predicted increased importance of safe germination sites under high abiotic stress (Eriksson and Fröborg 1996, Cooper et al. 2004). Frost damage on seedlings is more frequent in open soils, and seedlings may have a higher survival probability in closed vegetation with a more stable soil and a protective shelter formed by other species (Billings and Mooney 1968, Coulson et al. 1993). Under warmer conditions inside the OTCs on the other hand, the patches of bare soil may be colonized because of more stable soil, less risk of frost damage, and because they lack potential competitors. Soil moisture increased invasibility under elevated and ambient temperature conditions, which is in line with (Jumpponen et al. 1999), who found that soil moisture increased germination and seedling survival in primary succession. Higher maximum temperatures inside the OTCs may increase drought stress here, and the slightly stronger positive relationship between soil moisture and invasibility under experimental warming, may suggest that soil moisture will be more important for recruitment processes under climate warming.

The community parameters were not under experimental control in this study, and other unmeasured variables, or the variables removed from the analyses due to collinearity, may explain the variations in the invasibility.

Impacts of climate warming

Climate warming may increase germination, seedling survival and establishment success for some species in the alpine region. The species added as propagules to the *Dryas* heath established in 32.8 % more plots under elevated than under ambient temperature conditions. Furthermore, experimental warming increased the total seedling density (although not statistical significant), and the seedling density and abundances for some of the added species. This is in line with studies in the high arctic which have shown that seed germination increase under warmer conditions (Wookey et al. 1995, Cooper et al. 2004). However, because of the relatively small effects of the simulated warming on the colonization processes, even without climate change, there may be changes in species richness if dispersal limitation is overcome.

Local interactions were more important for colonization than temperature conditions at Finse, suggesting that biotic interactions are more important for alpine plant community structure than previously suggested for environmentally harsh communities unsaturated with species (Grime 1979, Huston 1999, Zobel et al. 2000, Foster 2001). However, the stronger negative relationship between vascular, in particular graminoid species richness, and invasibility under experimental warming, suggests that climate change may increase the role of interspecific competition on alpine plant community structure, and thus alter the long-term effects of biotic interactions on invasibility and diversity. Because of the limited dispersal abilities of the regional species, and the competitive exclusion of invaders by resident species, global warming alone may not result in a rapid colonization of alpine *Dryas* heaths. However, the recent migration of species on European mountains (e.g. Grabherr et al. 1994, Kullmann

2002, Klanderud and Birks 2003), but the minor effects of climate warming on colonization processes found in our study, may suggest that climate is a driver of species distributions on large temporal and spatial scales, whereas propagule availability and local interactions limit colonization processes over a shorter time-span and smaller spatial scales. Due to the slow growth of alpine plants (Billings and Mooney 1968), long-term experiments are needed to assess if invading species will be a threat to the richness and abundances of the resident species in alpine habitats.

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Figure legends

Fig. 1. Simple linear regressions of the number of species added as propagules (independent) and (a-c) seedling species richness and (d-f) log+1 seedling density per plot (0.18 m^2) (dependent) under ambient (control: solid circle, solid line) and elevated (T: open circle, dashed line) temperature conditions in 2001, 2002, and 2003. R^2, β (Std. regression coefficients), and *P*-values are given.

Fig. 2. Simple linear regressions of the number of species added as propagules (independent) and the number of vascular species in 2004 (dependent) under ambient (control: solid circle, solid line) and elevated temperature (T: open circle, dashed line) conditions. R^2, β (Std. regression coefficients), and *P*-values are given.

Table 1. Species added as propagules, their life-form, number of plots to which they were added, number of these in which they were present in 2000 and 2004, average frequency abundances in 2000 and 2004 across all plots to which they were and were not added as propagules under ambient (C) and elevated (T) temperature conditions.

