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## Ontogenetic niche shifts in three *Vaccinium* species on a sub-alpine mountain side

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**Background:** Climate warming in arctic and alpine regions is expected to result in the altitudinal migration of plant species, but current predictions neglect differences between species' regeneration niche and established niche.

**Aims:** To examine potential recruitment of *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea* on a mountain slope in northern Sweden in relation to current adult occurrence.

**Methods:** We combined a seed-sowing experiment in seven community types with adult occurrence observations and species distribution mapping.

**Results:** Emergence of *V. myrtillus* and *V. vitis-idaea* seedlings was significantly related to community type, while *V. uliginosum* was indifferent, but exhibited the highest average emergence. Adult occurrence was related to community, and ontogenetic niche shifts were observed for all three study species. *V. myrtillus* was shown to have the highest potential recruitment in habitats at altitudes above its current populations.

**Conclusions:** The potential for migration exists, but incongruence between regenerative and established niches presents a challenge for colonisers, as well as for plant migration modelling.

**Keywords:** climate; established niche; germination; mapping; regeneration niche; *Vaccinium*

### Introduction

During the second half of the twentieth century, the most rapid climatic warming has occurred at northern latitudes, and the Arctic region is predicted to experience the most pronounced climatic change in the future (Anisimov et al. 2007). This is thought to cause plant communities to shift to higher altitudes and latitudes (Lenoir et al. 2008; Wolf et al. 2008). Re-sampling studies in alpine regions have, however, found that despite altitudinal range shifts, upward migration of plant species was rarely as rapid as expected from the warming, and well below rates predicted by bioclimatic envelope models (Grabherr et al. 1994; Klanderud and Birks 2003; Pauli et al. 2003; Moen and Lagerström 2008), though long-distance dispersal events do occur (Alsos et al. 2007). Predictions of plant distribution shifts with climatic change suffer criticisms for the lack of dispersal parameters (Higgins et al. 2003; Guisan and Thuiller 2005; Neilson et al. 2005), with range shift simulations assuming either unlimited or no dispersal (Thomas et al. 2004; Thuiller 2004).

Arctic and alpine plant communities are dominated by clonal plants, with vegetative propagation as the most common form of reproduction (Körner 2003). The scale of latitudinal and altitudinal migration predicted by bioclimatic envelope models, however, requires reproduction by

detached propagules such as seeds (Molau and Larsson 2000). A key stage in the dispersal of and colonisation by a species is seedling recruitment (Harper 1977; Eriksson 2000), and therefore investigations on that topic might help to explain the differences between predicted and realised altitudinal migration.

The stages of seedling recruitment in alpine plants include breaking of dormancy, germination, seedling emergence and seedling survival. These stages are affected by a number of variables, including temperature (Baskin et al. 2000; Körner 2003), light availability (Giba et al. 1993; Shimono and Kudo 2005), soil moisture (Bell and Bliss 1980; Forbis 2003; Shimono and Kudo 2005) and the availability of various nutrients (Chambers et al. 1990; Hawkins and Henry 2004). These factors are partially controlled by the structure and composition of plant communities, influencing seedling establishment in the field (Welling and Laine 2002; Shimono and Kudo 2003; Gough 2006), with neighbour interactions working in tandem with the effects of climatic change to facilitate expansion or reinforce barriers for migration (Davis et al. 1998; Dona and Galen 2006).

*Vaccinium* dwarf shrubs dominate the field layer of many temperate, boreal and alpine communities across the northern hemisphere and are known to have different

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altitudinal distributions (Molau and Larsson 2000; Frak and Ponge 2002; Welling and Laine 2002), as well as displaying considerable variation in growth, reproduction, dispersal and germination (Shevtsova et al. 1995; Vander Kloet and Hill 2000). It has been suggested that *Vaccinium myrtillus* L. would invade higher altitudes under warmer conditions (Heegaard 2002; Fosaa et al. 2004; Sundqvist et al. 2008), although results from re-sampling studies have been inconclusive, ranging from considerable expansion to marginal contraction of altitudinal limits over the past century (Klanderud and Birks 2003; Moen and Lagerström 2008).

