

# Gap dynamics in perennial subalpine grasslands: trends and processes change during secondary succession

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## Abstract

**1** This study examines how gap revegetation processes – the creation and filling of free space in a closed vegetation sward - affect the floristic composition of subalpine grasslands during secondary succession. Four hypotheses addressing overall effects, changes during secondary succession, and gap-size and edge effects are tested.

**2** In a field experiment, 216 gaps and controls of two different sizes (625 cm<sup>2</sup> and 39 cm<sup>2</sup>) were established at six sites representing a replicated successional series (0, 10, and 40 years after abandonment). The floristic composition was monitored twice yearly over four growing seasons. In the first growing season, the relative importance of seed and vegetative gap colonisation was quantified.

**3** The four hypotheses were tested using Principal Response Curves (PRC), a recent derivative of partial redundancy analysis specifically designed for the analysis of time-dependent compositional response data from BACI (Before – After, Control – Impact) design experiments. PRC has several advantages over previous methods. It provides quantification and Monte Carlo testing of compositional responses through time, efficient graphical displays, and it allows the behaviours of individual species to be related to the overall pattern.

**4** All four hypotheses were corroborated by the experimental results. Micro-successions in gaps account for a high fraction of the compositional variance, 21.6%, and 8.8 – 12.2% at the 625 cm<sup>2</sup> and 39 cm<sup>2</sup> scales, respectively. Size effects add 3.3 – 5.5% to the explained variance per successional stage, indicating that small and large gaps are colonised by partially distinct assemblages of species. Edge effects appear in the mid-successional stage only, indicating that clonal ingrowths and vegetative encroachment is stronger here. The compositional effects are relatively weak, however, adding only 1.6% to the explained variance. Gap revegetation is slow; both small and large gaps are still significantly different from undisturbed control plots more than three years after gaps were created.

**5** Most of the species, 74%, are affected by gaps in at least one of the successional stages. Species responses are not consistent across successional stages; species that are gap-dependent in the 0-year successional stage tend to disappear, while other species become gap-dependent with successional time. Species that colonise gaps as seedlings, not as clonal ingrowths, become more dependent on gaps during secondary succession (Seed recruitment fraction and gap response: Pearson's  $r_p = -0.30, -0.44, \text{ and } -0.68$  per stage). Across sites, locally rare species tend to increase in relative abundance in gaps, while common species decrease (Pearson's  $r_p = 0.66, 0.72, \text{ and } 0.82$  per successional stage,  $p < 0.001$ ).

**6** It is concluded that gap revegetation processes have substantial effects on the floristic composition of these perennial grasslands. Between-species differences in gap colonisation ability are important sources of small-scale variability. During secondary succession, changes in disturbance regime affect the gap revegetation processes, as well as the probability for local population persistence for gap-dependent species.

*Keywords:* Competition, disturbance, edge effect, gap revegetation, ordination, Principal Response Curves, size effect, secondary succession.

## Introduction

It is central to ecological theory that disturbance should affect the populations and communities subjected to it. The effects are obvious in the case of large-scale disturbances such as wildfires, floods, storms, landslides, or bulldozers, which may transform entire landscapes from one day to the next. However, less conspicuous, fine-scale

disturbances within intact vegetation may have important consequences for the survival, growth, and fecundity of individual plants (Fowler 1988, Carlton & Bazzaz 1998), for population dynamics (DeSimone & Zelder 1999, King & Grace 2001, Rydgren *et al.* 2001), and for the outcome of biological interactions (Huston 1979, Pickett & White 1985, Pacala & Levin 1997, Suding & Goldberg 2001). In communities with a continuous