Species	Life form *	No. plots added	No. plots present 2000		No. plots present 2004		Abundance 2000		Abundance 2004 Propagules added §		Abundance 2004 No propagules added #	
			C	T	C	T	C	T	C	T	C	T
Antennaria dioica	F	38	19	18	19	24	0.05	0.06	0.07	**0.10**	0.06	**0.04**
Antoxanthum odoratum	G	42	0	0	3	0	0.00	0.00	0.04	0.00	0.02	0.003
Arabis alpina	F	44	0	0	1	0	0.00	0.00	0.002	0.00	0.001	0.00
Bistorta vivipara	F	42	39	40	40	40	0.85	0.90	0.9	0.9	0.90	**0.95**
Carex atrofusca	G	48	5	5	8	7	0.01	0.01	**0.02**	0.03	0.04	0.03
C. capillaris	G	36	4	5	5	8	0.01	0.02	0.01	0.03	0.02	0.04
Cerastium alpinum	F	46	22	12	28	23	0.08	0.03	**0.18**	**0.15**	**0.04**	**0.02**
C. cerastoides	F	36	0	0	4	2	0.00	0.00	0.01	0.003	0.00	0.00
Epilobium anagalidifolium	F	40	0	0	5	7	0.00	0.00	**0.01**	**0.01**	**0.00**	**0.00**
Erigeron uniflorus	F	42	19	13	32	30	0.05	0.04	**0.22**	**0.26**	**0.03**	**0.06**
Festuca vivipara	G	38	34	27	32	33	0.34	0.15	0.23	0.19	0.16	0.14
Leontodon autumnalis	F	38	0	0	13	10	0.00	0.00	**0.05**	**0.05**	**0.00**	**0.00**
Luzula spicata	G	44	23	23	22	20	0.07	0.07	0.08	0.07	0.08	0.07

Omaloteca supina	F	44	0	0	7	8	0.00	0.00	**0.01**	**0.01**	**0.00**	**0.00**
Oxyria digyna	F	44	0	0	6	9	0.00	0.00	**0.01**	**0.02**	**0.00**	**0.00**
Oxytropis lapponica	L	30	18	7	21	18	0.17	0.04	0.26	**0.22**	**0.06**	**0.03**
Parnassia palustris	F	46	0	1	10	11	0.00	0.001	**0.04**	**0.03**	**0.001**	**0.00**
Poa alpina	G	30	6	3	4	7	0.02	0.01	0.01	0.02	0.003	0.01
Potentilla crantzii	F	36	25	23	26	32	0.12	0.10	**0.26**	**0.28**	**0.11**	**0.10**
Ranunculus acris	F	54	0	0	28	27	0.00	0.00	**0.20**	**0.25**	**0.00**	**0.001**
Rumex acetosa	F	42	0	0	0	0	0.00	0.00	0.00	0.00	0.00	0.00
Saxifraga cespitosa	F	36	2	1	1	1	0.003	0.003	0.001	0.001	0.00	0.003
S. oppositifolia	F	44	6	7	9	6	0.02	0.01	0.03	0.01	**0.004**	0.01
Silene acaulis	F	38	35	38	37	39	0.30	0.37	**0.37**	0.39	0.31	0.34
Taraxacum sp.	F	40	0	0	19	21	0.00	0.00	**0.12**	**0.16**	**0.003**	**0.001**
Thalictrum alpinum	F	34	40	40	40	40	0.76	0.76	0.74	0.70	**0.68**	0.72
Veronica alpina	F	36	0	0	10	8	0.00	0.00	**0.02**	**0.01**	**0.00**	**0.00**

* F, nonlegume forb; L, legume; G, graminoid

§ Boldface values indicate that 2004 abundance differ significantly from 2000 abundance (*t*-test, $P < 0.05$).

\# Boldface values indicate that 2004 abundance in propagule-addition plots differ significantly from 2004 abundances in plots not receiving propagules (*t*-test, $P < 0.05$).