*Vaccinium* species produce numerous seeds, which are dispersed endozoochorously by a variety of birds and mammals (e.g. Traveset and Willson 1997; Graae et al. 2004; Bruun et al. 2008), and can remain viable after several years of burial (Granström 1987; Hill and Vander Kloet 2005). Despite this, they lack germinable seed banks across much of their geographical range (Vander Kloet and Hill 1994; Molau and Larsson 2000; Alsos et al. 2003; Cooper et al. 2004; but see Granström 1982). Work in boreal forest systems by Eriksson and Fröberg (1996) and Eriksson (2002) has suggested that *Vaccinium* species depend on narrow 'windows of opportunity' for germination, using widespread dispersal as a strategy to find appropriate sites for colonisation, as well as exhibiting ontogenetic niche shifts implying different environmental optima for germination, seedling and juvenile survival, and adult occurrence. It is possible that the availability of such 'windows' outside of the adult population range limits migration as much as the production and dispersal of viable seeds. In sub-alpine areas, variables such as topography, soil chemistry and microclimate control the distribution of plant communities which in turn may facilitate or hinder colonisation by seed (Billings and Bliss 1959; Körner 2003; Darmody et al. 2004; Björk et al. 2007).

In this study we used a seed-sowing experiment and adult occurrence observations in different community types to compare community preferences of two life stages of three *Vaccinium* dwarf shrubs, as well as to map seedling emergence and adult occurrence on a mountain face in northern Swedish Lapland. Specific questions asked were: (1) Does the regeneration niche of *Vaccinium* dwarf shrubs correspond to the established niche in alpine and sub-alpine habitats? and (2) Does the availability of regeneration sites for these species limit altitudinal migration?

## Methods

### Study area

The Abisko valley is situated south of lake Torneträsk, 200 km north of the Arctic circle in the far north of Sweden, in the sub-Arctic ecotone between the boreal forest and the tundra zone. The 1961–1990 average annual temperature in Abisko was approximately  $-0.8$  °C. July is on average the warmest month ( $+11$  °C) and January the coldest ( $-11.9$  °C). Mean annual precipitation 1961–1990

was 304 mm (Alexandersson and Eggertsson Karlström 2001).

Mount Njulla (also Nuolja) and Tältlägret are both situated in the Abisko valley, at  $68^{\circ} 22' N$ ,  $18^{\circ} 41' E$  and  $68^{\circ} 17' N$ ,  $18^{\circ} 45' E$ , respectively. Njulla peaks at 1169 m above sea level (a.s.l.), with the treeline of *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman. found at around 650 m a.s.l. on the east-facing slope. The area around Tältlägret is situated just above the treeline, between 650 and 800 m a.s.l. Both areas are visited by walkers during the summer, and Njulla hosts off-piste skiing in the winter. Herded reindeer are known to graze throughout the area. The three study species, *Vaccinium myrtillus*, *V. uliginosum* L. and *V. vitis-idaea* L. have long been identified among the dominant dwarf shrub species in Abisko (Fries 1925; Phoenix et al. 2001).

### Seed-sowing experiment

This study used a combination of two seed-sowing experiments from the same year, using the same seed pools, but slight differences in experimental design exist between the two study areas. Ripe fruits of *V. myrtillus* and *V. uliginosum* were collected from populations in the Abisko valley, while *V. vitis-idaea* fruits were collected in Norway at the same latitude, from which plump seeds were extracted in the laboratory.

In September and October 2005, these seeds were sown in sites distributed within seven community types (Table 1). Five communities were situated at Tältlägret, where the habitat mosaic implied that the communities were separated by only a few hundred metres. Here, four sites were chosen which contained each of the five non-forested communities. At each site, a plot  $0.1 \text{ m} \times 0.1 \text{ m}$  in size was disturbed (see below) in each community type, and the study species were randomly assigned to a  $0.025 \text{ m} \times 0.025 \text{ m}$  subplot where 30 seeds were sown. One Lichen Heath plot was later found to be waterlogged during the summer, and therefore did not match our habitat definition, so seedling emergence data from this plot were not analysed.

The below-treeline Forest Heath and Forest Meadow communities were placed on the east face of Njulla, approximately 1 km apart, separated by 200 m altitude. In each community, five  $0.05 \text{ m} \times 0.05 \text{ m}$  plots were disturbed within the same  $5 \text{ m} \times 5 \text{ m}$  area. Sites with low canopy cover, which were at least 25 m from any signs of regular anthropogenic disturbance, were chosen. Fifty seeds of each species were placed in a randomly predetermined  $0.025 \text{ m}$  quarter of the disturbed square plot, with the remaining left bare as a control. Similar plots in *Salix* Meadow, Low Meadow and Poor Heath communities on Njulla were used to test correspondence between the two study areas.