vegetation cover and a large proportion of perennial species, an important effect of fine-scale disturbance is to create temporary competitor-free microsites – gaps – in the closed sward. Coexisting species often differ in their capacity to colonise bare ground (Goldberg 1987, Hillier 1990, Williams 1992, Bullock *et al.* 1995, Burke and Grime 1996, Kotanen 1997a, Pakeman *et al.* 1998, Vandvik & Elven 2002), and gap revegetation processes – the creation, colonisation and filling of free space – may therefore be an important source of fine-scale temporal and spatial variability. Recruits may originate from newly dispersed seeds, a persistent seed bank, or vegetative shoots, and colonisation capacity can to some extent be predicted from vegetative traits such as persistence, growth, and clonality, and from regeneration traits such as seed production, dispersal, seed bank longevity, and germination behaviours (Lavorel *et al.* 1994, 1999, Thompson *et al.* 1996). Gaps differ in size, shape, micro-topography, and time of occurrence, and this affects the light, moisture, and temperature environment (Thompson *et al.* 1977, Goldberg & Werner 1983, Morgan 1997, Kotanen 1997a) as well as competitive effects within the gaps (Miles 1974, Bullock 2000). Consequently, revegetation dynamics may differ considerably between large and small gaps (Goldberg & Werner 1983, Williams 1992, Ryser 1993, Morgan 1997, Britton *et al.* 2000), between gaps of different shapes (Kotanen 1997b), from the gap edge to centre (Bullock *et al.* 1995), with micro-topography (Carlton & Bazzaz 1998, Vivian-Smith 1997, Suding & Goldberg 2001), and between gaps created in different seasons (Fowler 1988, Hillier 1990).

The continuous creation, colonisation, and filling of bare-ground gaps within a closed sward may be seen as series of micro-successions that are part of the ‘everyday dynamics’ of many plant communities. Such communities can be seen as patchworks of microsites in different stages of revegetation, whose spatial structure and age distribution are determined by the frequencies with which gaps are opened up in the landscape. The overall disturbance regime will thus affect the probability for long-term survival, especially of relatively short-lived species, providing a link between the effects of localised small-scale disturbances and ecosystem properties such as long-term stability or successional change. For example, it is well established that changes in extensive, low-intensity disturbance regimes such as those of traditionally managed semi-natural grasslands, may initiate rapid successional change and a considerable loss of diversity (Bernes 1993, Stanners & Bordeau 1995, Fremstad & Moen 2001). It has been shown that these effects are generally more dramatic in systems with high diversity and long ecological histories (Hobbs &

Hunneke 1992, Milchunas 1993). While the overall successional pathways in these secondary successions – *grassland to forest or shrub* – and the ultimate cause – *decreased frequency of fine-scale disturbances resulting from the cessation of land-use* – are well established, the consequences for small-scale dynamics and ongoing ecological processes within the landscapes are less clear. One could, for example, expect that the species loss and change in functional types along a large-scale secondary successional sequence (Prach *et al.* 1997) should have consequences for the mode, rate, and direction of micro-successions occurring in gaps within these landscapes. Further, the major constraints for population persistence could be expected to switch from regeneration to established life stages with the decrease in gap frequency during succession. In other words, it is unclear whether the behaviours of species, life stages, and functional types are constant, or if they change with the successional context. These are important questions for understanding how changing disturbance regimes and successional change affect vegetation processes, population persistence, and diversity. It has been shown that the trends and processes of gap colonisation and filling vary across landscapes, such as between vegetation types (Williams 1992, DeSimone & Zelder 1999, Britton *et al.* 2000), along climatic gradients (Umbanhowar 1995), and with the range of life histories available in the local species pool (Reader & Buck 1990, Kotanen 1995, 1997). There are, however, no studies that I am aware of that investigate the trends and processes of gap revegetation in different successional stages.

This study aims to assess the effect of micro-successions occurring after fine-scale disturbances on the floristic composition of subalpine perennial grasslands, and further to assess whether micro-successional trajectories and the underlying processes change along a secondary successional (time) gradient. Below, this overall aim is broken down into a hierarchy of hypotheses that are tested in a gap revegetation experiment.

*Hypothesis 1: The composition of the vegetation that develops in bare-ground gaps is different from the surrounding grassland.* When a gap is created, plant shoots are killed. While detrimental for the individual plant, this will only affect the local community composition if the recruitment of species into gaps is not proportional to their relative abundance in the vegetation. Such differential colonisation of gaps is expected if species differ in life-history traits such as vegetative persistence, clonal growth, seed production, germination responses, or seedling survival. Previous studies report that perennial grassland gaps are largely colonised by ramets of clonal origin (Fowler 1981,

Rusch & van der Maarel 1992, Milberg 1993, Arnthórsdóttir 1994). The relative quantity of clonal and seed recruits is not necessarily proportional to their overall importance for population persistence and community dynamics, however.