Table 2. Multiple regressions of the relationships between different community parameters and community invasibility (species richness in 2004 minus 2000) under ambient (control) and elevated (OTC) temperature conditions. (A) Parameters, standardized regression coefficients (β) and t-test for H_0 that each regression parameter differs from 0. Asterisks indicate significant interaction (* = $P < 0.1$, ** = $P < 0.05$) between the OTC factor and the parameter in an ANCOVA. (B) ANOVAs on overall multiple regressions.

A)	Control				OTC			
Parameters	df	β	*t*	*P*	df	β	*t*	*P*
Species added	1	0.54	4.14	< 0.001	1	0.49	4.96	< 0.001
Vascular richness*	1	-0.48	-3.00	0.005	1	-0.49	-4.73	< 0.001
Dryas cover	1	-0.36	-2.68	0.011	1	-0.26	-2.45	0.020
Bare soil	1	0.21	1.56	0.129	1	0.28	2.67	0.012
Soil moisture	1	0.39	2.52	0.017	1	0.59	3.80	0.001
NH_4+NO_3**	1	-0.37	-2.77	0.009	1	-0.27	-1.88	0.068

B) Analysis of variance

Source	df	*F*	*P*	R^2	df	*F*	*P*	R^2
Model	6	6.16	< 0.001	0.574	6	13.21	< 0.001	0.701
Error	33				33			

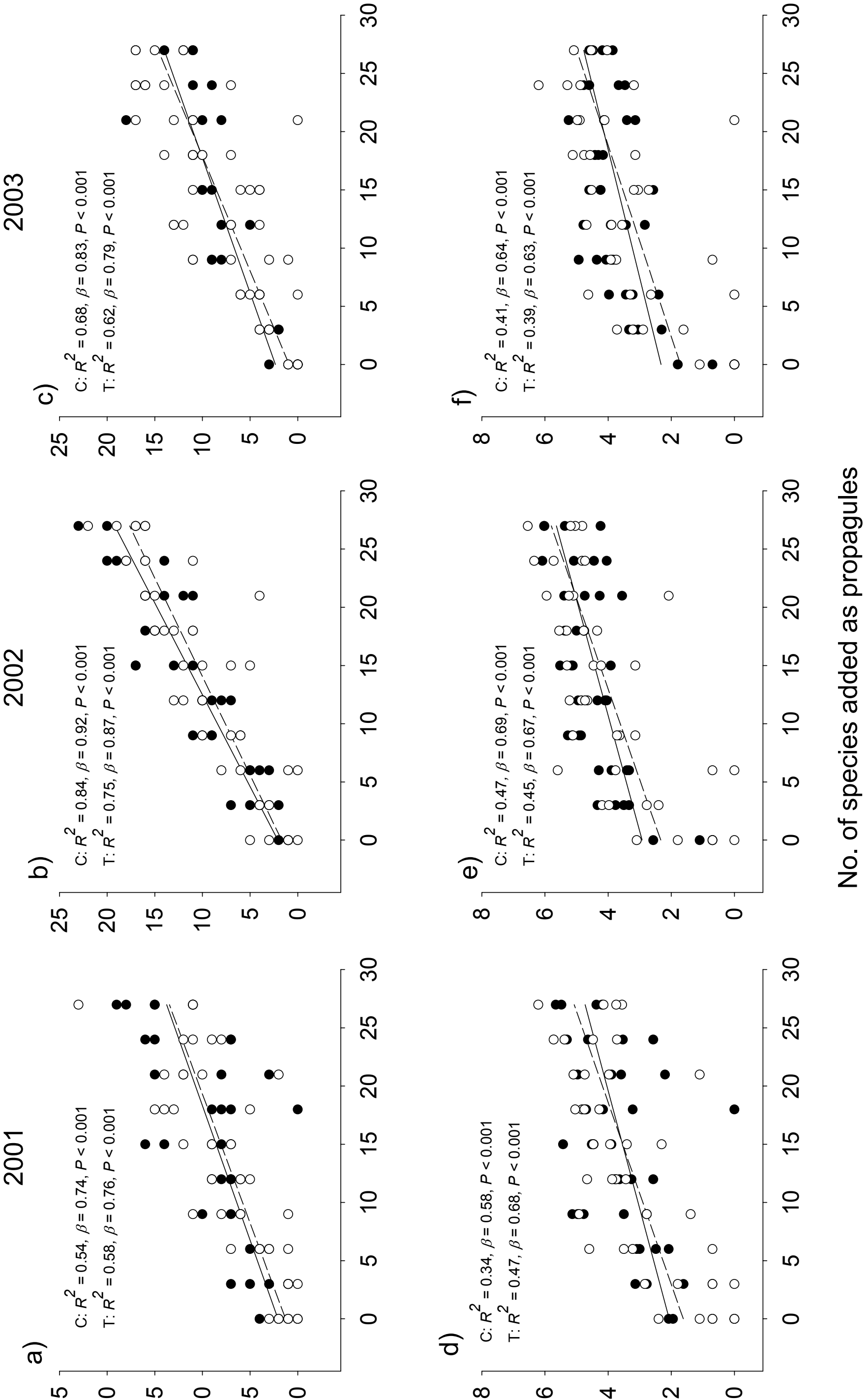
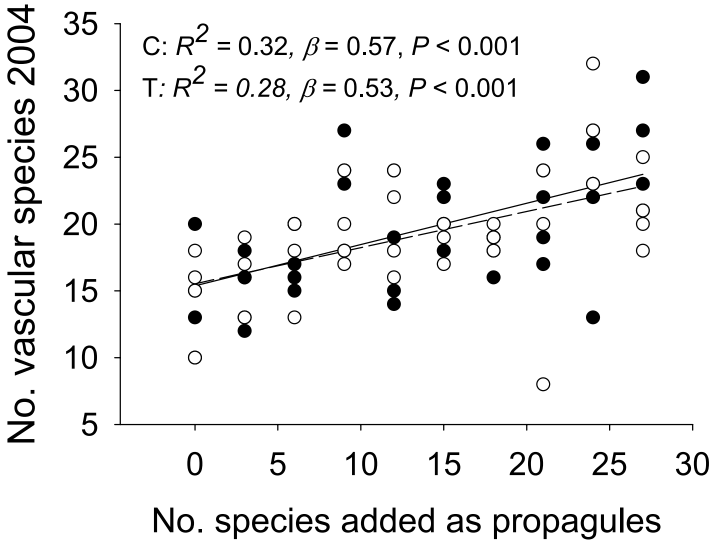