The disturbance treatment was designed to mimic natural disturbance events by herbivores in the forest–tundra ecotone, where plants are removed, and the organic or mineral soil exposed (Olofsson et al. 2005). To do this, we

Table 1. Plant communities in the Abisko valley and associated dominant or typical vascular plant species. In addition to vegetation, communities varied with regards to soil and moisture, with meadow communities characterised by higher soil moisture and productivity than were the heath communities, with the above-treeline heath communities declining in soil quality, moisture and productivity from Rich Heath (RH) to Poor Heath (PH) to Lichen Heath (LH).

Community	Location	Dominant or typical species
Forest Heath (FH)	Njulla	<i>Betula pubescens</i> ssp. <i>tortuosa</i> , <i>Empetrum nigrum</i> spp. <i>hermaphroditum</i> , <i>Vaccinium vitis-idaea</i> , <i>V. myrtillus</i> , <i>Linnaea borealis</i>
Forest Meadow (FM)	Njulla	<i>Betula pubescens</i> ssp. <i>tortuosa</i> , <i>Geranium sylvaticum</i> , <i>Deschampsia flexuosa</i> , <i>Viola biflora</i> , <i>Dryopteris</i> spp.
<i>Salix</i> Meadow (SM)	Njulla/Tältlägret	<i>Anthoxanthum odoratum</i> , <i>Equisetum arvense</i> , <i>Salix</i> spp., <i>Saussurea alpina</i> , <i>Trollius europeus</i> , <i>Viola biflora</i>
Low-growing Meadow (LM)	Njulla/Tältlägret	<i>Anthoxanthum odoratum</i> , <i>Bartsia alpina</i> , <i>Carex vaginata</i> , <i>Deschampsia flexuosa</i> , <i>Salix herbacea</i> , <i>Sibbaldia procumbens</i> , <i>Vaccinium myrtillus</i>
Rich Heath	Tältlägret	<i>Empetrum nigrum</i> sp. <i>hermaphroditum</i> , <i>Betula nana</i> , <i>Vaccinium vitis-idaea</i>
Poor Heath	Njulla/Tältlägret	<i>Empetrum nigrum</i> sp. <i>hermaphroditum</i> , <i>Vaccinium uliginosum</i> , <i>V. vitis-idaea</i>
Lichen Heath	Tältlägret	<i>Vaccinium uliginosum</i> , <i>Diapensia lapponica</i> , <i>Empetrum nigrum</i> sp. <i>hermaphroditum</i>

cleared existing surface vegetation, and major roots from the top 0.1 m of soil to prevent re-shooting. Extra soil from the immediate area was cleared similarly and added if required to ensure that plots were level with the surroundings.

Once sown, seeds were left to stratify naturally in the field over winter, and both sites were revisited on five occasions during the following summer and seedling emergence was recorded.

#### Plant community mapping and adult occurrence records

During the summer of 2006, community type was recorded systematically by visual inspection in the field at a resolution of 50 m over a predetermined area of 2.1 km<sup>2</sup> on the east face of Njulla, ranging from 350–1050 m a.s.l. The community types used matched those used for the seed-sowing experiment described in Table 1. Adult occurrence of the three *Vaccinium* species was recorded within the same area using a 0.5 m × 0.5 m quadrat at plots spaced by 100 m.

#### Data analyses

Seedling emergence is defined here as the number of individual seedlings counted during the five observation dates. It was not possible to mark seedlings individually, so in order to prevent double counting, and only the positive change in seedling number from the previous recording date were counted. This means that emergence may be underestimated due to mortality. Emergence from the three community types common to both Njulla and at Tältlägret was plotted (Figure 1) and judged subjectively to be sufficiently comparable to allow the inclusion of the Forest Heath and Forest Meadow communities in the analysis.

