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Plant community type and small-scale disturbances, but not altitude, influence the invasibility in subarctic ecosystems

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Summary

- Little of our knowledge about invasibility comes from arctic and alpine ecosystems, despite increasing plant migration and invasion in those regions. Here, we examine how community type, altitude, and small-scale disturbances affect invasibility in a subarctic ecosystem.
- Over a period of 4 yr, we studied seedling emergence and establishment in 17 species sown in gaps or undisturbed vegetation in four subarctic community types (*Salix* scrub, meadow, rich heath, poor heath) along an elevation gradient.
- Invasibility was lowest in rich heath and highest in *Salix* scrub. Small disturbances significantly increased the invasibility in most communities, thereby showing the importance of biotic resistance to invasion in subarctic regions. Unexpectedly, invasibility did not decrease with increasing elevation, and it was also not related to summer temperature.
- Our data suggest that biotic resistance might be more important than abiotic stress for invasibility in subarctic tundra and that low temperatures do not necessarily limit seedling establishment at high altitudes. High elevations are therefore potentially more vulnerable to invasion than was originally thought. Changes in community composition as a result of species migration or invasion are most likely to occur in *Salix* scrub and meadow, whereas *Empetrum*-dominated rich heath will largely remain unchanged.

Introduction

In subarctic regions, the climate is now warming rapidly (Callaghan *et al.*, 2010) and further temperature increases are expected to be substantially greater than the global average (ACIA, 2004). This may lead to upward movement of native plant species (Kullman, 2002; Klanderud & Birks, 2003; Lenoir *et al.*, 2008) and improved climatic conditions for the establishment of alien species (Dukes & Mooney, 1999; Rose & Hermanutz, 2004; Walther *et al.*, 2009; Ware *et al.*, 2012). To date, we have very limited knowledge on where in the subarctic landscape migrating native or introduced alien species are most likely to establish, and thus where changes in plant community composition are likely to occur. This information, however, is needed to better predict ecosystem responses to climate change (Wookey *et al.*, 2009) and to improve models of species migration and invasion (Guisan & Thuiller, 2005; Pellissier *et al.*, 2010).

Invasibility (i.e. the susceptibility to the establishment of new species – this can be either natives or aliens; Burke & Grime, 1996) has rarely been examined in arctic or alpine ecosystems. Probably, this is because of earlier assumptions that native species rarely establish from seed in biomes dominated by clonal propagation (Billings & Mooney, 1968; Billings, 1987; Totland, 1997) and that invasion by alien species is strongly limited in

harsh environments (Millennium Ecosystem Assessment, 2005). However, the importance of sexual reproduction in cold ecosystems has now been acknowledged (Forbis, 2003; Erschbamer *et al.*, 2008; Venn & Morgan, 2009; Douhovnikoff *et al.*, 2010), and recent studies describe rapid increases of alien plant introductions and establishment in arctic and alpine ecosystems (Morgan & Carnegie, 2009; Alexander *et al.*, 2011; McDougall *et al.*, 2011; Ware *et al.*, 2012). Our current knowledge comes either from short (1 yr) experimental studies (Paiaro *et al.*, 2007; Eckstein *et al.*, 2011; Soudzilovskaia *et al.*, 2011) or from observational studies (Welling & Laine, 2002; Forbis, 2003; Venn & Morgan, 2009), which inherently suffer from differences in propagule pressure between the examined communities or habitats (Catford *et al.*, 2012). Here, we examined in a 4 yr study how plant community type, altitude and disturbance influenced invasibility in a subarctic ecosystem and how they interacted. We focused on easy-to-measure factors because they have the potential to be incorporated into species distribution models.

The most common plant community types in subarctic tundra are rich heath, poor heath, meadow and *Salix* scrub (Graae *et al.*, 2011). These community types do not only differ in species composition, but also in their occurrence along fine-scale topographic gradients which influence patterns of snow depth and duration, leading to strongly contrasting growing conditions (Forbis, 2003;

Körner, 2003; Graae *et al.*, 2011, 2012). As a result, we find relatively productive and species-rich plant communities in the more benign sheltered depressions (*Salix* scrub and mesic meadow), *Empetrum*-dominated dwarf shrub communities at intermediate habitats (rich heath), and low-growing species-poor heath communities, including a lot of lichens, on wind-exposed ridges (poor heath; Graae *et al.*, 2011). Prediction of which communities should have the highest invasibility is not straightforward, because they all have characteristics that could either benefit or hamper invasion. For instance, subarctic meadow communities are moist, have a reasonable amount of nutrients and are protected from subzero temperatures during winter, suggesting they have a higher invasibility than poor heath communities, which are dry, nutrient-poor and experience a lot of winter frost (Forbis, 2003; Graae *et al.*, 2011; Sundqvist *et al.*, 2011). On the other hand, considering the very short growing season in meadow (Körner, 2003; Graae *et al.*, 2011) and its higher species richness than in poor heath (higher diversity is often linked to lower invasibility; Knops *et al.*, 1999), one could also expect the opposite pattern. However, based on the assumption that subarctic plant communities are not yet saturated with species (Stohlgren *et al.*, 2008; Hoffmann, 2012), the knowledge that more species-rich places often support larger numbers of colonizers or invaders ('the rich get richer'; Stohlgren *et al.*, 2003), and the fact that the results from two studies show higher seedling numbers in meadow and *Salix* communities than in heath vegetation (Welling & Laine, 2002; Graae *et al.*, 2011), we expect a higher invasibility in the more sheltered and species-rich communities (i.e. meadow and *Salix* scrub) than in the more exposed communities (rich heath and poor heath).

Although altitude *per se* is not a perfect substitute for environmental harshness (Körner, 2007), the air temperature and the duration of the growing season usually decline with increasing elevation in high-latitude mountains, especially if other factors such as moisture regime are held constant (Körner, 2007). In particular, the transition from the forested montane zone to the treeless alpine zone is commonly related to a decrease in temperature and nutrient concentrations, and an increase in wind speed and the amount and duration of the snow cover (Körner, 2003; Sundqvist *et al.*, 2011), and therefore plant colonization might be hampered above the tree line. It is often assumed that invasibility decreases with increasing elevation (Pauchard & Alaback, 2004; Marini *et al.*, 2009), which is supported by observed lower numbers of alien species with increasing altitude (Alexander *et al.*, 2011; Pysek *et al.*, 2011). This pattern, though, could also arise from lower propagule pressure (i.e. the number of introduced seeds and/or number of introduction events; Colautti *et al.*, 2006) and less anthropogenic disturbances at high altitudes (Pysek *et al.*, 2011), and is thus not necessarily linked to differences in abiotic growing conditions. Moreover, reduced competition (Callaway *et al.*, 2002) and a higher small-scale heterogeneity at high- vs low-elevation sites (Davies, 2011) could potentially increase the invasibility at high altitudes. However, because abiotic factors (e.g. climatic conditions) often dominate over biotic factors (e.g. competition) in determining colonization or invasion success (D'Antonio *et al.*, 2001; Milbau *et al.*, 2009b), we expect that the invasibility decreases with increasing elevation, or at least declines from the montane to the alpine zone.