2001
2002
2003
a)
b)
c)
d)
e)
f)
C: $R^2 = 0.54$, $\beta = 0.74$, $P < 0.001$
T: $R^2 = 0.58$, $\beta = 0.76$, $P < 0.001$
C: $R^2 = 0.84$, $\beta = 0.92$, $P < 0.001$
T: $R^2 = 0.75$, $\beta = 0.87$, $P < 0.001$
C: $R^2 = 0.68$, $\beta = 0.83$, $P < 0.001$
T: $R^2 = 0.62$, $\beta = 0.79$, $P < 0.001$
C: $R^2 = 0.34$, $\beta = 0.58$, $P < 0.001$
T: $R^2 = 0.47$, $\beta = 0.68$, $P < 0.001$
C: $R^2 = 0.47$, $\beta = 0.69$, $P < 0.001$
T: $R^2 = 0.45$, $\beta = 0.67$, $P < 0.001$
C: $R^2 = 0.41$, $\beta = 0.64$, $P < 0.001$
T: $R^2 = 0.39$, $\beta = 0.63$, $P < 0.001$
Seedling species richness
Seedling density/plot (log+1)
No. of species added as propagules
0
5
10
15
20
25
30
0
2
4
6
8

Figure 1



C: $R^2 = 0.32$, $\beta = 0.57$, $P < 0.001$
T: $R^2 = 0.28$, $\beta = 0.53$, $P < 0.001$
No. vascular species 2004
35
30
25
20
15
10
5
0
5
10
15
20
25
30
No. species added as propagules

Figure 2

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