Community effect upon emergence and adult occurrence were investigated for each species separately. Emergence response to community was investigated by using generalised

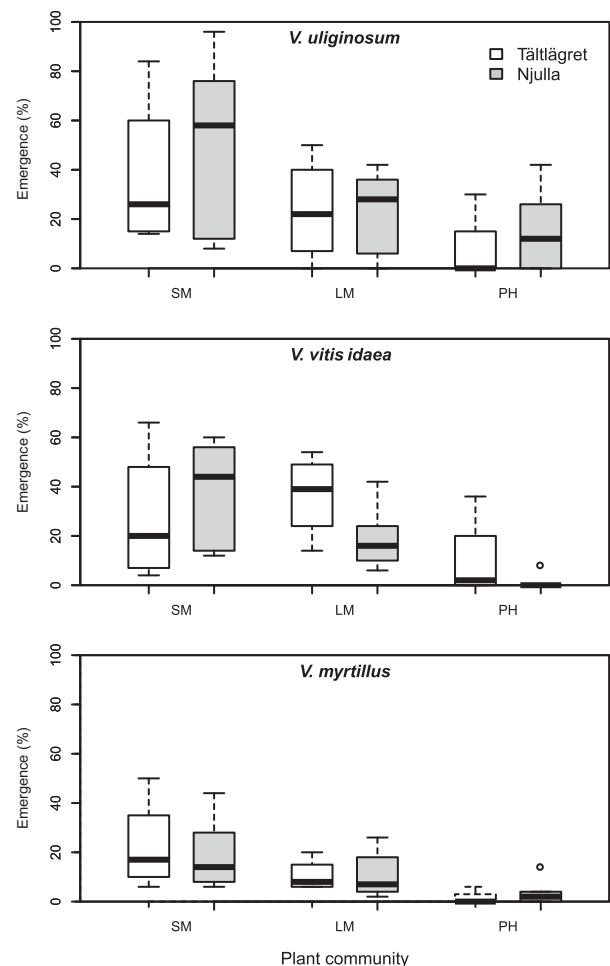


Figure 1. Comparison of seedling emergence in matching community types on Njulla and at Tältlägret. Boxes represent the upper and lower quartiles, the thick line represents the median, and the whiskers show the range of the dataset without outliers. Outliers (where an observation falls outside the upper or lower quartiles  $\pm 1.5 \times$  the interquartile range) are represented by open circles.

linear models (GLMs) with negative binomial distribution for all three species. Negative binomial distributions were preferred to binomial distributions because of a strong overdispersion and a large proportion of zeros in the data. We used the percentage of seeds that had emerged per plot, because of the difference in the amount of seeds sown at Njulla and Tältlägret. Community effect upon adult occurrence was investigated using GLMs with binomial error for *V. myrtillus* and *V. uliginosum*. GLMs with negative binomial error were used for *V. vitis-idaea* because of overdispersion.

For both seedling emergence and adult occurrence, the importance of habitat type was assessed by using analysis of deviance tests (chi-square statistic). The  $D^2$  values, expressed here as Residual deviance/Total deviance, were extracted to assess effect sizes. Post-hoc comparison between the effects of the seven habitat types was investigated using Behrens–Fisher non-parametric multiple comparison tests (Munzel and Hothorn 2001).

Germination and adult occurrence within each habitat was represented by mean seedling emergence and mean observed adult occurrence per community, and was mapped over the sampling area using ArcGIS 9.2. Statistical tests were carried out with R 2.8.1 (R Development Core Team 2006), GLMs were built using the MASS package, version 7.2–45 (Venables and Ripley 2002), and the npmc (Non-parametric Multiple Comparisons) package version 1.0–7 (Helms and Munzel 2008) was used for the Behrens–Fisher tests.

## Results

### Recruitment

The highest seedling emergence from the seed-sowing experiment was recorded for *Vaccinium uliginosum* (17%), lower in *V. vitis-idaea* (15%) and the lowest in *V. myrtillus* (8%). Community had a significant effect on the emergence of *V. myrtillus* ( $P < 0.001$ ,  $D^2 = 0.61$ ) and that of *V. vitis-idaea* ( $P = 0.046$ ,  $D^2 = 0.28$ ). For both species, most seedlings emerged in the meadow communities, and least in the heath communities. The Behrens–Fisher tests showed significantly lower emergence in the three non-forested heathland communities outside the forest compared with the three meadow communities for *V. myrtillus* (Figure 2(a)) and separated the meadow communities above the treeline from Lichen Heath, and the Forest Heath from the Low Meadow for *V. vitis-idaea* (Figure 2(b)). For *V. uliginosum* the patterns in germination among communities were generally similar to those for *V. myrtillus* and *V. vitis-idaea*; however, the emergence of seedlings in *V. uliginosum* in heath communities was higher and the differences among communities not significant ( $P = 0.2$ ) (Figure 2(c)).