Disturbance is a strong driver of invasion in general (D'Antonio *et al.*, 1999) and small-scale disturbances play an important role in community invasibility by creating new microhabitats and directly removing or decreasing populations of competitor species (Kotanen, 1997; Byers, 2002). In subarctic environments, disturbances at the community scale are mainly created through grazing and trampling by reindeer, burrowing by lemmings and voles, and by cryogenic processes resulting in bare soil patches (Gough, 2006; Vistness & Nellemann, 2008). In various arctic and alpine communities, a positive effect of disturbance on colonization has been demonstrated (Welling & Laine, 2002; Lindgren *et al.*, 2007; Olofsson & Shams, 2007; Cichini *et al.*, 2011; Graae *et al.*, 2011), but it is not known how the role of disturbance differs between community types or along an elevation gradient. Here, we expect that disturbance will mainly increase the invasibility in the more productive sites (Graae *et al.*, 2011), and thus at low elevations and in meadow and *Salix* scrub. At higher elevations or in exposed communities (poor heath), disturbance could potentially disrupt facilitative interactions needed for plant colonization (Cavieres *et al.*, 2005), and we would therefore expect neutral or negative effects there. It must be noted, though, that Paiaro *et al.* (2007) found the opposite pattern, with disturbance reducing seedling emergence at all but the highest elevations, where the effect was positive.

We conducted a 4 yr fully factorial seed-sowing experiment in a subarctic ecosystem to examine if community type, altitude and small-scale disturbances affected invasibility, and how these factors interacted. Because we were interested in differences in invasibility (i.e. which habitats/biological communities are most susceptible to species establishment), and not in habitat preferences of individual species, we examined the germination and establishment success of a broad species pool, including different genera, growth forms and functional types. Further, we examined how the communities and altitudes differed in abiotic and biotic characteristics and whether any of those were closely correlated to invasibility.

Materials and Methods

Study site

The study was carried out between 500 and 900 m asl on the northeast-facing slope of Mt Suorooaivi (1193 m), located *c.* 20 km southeast of Abisko, *c.* 200 km north of the Arctic Circle in northern Sweden (68°21′N, 18°49′E). The bedrock consists of salic igneous rock and quartic and phyllitic hard schists (Sundqvist *et al.*, 2011). The site is characterized by a subarctic climate, with a mean annual air temperature of −0.6°C (Abisko Scientific Research Station, 1913–2006). The mean annual precipitation in the region is 303 mm yr^{-1} (Abisko Scientific Research Station, 400 m asl, 1913–2006). The growing season lasts for *c.* 130 d (Karlsson & Callaghan, 1996) and the tree line at the study site is situated at *c.* 550 m asl and formed by *Betula pubescens* ssp. *czerepanovii* (mountain birch). Reindeer range freely in the area.

Seed material

To compare the invasibility between plant communities or altitudes, we used the same seed mix in all treatments (Milbau *et al.*, 2003; Catford *et al.*, 2012). We used 22 species belonging to different functional types and varying in latitudinal range (Table 1). Apart from *Betula pubescens* ssp. *pubescens*, *Calamagrostis purpurea* and *Pinus sylvestris*, all species occurred in the study area, where we collected the seeds between 15 August and 13 September 2007. *P. sylvestris* and *Vicia cracca* are naturalized alien species in Sweden, whereas the other species are native to the area. Seeds of *P. sylvestris* were ordered from a seed company in Karesuando (68°20′N, 21°53′E) and seeds from *B. pubescens* ssp. *pubescens* and *C. purpurea* were collected in Umeå (63°49′N, 20° 15′E). All seeds were stored at room temperature until sowing. Five species showed very low germination in this study and in a related laboratory experiment (Milbau *et al.*, 2009a) and were therefore excluded from the analyses (Table 1).

Experimental design and treatments

At each of five elevations (500, 600, 700, 800 and 900 m asl), we selected three replicate plots per community type, that is *Salix* scrub, meadow, rich heath and poor heath, which differ in their occurrence along fine-scale topographic gradients (Forbis, 2003; Graae *et al.*, 2011; see Supporting Information, Table S1, for species composition). At the site at 500 m asl, there were no poor heath communities, as a result of the mild and sheltered conditions in the birch forest. The selected altitudinal gradient (500–900 m asl) ranged from just below the forest line to near the limit of vascular plant growth. Summer air temperatures

measured along the gradient at 400, 700 and 1000 m asl were, respectively, 13.3, 12.4 and 10.6°C in July 2008, and 9.6, 8.2 and 6.3°C in August 2008 (Sundqvist *et al.*, 2011).

In each of the 57 plots, we used three degrees of disturbance: undisturbed, gaps of 3 cm diameter, and gaps of 6 cm diameter. These treatments were applied to each of the 22 study species individually. Each plot thus contained 22 gaps of 3 cm, 22 gaps of 6 cm and 22 permanently marked undisturbed microplots. Because we were mostly interested in small disturbances, for instance created by animals in an otherwise undisturbed landscape, we chose gap sizes of 3 and 6 cm diameter. We expected these diameters to be large enough to affect target–neighbour interactions in subarctic communities (Milbau, *et al.*, 2007). We created the gaps by removing all above-ground vegetation and the top (*c.* 1 cm) of the soil layer with a core saw-drill of the correct diameter. Within each plot, large and small gaps were positioned randomly and all gaps were at least 20 cm apart. Between 27 September and 9 October 2007, 30 seeds per species were put in the centre of each gap, or in between two marker pins for the undisturbed treatment. Because of large seed sizes and high germination percentages in *P. sylvestris* and *V. cracca* (Milbau *et al.*, 2009a), only 10 seeds per gap were used for those species.

Seedling emergence and seedling establishment

We recorded seedling emergence in all 3762 microplots in June, July and August 2008, and recorded seedling survival in June and August 2009, and in July 2010. The total number of newly emerged seedlings ('seedling emergence') was calculated per plot and per disturbance treatment (i.e. undisturbed, 3 cm gap, 6 cm

Table 1 List of the species added as seeds to the studied plant communities

Species	Functional type	Seed origin	Latitudinal range	Excluded from analyses
Astragalus frigidus (L.) A.Gray	Forb (legume)	Abisko	Narrow	
Betula nana L.	Shrub	Abisko	Narrow	
Betula pubescens ssp. *pubescens* Ehrh.	Tree	Umeå	Broad	
Betula pubescens ssp. *czerepanovii* (Orlova) Hämet-Ahti	Tree	Abisko	Narrow	
Calamagrostis lapponica (Wahlenb.) Hartm.	Grass	Abisko	Narrow	
Calamagrostis purpurea (Trin.) Trin.	Grass	Umeå	Broad	×
Carex rostrata Stokes	Sedge	Abisko	Broad	×
Carex saxatilis L.	Sedge	Abisko	Narrow	×
Deschampsia flexuosa (L.) Trin.	Grass	Abisko	Broad	
Dryas octopetala L.	Dwarf shrub	Abisko	Narrow	
Empetrum hermaphroditum Lange ex Hagerup	Dwarf shrub	Abisko	Broad	×
Epilobium angustifolium L.	Forb	Abisko	Broad	
Festuca ovina L.	Grass	Abisko	Broad	
Pinus sylvestris L.	Tree	Karesuando	Broad	
Salix glauca L.	Shrub	Abisko	Broad	×
Silene acaulis (L.) Jacq.	Forb	Abisko	Narrow	
Silene dioica (L.) Clairv.	Forb	Abisko	Broad	
Solidago virgaurea Praecox	Forb	Abisko	Broad	
Vaccinium myrtillus L.	Dwarf shrub	Abisko	Broad	
Vaccinium uliginosum L.	Dwarf shrub	Abisko	Narrow	
Vaccinium vitis-idaea L.	Dwarf shrub	Abisko	Narrow	
Vicia cracca L.	Forb (legume)	Abisko	Broad	

gap). Further, we calculated, per plot and disturbance treatment, the total number of seedlings ('seedling establishment') and the number of seedling species ('seedling richness') present in 2010. Seedling establishment and seedling richness were used as a measure of invasibility. Seedling mortality was calculated as the difference between the maximum and the final number of seedlings divided by the maximum number of seedlings (i.e. % mortality).