*Hypothesis 2: In grasslands undergoing secondary succession, the overall compositional effect of gaps increases over time, and the identity of gap regenerators changes.* The density and frequency of bare-ground gaps will decrease during secondary succession in grasslands, partly because of the decreased disturbance from the ungulate grazers, but also because relatively short-lived early-successional species are replaced by more long-lived species (Prach *et al.* 1997). This should affect the probability for long-term local population persistence of gap-regenerating species. At the same time, the probability for successful seed regeneration outside gaps decreases as the vegetation becomes taller and denser during succession. Short-lived species will have a higher probability of local extinction, and the creation of gaps in the closed sward should become more important for the persistence of these species with successional age.

*Hypothesis 3: Gaps of different sizes are filled with different assemblages of species.* With increasing gap size the light, moisture, wind, and competition environment within the gaps becomes progressively more different from the closed vegetation environment. Rather than being an on-off effect, gaps may therefore be seen as a gradient from closed vegetation through small to larger gaps. Compositional differences between large and small gaps are predicted to result from between-species differences in clonal growth, seed production, dispersal, or germination behaviour. During secondary succession, the predicted decrease in the diversity of gap-regenerating species will result in a reduced potential for gap-size differentiation.

*Hypothesis 4: Within relatively large gaps edge effects operate, so that the centre and periphery will be colonised by different species.* Analogous to the gap size effect, considerable environmental and competitive variation may occur within large gaps. This variation can be summarised as an edge-to-centre gradient. Species may colonise different parts of this gradient, but the potential for differentiation will be reduced as the diversity of gap-regenerating species decreases during secondary succession.