### Adult occurrence

Adult occurrence of all three *Vaccinium* species varied significantly with community (*V. myrtillus*:  $P < 0.001$ ,  $D^2 = 0.40$ ; *V. uliginosum*:  $P < 0.001$ ,  $D^2 = 0.13$ ; *V. vitis-idaea*:  $P < 0.001$ ,  $D^2 = 0.15$ ).

*V. myrtillus* (Figure 2(d)) was significantly more frequent in the forest communities, than in communities above the treeline. *Salix* Meadow was also significantly preferred to both Low Meadow and Rich Heath areas, where no individuals were recorded.

*V. vitis-idaea* (Figure 2(e)) was mainly found growing in the Forest Heath community and was less frequent in the Low Meadow and *Salix* Meadow communities. Adult occurrence differed significantly between Forest Heath and all meadow communities, forest meadow and the other meadow communities, Low Meadow and Poor and Rich Heath communities, and *Salix* Meadow and Poor Heath communities.

*V. uliginosum* (Figure 2(f)) was most frequently recorded in Rich Heath community and was less frequent in the meadow plots. Adult occurrence of this species differed significantly between the Low Meadow plot and all heath-like communities, and between Rich Heath to Forest Meadow and *Salix* Meadow communities.

### Ontogenetic niche shifts

Comparing Figures 2(a) and 2(d) and Figures 2(b) and 2(e) shows that the seedling emergence and adult occurrence for both *V. myrtillus* and *V. vitis-idaea* differed with regard to community. For these two species, the highest emergence counts were recorded in the *Salix* Meadow community, whereas adults were found in less than a quarter of the survey plots in this community type. Likewise, adults were rarely found in the herbaceous community plots, which however had the second and third highest seedling emergence. *V. uliginosum* demonstrated no significant community preference for seedling emergence, and therefore had a wider regeneration niche than the other two species, despite a more frequent adult occurrence in the heath communities, as described above.

### Mapping

The habitat map for the study area on Mount Njulla is shown in Figure 3(a). Forest habitats are found at lower altitudes, interspersed with some Rich Heath patches around wetter areas. The *Salix* Meadow belt lies just above the forest from around 600–650 m a.s.l., and is replaced between 700 and 800 m a.s.l. by a Rich Heath belt, dominated by *Empetrum nigrum* L. spp. *hermaphroditum* and *Betula nana* L. At the next level the Low Meadow zone can be found, a moister area containing a mix of graminoids, sedges and low herbs, probably relating to moderate snowbeds. Finally, the vegetation changes at around 800 m a.s.l. to Poor Heath and Lichen Heath on approaching the summit.

Mapping the results of the seed-sowing experiment and adult occurrence observations (Figures 3(b)–3(g)) allows us to observe the described ontogenetic niche shifts more clearly. *Vaccinium uliginosum* and *V. vitis-idaea* adults (Figure 3(b)) were most regularly found in heathland communities, generally occurring at higher altitudes. The two species were also frequently observed in the Forest Heath