Abiotic and biotic characteristics of the communities

In each community type and at each elevation, we measured soil temperature (°C) in the top 2 cm of the soil layer with three temperature sensors (ECT; Decagon Devices, Pullman, WA, USA), and soil volumetric moisture content (VWC, $m^3 m^{-3}$) in the top 5 cm soil layer with two soil moisture sensors (EC-5; Decagon Devices). We used several sensors per plot because they easily break down or get damaged by rodents or other animals. Soil temperature and soil moisture were measured every min and mean values h^{-1} were stored (Em50 data logger; Decagon Devices). We calculated average values over all working sensors in each plot. In the analyses, we used the mean soil temperatures from January 2008 (coldest month, 'winter temperature') and August 2008 (warmest month, 'summer temperature'). For soil moisture, averages were calculated over June, July and August 2008 ('summer moisture'). Snow depth was measured in March 2009, by putting a measuring pole in two locations per plot and averaging the values per plot.

Bioavailable amounts of NO_3^- and NH_4^+ were determined by burying three resin capsules (PST-1; Unibest, Bozeman, MT, USA) in each plot and allowing them to adsorb ions during 2 months (July and August 2008). The capsules were then collected and extracted in 2 M KCl. The KCl extractable concentrations of NH_4^+ and NO_3^- were determined by colorimetry and total N was calculated by adding NO_3-N and NH_4-N. For determination of soil pH, in each plot we collected three soil cores (4.5 cm diameter) of the top 5 cm soil layer and stored them at $-15°C$ until carrying out the analyses. We merged the three samples per plot and sieved them through a 2 mm sieve. Soil pH was measured in the soil suspension (6 g of soil in 50 ml deionized water) after shaking for 18 h using a MP220 pH meter (Mettler Toledo, Stockholm, Sweden).

The extent to which vegetation shaded seeds and seedlings was measured as photosynthetically active radiation (PAR, 400–700 nm) above the canopy and at the soil surface, yielding percentage PAR transmittance. This was done in July 2008, at the peak of the growing season, by measuring at four points in each plot with a PAR sensor (JYP 1000; SDEC, Reignac-sur-Indre, France). We carried out measurements on overcast days because this improves the results (Sinoquet et al., 1990). During August 2008, we determined species composition and cover in each plot in a representative square of 50 × 50 cm, with a frame split into 25 small squares. From these data, we also determined the species richness in each plot.

Statistical analyses

We used discriminant analysis (DA) to examine how the plant communities differed in the measured abiotic and biotic factors (summer temperature, winter temperature, summer moisture, snow depth, soil pH, total N, PAR transmittance, species richness), and a similar analysis was done to test for differences between altitudes.

We performed four linear mixed-model ANOVAs with seedling emergence, seedling establishment, seedling richness and seedling mortality as dependent variables, to test how community type, altitude and disturbance type affected the invasibility of the plots. Community type, altitude and disturbance and all possible interactions were entered as fixed factors. Plot nested within altitude × community type was used as a random factor in the analyses. Differences among means were further analysed by pairwise comparisons, using least significant differences.

Because most of the measured abiotic and biotic factors were correlated, we used a principal component analysis (PCA) regression approach (Jolliffe, 2002; Zuur et al., 2007) to assess which of these variables were most important for seedling emergence, seedling establishment and mortality. Because all measurements were done in intact vegetation (i.e. not in the gaps), seedling data from the undisturbed treatment were used as dependent variables. First, we conducted PCA on all explanatory variables (summer temperature, winter temperature, summer moisture, snow depth, soil pH, total N, PAR transmittance, species richness), which were normalized (i.e. mean = 0, SD = 1) before the PCA. Then we used all uncorrelated PCA axes as explanatory variables in the linear regression model, and with backward selection we selected those axes that were significantly related to the dependent variable. Following Zuur et al. (2007), we then used the estimated regression parameters of the axes that were retained in the model and their loadings (these told us how each axis was composed in terms of the eight original explanatory variables) to infer which of the original variables were most important. First, we multiplied the regression coefficient of each axis with the loadings for that axis. Then, we added up the multiplied loadings of all axes for each explanatory variable. This resulted in a final regression model that allowed us to assess which of the variables were important while avoiding problems with multicollinearity (Zuur et al., 2007).

Seedling emergence and seedling establishment were square-root-transformed in all analyses to improve normality of the data and homogeneity of variance. DA and PCA were performed using XLSTAT 2012.4.12 (Addinsoft, Paris, France) and all other statistical analyses with SPSS 18.0 (SPSS, Chicago, IL, USA).

Results

Plant communities and altitudes

Plant communities were well separated by the measured biotic and abiotic variables (DA, Wilk's lambda test, $P < 0.0001$; Fig. 1). Along the first axis, which represented 68% of the variation, Salix scrub showed the highest and poor heath the lowest values for soil moisture, pH, winter temperature, species richness, snow depth, total N and summer temperature (variables with discriminant function coefficients > 0.3, given in order of decreasing importance). For PAR transmittance, the highest values occurred in poor heath communities. The second axis represented 26% of

the variation and indicated higher values for species richness, PAR transmittance, snow depth, summer temperatures and pH in meadow compared with the other community types.

Also the altitudes varied significantly in abiotic and biotic variables (DA, Wilks' λ test, $P < 0.0001$; Fig. 2). The first axis, which accounted for 53% of the variation, indicated that the lowest elevations (500 and 600 m asl) had higher summer and winter temperatures, higher pH, higher soil moisture and lower PAR transmittance than the higher elevations. Contrary to our expectations, the highest altitude (900 m asl) was not positioned at the coldest end of this gradient, but was similar to the site at 700 m asl. The second axis accounted for 37% of the variation and was mainly correlated with soil moisture and snow depth, indicating high soil moisture at the 900 m site and high snow accumulation at the 700 m site.