## Methods

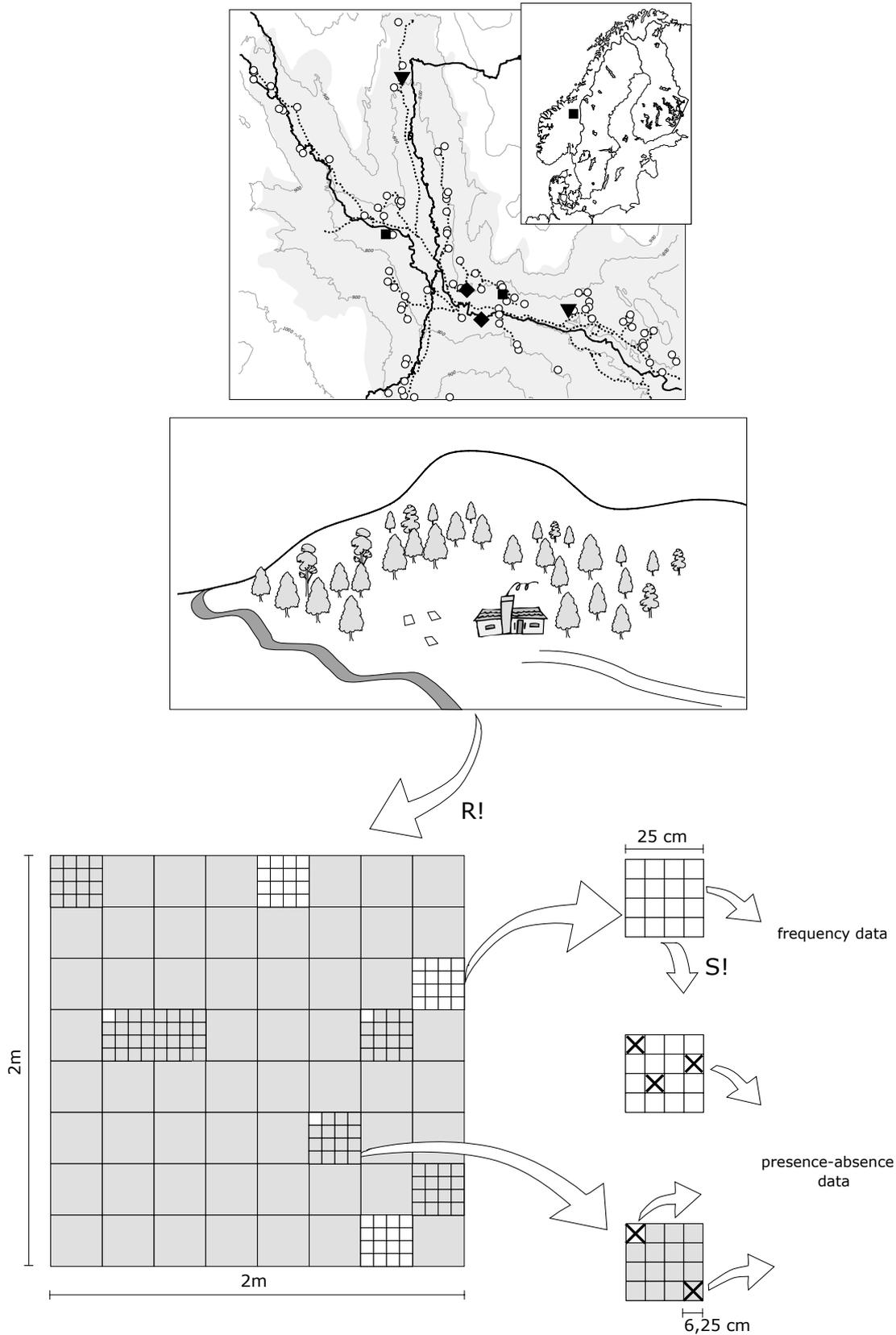
### STUDY AREA

In the Norwegian mountains, the total biomass harvested by grazing and mowing decreased by 61% from 1939 to 1996 (Edelmann 1997). This trend is not uniform, however, as the intensity of land-use varies at all spatial scales, from regions and landscapes to vegetation patches. A range of different factors, including ecological factors such as climate and bedrock, political factors such as government subsidy policy and regional development programmes, as well as the interests and private economy of different landowners, influences this variation. As a result, the Norwegian sub- and low-alpine landscapes of today are comprised of patches of formerly grazed or mown vegetation that are in intensive use, in traditional use, and in different stages of secondary succession after abandonment (Austrheim 1999, Austrheim & Eriksson 2002, Vandvik & Birks 2002a, 2002b). This study was carried out in the Vangrøftdalen valley, Os Municipality, eastern Norway (10°49'E, 62°37'N) (Fig. 1). The valley system covers an area of ca. 60 km<sup>2</sup> at altitudes between 700 – 800 metres above sea level (m.a.s.l.), and is surrounded by mountains reaching 1100 – 1200 m.a.s.l. The landscape is characterised by semi-natural subalpine birch forest and extensive mire systems, with summer farms scattered throughout. The 87 historical summer farms in the area are in different secondary successional stages from farms in current use, with free-ranging grazing animals, to farms abandoned more than 100 years ago (V. Vandvik, unpublished data).

### EXPERIMENTAL DESIGN AND SAMPLING

The study sites comprise a set of semi-natural grasslands within summer farms that represent a twice replicated chronosequence of farms in current use, farms abandoned ca. 10 years ago, and farms abandoned ca. 40 years ago (i.e. six farms). The farms are situated 1 – 6 km apart, at altitudes of 730 – 800 m.a.s.l. Within each site, regeneration in experimentally created gaps of two different sizes was investigated in a four-year experiment with a BACI (Before-After Control-Impact) design (Fig. 1).

The study was initiated in 1997, when three *blocks* (2 m x 2 m = 4m<sup>2</sup>) were laid out at each site. Six *large plots* (25 cm x 25 cm = 625 cm<sup>2</sup>) and three pairs of *small plots* (6.25 cm x 6.25 cm = 39 cm<sup>2</sup>) were laid out in random positions within each block (Fig. 1). These plots, 216 in total, were marked with 10 cm metal tubes. A 25 x 25 cm metal frame, divided into 16 subplots, was fastened onto the tubes for the vegetation analyses. Frequency-in-subplot data were collected from



**Figure 1.** Geographical location of the study area, location of the six subalpine grassland sites, an example of how the experimental design was carried out within one of the 4 m<sup>2</sup> blocks, and sampling design within large (625 cm<sup>2</sup>) and small (39 cm<sup>2</sup>) gaps and controls (see also methods). R! = Randomised experimental design, S! = Systematic sampling. The 108 large gap/control plots, 108 small gap/control plots, and 162 central/side/corner plots within large gaps were sampled before treatment, and twice yearly for three years after gaps were created. On the map, 0-year experimental sites are shown as triangles, 10-year sites as circles, and the 40-year sites as squares. The area below the tree line is shaded light grey, and main roads and waterways are indicated. Contour intervals are 100 metres. In the 4 m<sup>2</sup> block, undisturbed vegetation is shaded grey and experimentally created gaps are white. X = data extracted for dataset II.