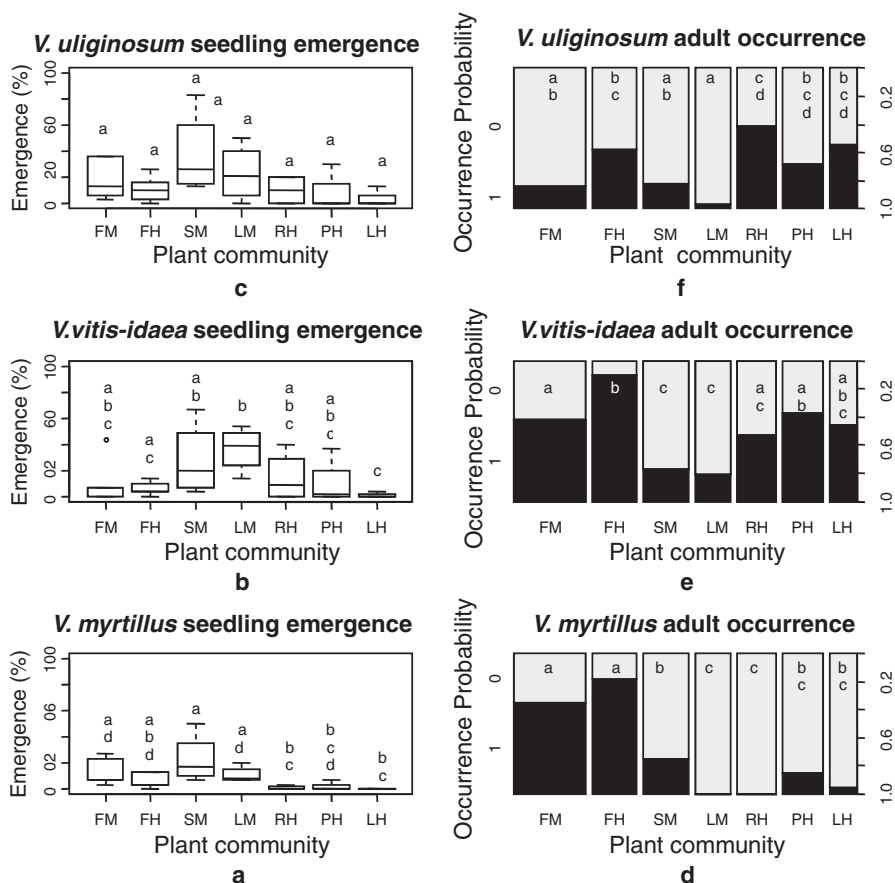


Figure 2. Germination and adult occurrence of *Vaccinium myrtillus*, *V. uliginosum*, and *V. vitis-idaea* in different communities types in the Abisko valley, northern Sweden. Species are listed top to bottom by decreasing altitudinal preference, and communities are listed left to right by altitudinal range. Letters (a–d) in common indicate no significant difference.

community situated in lower part of the area; the Low-growing Meadow and *Salix* Meadow communities, where the two species were rarely observed, formed a belt at mid-altitude. These two species obtained their higher seedling emergence scores in these communities, though not significant for *V. uliginosum* (Figure 3(c)). *Vaccinium myrtillus* (Figure 3(f)) was most frequently observed in communities situated below 700 m a.s.l., whereas the predicted seedling emergence (Figure 3(g)) was higher in the communities occurring above the treeline, between about 650 and 950 m a.s.l.

## Discussion

In this study, the three species of *Vaccinium* dwarf shrubs were found to differ in community affiliations with respect to seedling emergence and adult occurrence. Adult occurrence in all three species varied significantly with community type, conforming to biogeographical expectations of the species, as well as to historical descriptions of the local area (Du Rietz 1950; Ritchie 1955, 1956; Jacquemart 1996). In addition, *V. myrtillus* and *V. vitis-idaea* exhibited significant community differences with regard to seedling emergence. Our results support those of Eriksson and Fröberg (1996) and Eriksson (2002), who also found

recruitment in these species to differ between sites on a habitat gradient, though the latter paper also found this pattern to occur with *V. uliginosum*, a result not supported in the present study.

In our study, seedling emergence of *V. myrtillus* and *V. vitis-idaea* was apparently favoured in moist habitats, which has also been demonstrated for these species in boreal regions (Eriksson 2002), and is a common trend for seedling emergence of Arctic and alpine species in general (Bell and Bliss 1980; Oberbauer and Miller 1982; Welling and Laine 2002; Forbis 2003). Visual inspection of Figure 2 also suggests that seedling emergence in *V. uliginosum* follows this trend, although this was not statistically significant. In addition to the comparatively better moisture and nutrient status of the meadow communities over the heath communities, the relatively high seedling emergence of all three species in the *Salix* Meadow plots could be due to facilitation by the canopy provided by the *Salix* spp. present. Empirical support for this effect is ambiguous, however, as although the canopy can provide physical protection and mediate water availability for colonisation of alpine species (Dona and Galen 2006, 2007), shading and litter accumulation can hinder recruitment (Totland and Esaete 2002). All three study species have, however, some ability to germinate in darkness (Baskin et al. 2000).