Invasibility: effects of plant community type, altitude and small-scale disturbances

In undisturbed vegetation, *Salix* scrub showed the highest invasibility (measured as seedling emergence, seedling establishment or seedling richness) and the lowest values were found in the heath communities (Table 2; Fig. 3). Disturbance had a large effect on seedling emergence, establishment and richness, but there was no significant difference between 3 and 6 cm gaps (Table 2; Figs 3, 4). On average, three times as many seedlings became established in gaps compared with undisturbed vegetation. The beneficial effect of disturbance on seedling emergence was smaller in *Salix* scrub than in the other community types (significant disturbance × community type interaction; Fig. 3a), and the disturbance effect disappeared during seedling establishment in *Salix* scrub (Fig. 3b). The effects of disturbance on emergence, establishment and richness were similar in meadow, rich heath and poor heath (Fig. 3).

More seedlings emerged at 900 than at 800 m asl (Fig. 4a), but altitude did not affect seedling establishment or seedling richness

in intact communities (Fig. 4b,c). The effect of disturbance peaked at 600 m asl (Fig. 4), whereas at 500 m asl (i.e. in the birch forest) disturbance promoted seedling emergence (Fig. 4a), but not seedling establishment or richness (Fig. 4b,c). Disturbance had a smaller effect at 900 than at 700 and 800 m asl.

In general, seedling establishment and seedling richness were very strongly correlated (Pearson correlation test, $N = 171$, $P < 0.001$, $r = 0.921$), meaning that a high seedling number (i.e. 'seedling establishment') indicates that many species are able to establish, as opposed to many individuals of a particular species. During the first 3 yr, nearly 80% of all seedlings died (Fig. 5). Seedling mortality was not affected by the disturbance treatments, but there was a significant interaction between community type and altitude (Table 2, Fig. 5). Whereas in meadow the mortality decreased with increasing altitude, the pattern was the other way around in poor heath. In *Salix* scrub and rich heath, no clear altitudinal pattern was found.

For seedling emergence, four PCA axes were retained in the model ($P < 0.001$, $r^2 = 0.36$), and after multiplying the axes loadings with the regression coefficients (Zuur *et al.*, 2007), we obtained the following model: Emergence $= 3.44 + 0.15 \times$ total $N + 0.04 \times$ snow depth $- 0.19 \times T_{winter} + 0.12 \times T_{summer} + 0.55 \times$ soil moisture $+ 0.78 \times$ pH $- 0.48 \times$ PAR $+ 0.23 \times$ species richness. This suggests that high seedling emergence was most strongly associated with high pH, high soil moisture and low PAR transmittance. For seedling establishment, the model contained three PCA axes ($P = 0.009$, $r^2 = 0.17$), and establishment was most strongly associated with high pH, high species richness, high winter temperatures, and high soil moisture (establishment $= 1.52 + 0.06 \times$ total $N + 0.00 \times$ snow depth $+ 0.16 \times T_{winter} - 0.02 \times T_{summer} + 0.11 \times$ soil moisture $+ 0.41 \times$ pH $+ 0.06 \times$ PAR $+ 0.18 \times$ species richness). High seedling mortality was mainly associated with high snow depth, low winter temperatures and low species richness (mortality $= 81.84 + 2.67 \times$ total $N + 5.03 \times$ snow depth $- 4.81 \times T_{winter} + 0.07 \times T_{summer} + 2.08 \times$ soil moisture $+ 2.80 \times$ pH $+$
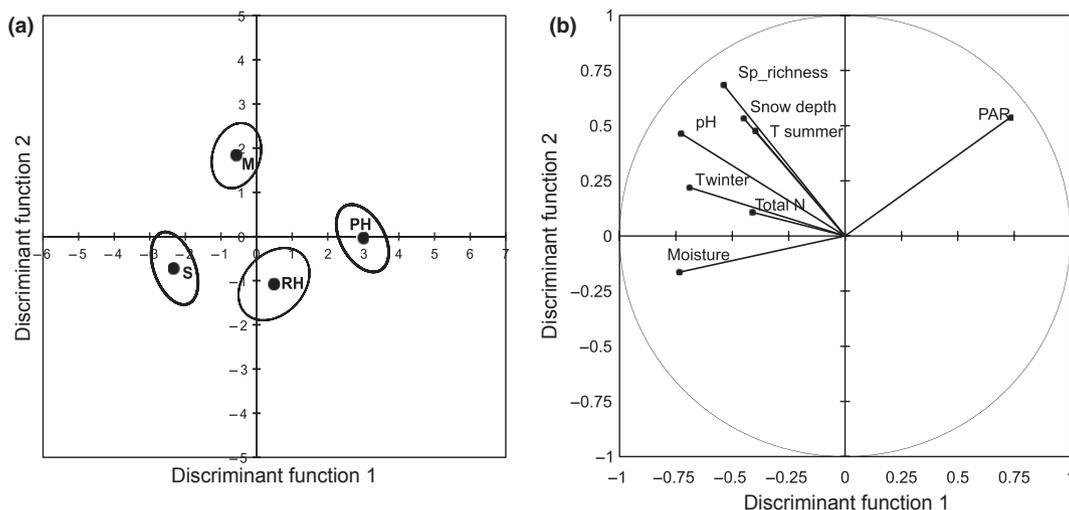

Fig. 1 (a) Plot of group centroids and confidence ellipses (95% confidence interval) for the different community types classified by discriminant analysis. S, *Salix* scrub; M, meadow; PH, poor heath; RH, rich heath. (b) Correlation between biotic and abiotic variables and the discriminant functions (DFs). DF1 = 68%, DF2 = 26%. PAR, photosynthetically active radiation.
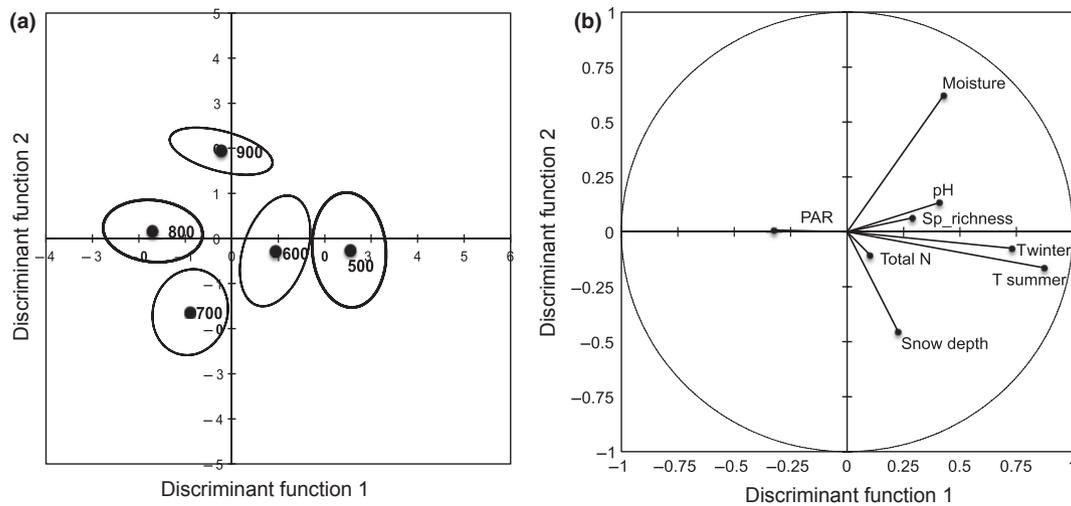
Fig. 2 (a) Plot of group centroids and confidence ellipses (95% confidence interval) for the different altitudes (500–900 m asl) classified by discriminant analysis. (b) Correlation between biotic and abiotic variables and the discriminant functions (DFs). DF1 = 53%, DF2 = 37%. PAR, photosynthetically active radiation.

Table 2 Effects of altitude, community type and disturbance type on seedling emergence, seedling establishment, seedling richness and seedling mortality in linear mixed models

Source of variation	Seedling emergence F_{df}	P	Seedling establishment F_{df}	P	Seedling richness F_{df}	P	Seedling mortality F_{df}	P
Altitude (A)	$1.242_{4,38}$	0.310	$2.990_{4,38}$	**0.031**	$2.918_{4,38}$	**0.034**	$1.382_{4,38}$	0.258
Community (C)	$1.962_{3,38}$	0.136	$1.240_{3,38}$	0.309	$2.312_{3,38}$	0.092	$1.817_{3,38}$	0.160
Disturbance (D)	$112.720_{2,76}$	**< 0.001**	$30.140_{2,76}$	**< 0.001**	$34.111_{2,76}$	**< 0.001**	$0.437_{2,75}$	0.648
A × C	$0.613_{11,38}$	0.806	$1.925_{11,38}$	0.067	$1.871_{11,38}$	0.075	$3.318_{11,38}$	**0.003**
A × D	$2.675_{8,76}$	**0.012**	$1.819_{8,76}$	0.086	$1.331_{8,76}$	0.241	$1.364_{8,75}$	0.226
C × D	$3.663_{6,76}$	**0.003**	$4.631_{6,76}$	**< 0.001**	$6.341_{6,76}$	**< 0.001**	$0.387_{6,75}$	0.885
A × C × D	$1.160_{22,76}$	0.309	$0.966_{22,76}$	0.514	$1.102_{22,76}$	0.364	$1.186_{22,75}$	0.286

P-values < 0.05 are in bold. Seedling emergence and seedling establishment were square-root-transformed before analyses.

$1.32 \times$ PAR $- 4.75 \times$ species richness), based on a model with two PCA axes ($P = 0.009$, $r^2 = 0.17$).

Discussion

Overall, invasibility in the subarctic was strongly affected by community type and disturbance, whereas altitude had no effect on invasibility in undisturbed vegetation. We will first discuss the influence of community type and altitude and then the effect of disturbance and how it interacts with community type and elevation.

In undisturbed vegetation, the invasibility was highest in *Salix* scrub and lowest in the two types of heath (Fig. 3), which is in agreement with our expectation of higher invasibility in more sheltered and benign communities. The discriminant analysis (Fig. 1) confirms the good overall growing conditions in *Salix* scrub, with high values for pH, winter temperature, soil moisture and nitrogen, and also a high species richness (Graae *et al.*, 2011). Our finding of low invasibility in intact rich heath communities is important, because this is by far the most dominant community type on poor acidic soils in the Northern

Hemisphere (Tybirk *et al.*, 2000; Pellissier *et al.*, 2010). Consequently, our results suggest that the current subarctic landscape might remain largely unchanged with a continued dominance of rich heath, and that *Salix* scrub and meadow will be the hotspots for community changes. We believe that this information should be used in species distribution models dealing with subarctic regions, as suggested, for instance, by Pellissier *et al.* (2010), who encourage integrating approaches from community ecology into models of species distribution.

Altitude did not affect the invasibility (seedling establishment and richness) of undisturbed communities (Fig. 4b,c), whereas we expected a higher invasibility at lower elevations (Pauchard & Alaback, 2004; Marini *et al.*, 2009). Even though the selected altitudinal gradient did not represent a perfect soil temperature gradient (Fig. 2), with the site at 900 m asl being milder than expected (Graae *et al.*, 2012; Tsyganov *et al.*, 2012), the invasibility at the coldest site (i.e. 800 m asl) was not lower than at other altitudes, nor was the invasibility higher in the warmer sites at 500 and 600 m asl. The lack of an overall altitude effect can be partly explained by the finding that summer soil temperature was only very weakly related to seedling emergence and establishment
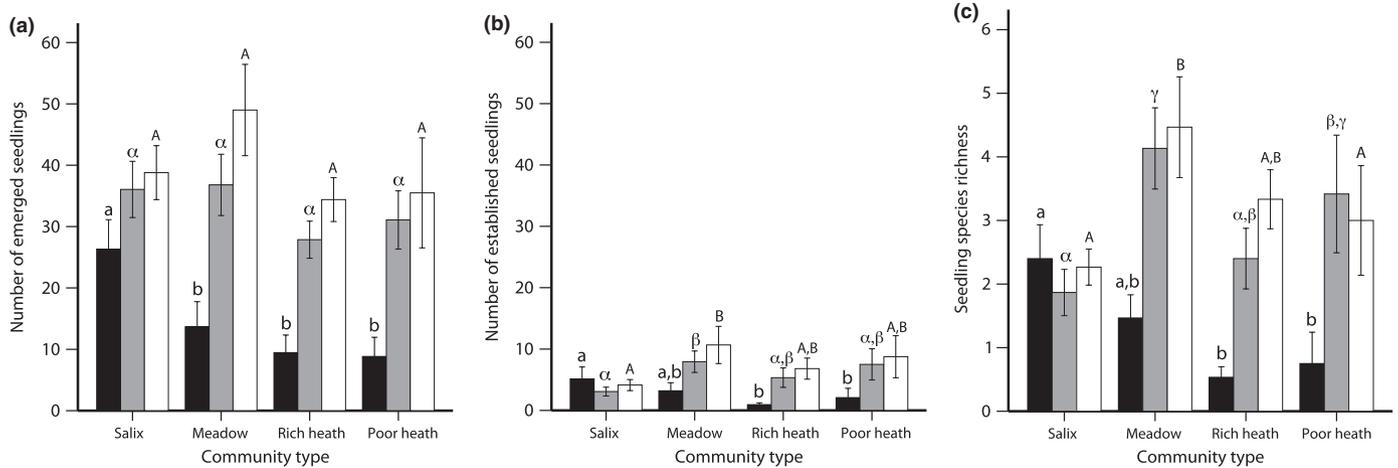
Fig. 3 Means (± 1 SE) for number of emerged seedlings (a), number of established seedlings (b), and seedling richness (c) in undisturbed vegetation (black bars), gaps of 3 cm diameter (grey bars), and gaps of 6 cm diameter (white bars) in the different community types. Different letters represent significant differences between community types (least significant difference (LSD), $P < 0.05$).

(PCA regressions), whereas factors that vary independently of elevation (e.g. pH or soil moisture) seemed more important. Our data thus suggest that colonization is not highly constrained by low summer temperatures, which is in accordance with earlier studies showing that warming had either no or a negative effect on the germination or early seedling establishment of arctic and subarctic species (Graae *et al.*, 2009; Milbau *et al.*, 2009a; Shevtsova *et al.*, 2009). It is important to note that we found seedlings from 14 out of the 17 sown species at the highest elevation, including species currently restricted to lower altitudes or latitudes, indicating that our findings are not restricted to cold climate specialist species.