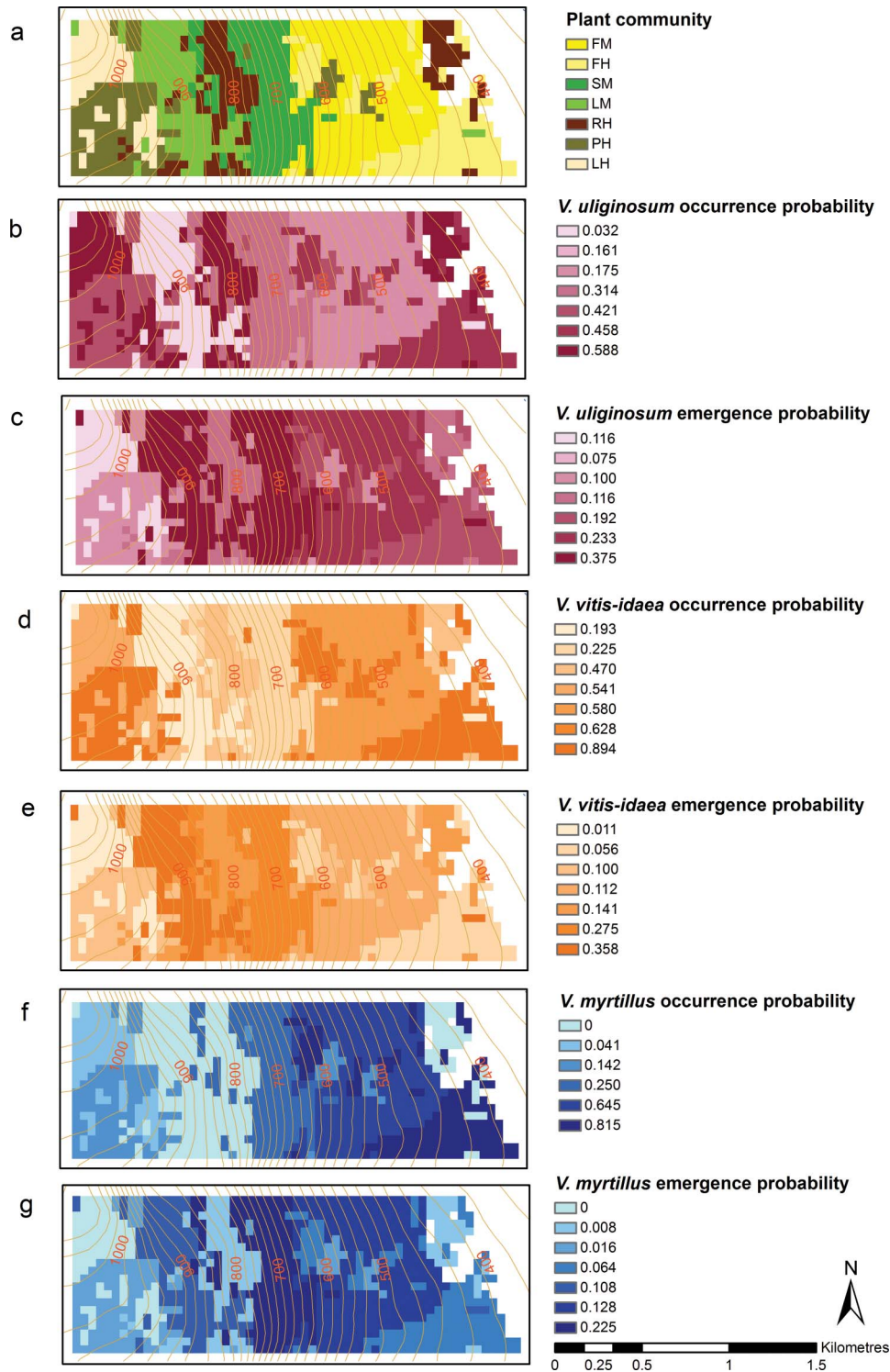


Figure 3. Maps showing community distribution (a) and probability of adult occurrence and seedling emergence of *V. myrtillus*, *V. uliginosum* and *V. vitis-idaea* (b)–(g) on mount Njulla.

General factors which can affect a species' adult occurrence but not seedling emergence in alpine regions can include herbivory (Olofsson et al. 2009) and seedling mortality, although this can be considered to be no more a limiting factor in recruitment in the alpine than in temperate regions (Forbis 2003). Our results, where *V. myrtillus*

and *V. vitis-idaea* seedlings emerged relatively well in communities where adults were absent, and adults were observed where seed addition resulted in little or no seedling emergence, support for the alpine tundra the finding of ontogenetic niche of *Vaccinium* dwarf shrubs from boreal ecosystems (Eriksson and Fröberg 1996; Eriksson 2002).