If temperature differences in the range of 2–3°C (*c.* 400 m elevational difference) are indeed not strongly affecting germination and seedling establishment, then the lower number of alien species occurring at high elevations (Alexander *et al.*, 2011) might be more strongly related to limited seed availability or reduced anthropogenic disturbances than to low temperatures. The high number and genetic diversity of alien plant species that are able to establish at high altitudes or latitudes (Morgan & Carnegie, 2009; McDougall *et al.*, 2011; Ware *et al.*, 2012), and the fact that they are mostly generalists instead of cold-climate specialists (Alexander *et al.*, 2011) supports this. This also suggests that the direct introduction of alien species to high elevations, for instance via mountain roads (Pauchard & Alaback, 2004), recreational activities (Johnston & Pickering, 2001; Morgan & Carnegie, 2009), or grazing (van Rees, 1982), poses a serious threat to the native mountain flora, especially once improved climatic conditions allow them to produce viable seeds. However, our results should not be extrapolated to the subnival zone or to high-arctic biomes, where more severe abiotic stress might seriously limit plant recruitment. Yet, we assume that our results are valid within the alpine zone in other mountain areas, at least where drought is not a limiting factor. This is supported by a study on mountain summits in southeastern Australia showing that natural seedling recruitment was not related to altitude (Venn & Morgan, 2009).

As expected (Cichini *et al.*, 2011; Graae *et al.*, 2011), small disturbances strongly increased the invasibility in our study system, with overall a threefold higher establishment in vegetation gaps than in undisturbed vegetation. Whereas past studies used gap sizes > 10 cm, we found that gap sizes of only 3 cm diameter were large enough to significantly increase the invasibility in the majority of community types and elevations. Yet, in the most productive plots, that is in *Salix* scrub or at 500 m altitude, neither the 3 cm, nor the 6 cm gaps had an effect on seedling establishment or richness, although they increased seedling emergence. Our results thus indicate that small-scale disturbances significantly improve the invasibility in most parts of the tundra landscape, but that larger disturbances may be needed to promote invasibility in more productive shrub- and tree-dominated subarctic communities (cf. Lindgren *et al.*, 2007). It must be noted, though, that *Empetrum*-dominated tundra (i.e. rich heath) is very resilient against disturbance and that *Empetrum* fails to recover only when it is 100% removed (Aerts, 2010). We therefore assume that even in the presence of herbivores, chances for invasion in rich heath will remain low. On the other hand, meadow (herbivory and burrowing) and poor heath (frost actions) show natural disturbances similar to those we simulated and therefore (climate-driven) changes in reindeer, vole and lemming populations (Kausrud *et al.*, 2008; Vors & Boyce, 2009) and in frost–thaw events may significantly affect the invasibility in these community types.

Contrary to our expectations, the disturbance effect did not decrease from the more productive *Salix* and meadow communities to the less productive heath communities. Differences in productivity and species richness alone could thus not explain differences in biotic resistance. Whereas the lack of a disturbance effect in the *Salix* scrub likely resulted from the small size of the vegetation gaps relative to the tall growing understorey vegetation, we assume that the strong effect of disturbance in the heath communities was related to their dominance by *Empetrum hermaphroditum* (see Table S1), a clonal evergreen species with a
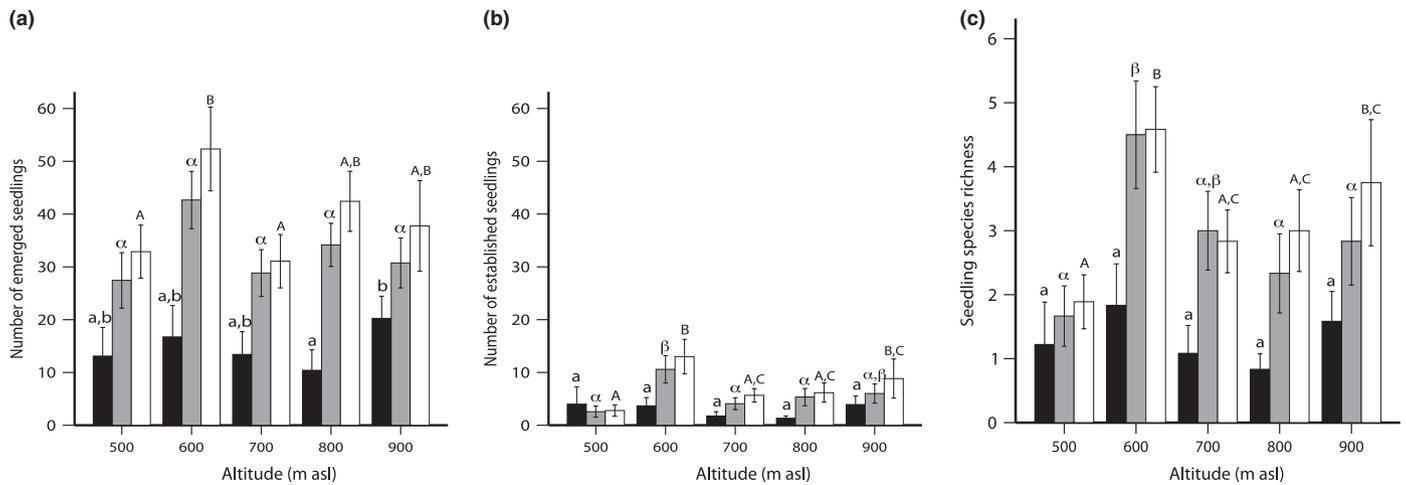
(a)

(b)

(c)

Fig. 4 Means (± 1) SE for number of emerged seedlings (a), number of established seedlings (b), and seedling richness (c) in undisturbed vegetation (black bars), gaps of 3 cm diameter (grey bars), and gaps of 6 cm diameter (white bars) at the different altitudes. Different letters represent significant differences between altitudes (least significant difference (LSD), $P < 0.05$).
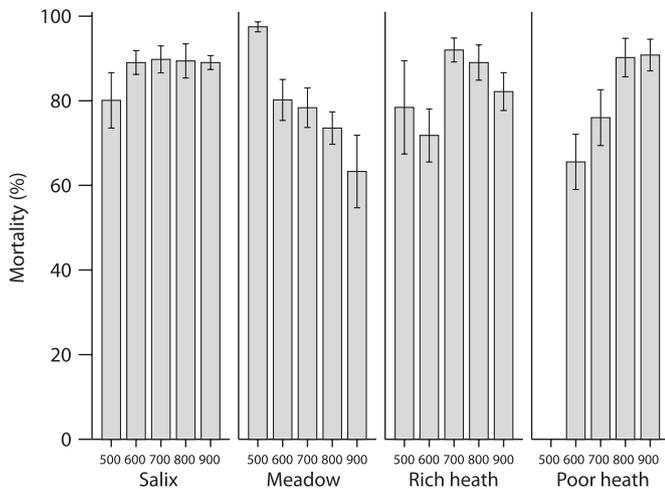

Fig. 5 Percentage seedling mortality (± SE) given per community type and altitude (m asl). There was no poor heath in the birch forest at 500 m.

very dense growth pattern and therefore a very strong competitor for space (Pellissier *et al.*, 2010). *E. hermaphroditum* also produces an allelopathic compound that potentially limits seedling growth and survival (Nilsson, 1994; Tybirk *et al.*, 2000; Aerts, 2010), but we did not observe higher seedling mortality in heath than in other community types (Fig. 5). Our results thus suggest that not only the productivity or diversity of invaded communities, but also their structure and species composition, determine the amount of biotic resistance against invasion. We argue that this should be more commonly taken into account in invasibility studies (cf. Dukes, 2002).