*Vaccinium uliginosum* was shown to have a wide regeneration niche, but was nevertheless significantly associated with the heath community types at the adult stage, which can also be viewed as an ontogenetic niche shift. Parrish and Bazzaz (1985) found variable niche widening and narrowing between seedling and adult stages in some annual old-field species on a number of environmental gradients, and our results indicate a reduction of the niche breadth in *V. uliginosum* between the seedling and adult stages at the community level. It is possible that *V. uliginosum* uses its ability to germinate relatively well in a range of community types as a strategy to ensure recruitment in sites such as the higher alpine and the wetter areas in the boreal region, where it faces less competition from other species at subsequent life stages.

*Vaccinium myrtillus* was the only species with clear adult preference for low altitude communities. This distribution confirms that it is a predominantly boreal forest species, whose invasion of higher altitudes has been predicted with climatic change (Heegaard 2002; Fosaa et al. 2004). Figure 3 shows that germination of *V. myrtillus* is most likely to take place at a higher altitude than its adult distribution. This suggests that existing alpine communities would not constitute a barrier for the initiation of altitudinal migration of *V. myrtillus* with future climatic change.

As *V. vitis-idaea* adults were found in communities both above and below the moister middle belt where germination was highest, our results do not suggest a migrational advantage to this species due to the ontogenetic niche shift shown within our study. Eriksson (2002) suggested that the preference for *V. vitis-idaea* to germinate in moister conditions might be a strategy whereby propagules rely on a temporary relaxation of drought conditions in the heath areas where adult plants dominate in order to recruit successfully, and therefore a higher germination in meadow communities could be expected, but survival and growth from recruitment to adulthood would be less likely to occur.

Other work examining the recruitment of *Vaccinium* dwarf shrubs with regard to climatic warming has produced contrasting results. Laboratory experiments have shown higher and more rapid germination with increased temperatures (Milbau et al. 2009), whereas field warming experiments simulating both short heatwaves (Graae et al. 2009) and season-long warming (Shevtsova et al. 2009) have resulted in significant reductions in recruitment. These, plus our data, which show how species of the genus in the same environment differ with regard to regenerative and established niches, illustrate some of the many difficulties facing modellers wishing to include quantitative measures of dispersal in bioclimatic envelope models, which usually predict vegetation changes at the community level.

Despite our study finding seedling emergence generally below 50% in all three species, *Vaccinium* dwarf shrubs are potentially good colonisers. Each fruit contains, on average, around 25 seeds for *V. myrtillus* and *V. uliginosum*, and 11 for *V. vitis-idaea* (Eriksson and Ehrlén 1991), and these are widely dispersed after ingestion and

defecation by a number of mammal and bird species (Traveset and Willson 1997; Graae et al. 2004; Bruun et al. 2008). Seeds should therefore be well dispersed throughout the landscape, allowing potential recruitment in different communities. The effective dispersal of *Vaccinium* dwarf shrubs, combined with their stress tolerance, could allow these species to colonise new areas before the arrival of competitive species. When more competitive species invade, stress-tolerant populations of *Vaccinium* species may escape by means of vegetative regeneration, eventually to more permanently stress-prone habitats. If this mechanism works in practice, it would imply an obvious selective benefit of the uncoupling of regenerative and established niches.

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### Notes on contributors

Alistair Auffret is a PhD student in physical geography, whose main research interests concern the dispersal of plant species through the Swedish rural landscape with a focus on land-use history and management.

Eric Meineri is a PhD student as part of the international SEED-CLIM project, focussing on the effects of climate change in the role of seed regeneration for plant populations.

Hans Henrik Bruun is an associate professor in macroecology, with research interests including population and evolutionary ecology, conservation and restoration. He has worked in temperate, alpine and arctic regions, at both the community and landscape scale.

Rasmus Ejrnæs is a senior researcher, and an official delegate in The European Platform for Biodiversity Research Strategy. His main research interests lie within the biodiversity of Scandinavian grasslands and wetlands.

Bente Graae is an associate professor in biology, researching the recruitment and colonisation potential of plant species at high latitudes in the face of climatic change. She is also a co-ordinator of FLEUR, a European network of researchers interested in the dynamics of forest plant species in a changing environment.

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