Whereas the gaps were probably too small to remove competition in the birch forest (i.e. at 500 m asl), the decreasing effect of disturbance in the alpine zone of the gradient (from 600 to 900 m asl) supports the idea of decreasing biotic resistance with increasing elevation. However, different from what was expected, there were no signs of facilitation in our study system. Indeed, even at the coldest and least productive site (800 m asl), close to

the subnival zone, we found positive disturbance effects. This supports the idea that in cold ecosystems, too, biotic competition might be an important driver of species assemblages (Klanderud & Totland, 2007; Eskelinen, 2010). However, because of the small size of our disturbances, we cannot completely exclude the presence of facilitative interactions, such as shelter from strong winds, by the extant vegetation.

Conclusions

Empetrum-dominated rich heath, the dominant community type in subarctic tundra, was very resistant against invasion, whereas meadow and *Salix* scrub were easier to invade. We therefore conclude that plant migration (or invasion) is not going to happen at the same speed anywhere in the subarctic landscape, and argue that species distribution models should incorporate differences in invasibility between plant community types. Small disturbances can considerably increase the invasibility of subarctic communities and we expect this to be mainly important in meadow and poor heath communities.

Unexpectedly, invasibility did not decrease with increasing altitude, and we found no indication that low temperatures limited colonization at high elevations. Biotic resistance, on the other hand, considerably reduced invasibility, even at the highest elevation and in the most exposed community type, where small vegetation gaps resulted in much higher seedling establishment. Our data thus suggest that, even in a harsh subarctic climate, biotic resistance might be more important than abiotic stress for community invasibility. Further, we found that biotic resistance depended more on vegetation structure and species composition than on community productivity or diversity, showing that species-poor communities are not necessarily easier to invade.

Our data suggest that altitude is not a strong limiting factor for colonization and invasion in subarctic tundra and therefore, given the influx of new (alien or native) seeds, significant changes in community composition and ecosystem functioning can be expected at high elevations in subarctic regions.

Acknowledgements

References

ACIA. 2004. *Impacts of a warming Arctic: Arctic climate impact assessment.* Cambridge, UK: Cambridge University Press.

Aerts R. 2010. Nitrogen-dependent recovery of subarctic tundra vegetation after simulation of extreme winter warming damage to *Empetrum hermaphroditum*. *Global Change Biology* 16: 1071–1081.

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN consortium. 2011. Assembly of non-native floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences, USA* 108: 656–661.

Billings WD. 1987. Constraints to plant growth, reproduction, and establishment in arctic environments. *Arctic and Alpine Research* 19: 357–365.

Billings WD, Mooney HA. 1968. The ecology of arctic and alpine plants. *Biological Reviews* 43: 481–529.

Burke MJ, Grime WJP. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776–790.

Byers JE. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97: 449–458.

Callaghan TV, Bergholm F, Christensen TR, Jonasson C, Kokfelt U, Johansson M. 2010. A new climate era in the sub-Arctic: accelerating climate changes and multiple impacts. *Geophysical Research Letters* 37: L14705.

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–848.

Catford JA, Vesk PA, Richardson DM, Pyšek P. 2012. Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Global Change Biology* 18: 44–62.

Cavieres LA, Quiroz CL, Molina-Montenegro MA, Munoz AA, Pauchard A. 2005. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspectives in Plant Ecology, Evolution and Systematics* 7: 217–226.

Cichini K, Schwienbacher E, Marcante S, Seeber GUH, Erschbamer B. 2011. Colonization of experimentally created gaps along an alpine successional gradient. *Plant Ecology* 212: 1613–1627.

Colautti RI, Grigorovich IA, MacIsaac HJ. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8: 1023–1037.

D'Antonio CM, Dudley TL, Mack M. 1999. Disturbance and biological invasions: direct effects and feedbacks. In: Walker LR, ed. *Ecosystems of disturbed ground.* Amsterdam, the Netherlands: Elsevier, 413–452.

D'Antonio CM, Levine J, Thomsen M. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. *Journal of Mediterranean Ecology* 2: 233–245.

Davies KF. 2011. Community invasibility: spatial heterogeneity, spatial scale, and productivity. In: Harrison SP, Rajakaruna N, eds. *Serpentine: the evolution and ecology of a model system.* Berkeley, CA, USA: University of California Press, 237–248.

Douhovnikoff V, Goldsmith G, Tape KD, Huang C, Sur N, Bret-Harte MS. 2010. Clonal diversity in an expanding community of Arctic *Salix* spp. and a model for recruitment modes of Arctic plants. *Arctic Antarctic and Alpine Research* 42: 406–411.

Dukes JS. 2002. Species composition and diversity affect grassland susceptibility and response to invasion. *Ecological Applications* 12: 602–617.

Dukes JS, Mooney HA. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution* 14: 135–139.

Eckstein RL, Pereira E, Milbau A, Graae BJ. 2011. Predicted changes in vegetation structure affect the susceptibility to invasion of bryophyte-dominated subarctic heath. *Annals of Botany* 108: 177–183.

Erschbamer B, Niederfriniger Schlag R, Winkler E. 2008. Colonization processes on a central Alpine glacier foreland. *Journal of Vegetation Science* 19: 855–862.

Eskelinen A. 2010. Resident functional composition mediates the impacts of nutrient enrichment and neighbour removal on plant immigration rates. *Journal of Ecology* 98: 540–550.

Forbis TA. 2003. Seedling demography in an alpine ecosystem. *American Journal of Botany* 90: 1197–1206.

Gough L. 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* 29: 44–56.

Graae BJ, De Frenne P, Kolb A, Brunet J, Chabrerie O, Verheyen K, Pepin N, Heinken T, Zobel M, Shevtsova A et al. 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. *Oikos* 121: 3–19.

Graae BJ, Ejrnæs R, Lang SI, Meineri E, Ibarra PT, Bruun HH. 2011. Strong microsite control of seedling recruitment in tundra. *Oecologia* 166: 565–576.

Graae BJ, Ejrnaes R, Marchand FL, Milbau A, Shevtsova A, Beyens L, Nijs I. 2009. The effect of an early-season short term heat pulse on plant recruitment in the Arctic. *Polar Biology* 32: 1117–1126.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.

Hoffmann MH. 2012. Not across the North Pole: plant migration in the Arctic. *New Phytologist* 193: 474–840.

Johnston FM, Pickering CM. 2001. Alien plants in the Australian Alps. *Mountain Research and Development* 21: 284–291.

Jolliffe IT. 2002. *Principal component analysis.* New York, NY, USA: Springer.

Karlsson PS, Callaghan TV. 1996. Plant ecology in the subarctic Swedish Lapland. *Ecology Bulletin* 45: 220–227.

Kausrud KL, Mysterud A, Steen H, Vik JO, Østbye E, Cazelles B, Framstad E, Eikeset AM, Mysterud I, Solhøy T et al. 2008. Linking climate change to lemming cycles. *Nature* 456: 93–97.

Klanderud K, Birks HJB. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene* 13: 1–6.

Klanderud K, Totland O. 2007. The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos* 116: 1279–1288.

Knops JMH, Tilman D, Haddad NM, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB, Siemann E, Groth J. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2: 286–293.

Körner C. 2003. *Alpine plant life: functional plant ecology of high mountain ecosystems.* Heidelberg, Germany: Springer.

Körner C. 2007. The use of 'altitude' in ecological research. *Trends in Ecology & Evolution* 22: 569–574.

Kotanen PM. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. *Journal of Applied Ecology* 34: 631–644.

Kullman L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* 90: 68–77.

Lenoir J, Gégout J-C, Marquet PA, de Ruffray P, Brisse H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320: 1768–1771.

Lindgren A, Eriksson O, Moen J. 2007. The impact of disturbance and seed availability on germination of alpine vegetation in the Scandinavian mountains. *Arctic, Antarctic, and Alpine Research* 39: 449–454.

Marini L, Gaston KJ, Prosser F, Hulme PE. 2009. Contrasting response of native and alien plant species richness to environmental energy and human impact along alpine elevation gradients. *Global Ecology and Biogeography* 18: 652–661.

McDougall K, Alexander J, Haider S, Pauchard A, Walsh N, Kueffer C. 2011. Alien flora of mountains: global comparisons for the development of local

preventive measures against plant invasions. *Diversity and Distributions* 17: 103–111.

Milbau A, Graae BJ, Shevtsova A, Nijs I. 2009a. Effects of a warmer climate on seed germination in the subarctic. *Annals of Botany* 104: 287–296.

Milbau A, Nijs I, Van Peer L, Reheul D, De Cauwer B. 2003. Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. *New Phytologist* 159: 657–667.

Milbau A, Reheul D, De Cauwer B, Nijs I. 2007. Factors determining plant–neighbour interactions on different spatial scales in young species-rich grassland communities. *Ecological Research* 22: 242–247.

Milbau A, Stout JC, Graae BJ, Nijs I. 2009b. A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biological Invasions* 11: 941–950.

Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: biodiversity synthesis.* Washington, DC, USA: World Resources Institute.

Morgan JW, Carnegie V. 2009. Backcountry huts as introduction points for invasion by non-native species into alpine vegetation. *Arctic, Antarctic, and Alpine Research* 41: 238–245.

Nilsson MC. 1994. Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. *Oecologia* 98: 1–7.

Olofsson J, Shams H. 2007. Determinants of plant species richness in an alpine meadow. *Journal of Ecology* 95: 916–925.

Paiaro V, Mangeaud A, Pucheta E. 2007. Alien seedling recruitment as a response to altitude and soil disturbance in the mountain grasslands of central Argentina. *Plant Ecology* 193: 279–291.

Pauchard A, Alaback PB. 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology* 18: 238–248.

Pellissier L, Bråthen KA, Pottier J, Randin CF, Vittoz P, Dubuis A, Yoccoz NG, Alm T, Zimmermann NE, Guisan A. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography* 33: 1004–1014.

Pysek P, Jarosik V, Pergl J, Wild J. 2011. Colonization of high altitudes by alien plants over the last two centuries. *Proceedings of the National Academy of Sciences, USA* 108: 439–440.

van Rees H. 1982. The diet of free-ranging cattle on the Bogong High Plains, Victoria. *Australian Rangelands Journal* 4: 29–33.

Rose M, Hermanutz L. 2004. Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. *Oecologia* 139: 467–477.

Shevtsova A, Graae BJ, Jochum T, Milbau A, Kockelbergh F, Beyens L, Nijs I. 2009. Critical periods for impact of climate warming on early seedling establishment in subarctic tundra. *Global Change Biology* 15: 2662–2680.

Sinoquet H, Moulia B, Gastal F, Bonhomme R, Varlet-Grancher C. 1990. Modelling the radiative balance of the components of a well mixed canopy: application to a white clover – tall fescue mixture. *Acta Oecologia* 11: 469–486.

Soudzilovskaia NA, Graae BJ, Douma JC, Grau O, Milbau A, Shevtsova A, Wolters L, Cornelissen JHC. 2011. How do bryophytes govern generative recruitment of vascular plants? *New Phytologist* 190: 1019–1031.

Stohlgren TJ, Barnett DT, Jarnevich CS, Flather C, Kartesz J. 2008. The myth of plant species saturation. *Ecology Letters* 11: 315–326.

Stohlgren TJ, Barnett DT, Kartesz JT. 2003. The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1: 11–14.

Sundqvist MK, Giesler R, Graae BJ, Wallander H, Fogelberg E, Wardle DA. 2011. Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos* 120: 128–142.

Totland Ø. 1997. Limits on reproduction in alpine *Ranunculus acris. Canadian Journal of Botany* 75: 137–144.

Tsyganov AN, Milbau A, Beyens L. 2012. Environmental factors influencing soil testate amoebae in herbaceous and shrubby vegetation along an altitudinal gradient in subarctic tundra (Abisko, Sweden). *European Journal of Protistology.* doi:10.1016/j.ejop. 2012.08.004.

Tybirk K, Nilsson M-C, Michelsen A, Kristensen HL, Shevtsova A, Tune SM, Johansson M, Nielsen KE, Riis-Nielsen T, Strandberg B et al. 2000. Nordic *Empetrum* dominated ecosystems: function and susceptibility to environmental changes. *Ambio* 29: 90–97.

Venn SE, Morgan JW. 2009. Patterns in alpine seedling emergence and establishment across a stress gradient of mountain summits in south-eastern Australia. *Plant Ecology & Diversity* 2: 5–16.

Vistness II, Nellemann L. 2008. Reindeer winter grazing in alpine tundra: impacts on ridge community competition in Norway. *Arctic, Antarctic & Alpine Research* 40: 215–224.

Vors LS, Boyce MS. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15: 2626–2633.

Walther G-R, Roques A, Hulme PE, Sykes MT, Pysek P, Kühn I, Zobel M, Bacher S, Botta-Dukat Z, Bugmann H et al. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* 24: 686–693.

Ware C, Bergstrom DM, Müller E, Alsos IG. 2012. Humans introduce viable seeds to the Arctic on footwear. *Biological Invasions* 14: 567–577.

Welling P, Laine K. 2002. Regeneration by seeds in alpine meadow and heath vegetation in sub-arctic Finland. *Journal of Vegetation Science* 13: 217–226.

Wookey PA, Aerts R, Bardgett RD, Baptist F, Bråthen KA, Cornelissen JHC, Gough L, Hartley IP, Hopkins DW, Lavorel S et al. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* 15: 1153–1172.

Zuur AF, Ieno EN, Smith GM. 2007. *Analysing ecological data.* New York, NY, USA: Springer.

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Plant species composition in the different plots

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