large plots, and presence-absence data from small plots. After the baseline analysis, the vegetation (above- and below-ground) was removed from 3 randomly chosen large plots and 3 small plots within each block; with the remaining 3+3 plots serving as controls. The plots were reanalysed at the beginning and end of the growth season (in the last week of June and August, respectively) in 1998, 1999, and 2000. In 1998, the number and origin (seed or vegetative) for all recruits appearing in gaps were noted. Although the bulbils of *Bistorta vivipara* are actually vegetative regenerative organs (Lid & Lid 1994), they function as seeds for the purposes of this study, and are denoted as such hereafter.

#### DATA SETS AND CODING OF TREATMENTS AND TIME

The data were compiled into two datasets (Fig. 1). *Dataset I* consists of frequency-in-subplot data from the 54 large gaps and 54 large controls at the seven recording dates ( $n = 756$ , plot area =  $625\text{cm}^2$ ). *Dataset II* consists of presence-absence data from the 54 small gaps and 54 small controls, and from three systematically sampled subplots within the 54 large gaps: 'corner', 'side', and 'centre' ( $n = 1890$ , plot area =  $39\text{cm}^2$ ). Explanatory variables that represent the three successional stages (0-year, 10-year, and 40-year), farms (F1 – F6), blocks (P1 – P18) treatments and controls (G and C), and time (T1 – T7) were compiled. For dataset II three additional variables represent the 'corner', 'side', and 'central' positions. All variables, including time, were coded as series of dummy variables. Time was not entered as a quantitative variable as I was interested in capturing the overall treatment effect through time, but have no reason to expect simple linear or unimodal trajectories. Interactions between variables (gap x time, gap x size x time etc.) were constructed when necessary for the statistical analyses. During the four years of the study, 17 control censuses and 7 gaps (=1.7% of the total data) were lost, either because the plots were destroyed by rodents or grazers, or because the metal tubes were not refound at one of the censuses. In order to maintain a balanced structure of the data, which is necessary for the Monte Carlo permutation tests in CANOCO 4 (ter Braak & Šmilauer 1998), all species that appeared in the plot at the sampling dates before and after the lost sample were entered as present in the lost sample as well.

#### NUMERICAL ANALYSES – PRINCIPAL RESPONSE CURVES (PRC)

Over the last few decades, the methodology for analysis and testing of temporal trends in species assemblages using numerical ordination has been

developed and refined (e.g. Austin 1977, Cramer & Hytteborn 1987, ter Braak & Wiertz 1994, Kotorova & Leps 1999). Many of the later applications utilise some form of constrained ordinations on sets of (dummy) variables (see ter Braak & Šmilauer 1998). Although such approaches allow precise quantification of effects and testing of hypotheses, they have weaknesses when it comes to visualisation and interpretation; diagrams are often cluttered, time is typically not displayed in a single direction, and the interpretation of the treatment effect becomes unclear. These difficulties are overcome in Principal Response Curves (PRC) (van den Brink & ter Braak 1997), a recent derivative of partial redundancy analysis (RDA) (Jongman, ter Braak & van Tongeren 1995). PRC zooms directly in on the compositional effect of treatments relative to controls at each sampling date. This is done by performing a partial RDA allowing for time-specific treatment effects, and then plotting the response of the community to the treatment against time. The time-specific treatment effect ( $C_{dt}$ ) quantifies the compositional effect of the treatment on the community at each sampling date, and temporal trends can be visualised plotting  $C_{dt}$  against time. The species weights ( $b_k$ ) can be interpreted as the affinity of the species with this diagram, where species with high positive values follow the overall community response to treatments and species with high negative values react in the opposite way. To evaluate the overall significance of the PRC diagram, whole time series can be permuted and the significance of the first constrained ordination axis tested. To evaluate how the effect changes through time, permutation tests can be performed for each point in time. See van den Brink & ter Braak (1999) for a detailed theoretical explanation, and ter Braak & Šmilauer (1998) for a description of computation and testing within the program CANOCO 4.

In its original form PRC quantifies and tests the effect through time of one or more treatments relative to a control. In this study I expand the approach by performing a series of PRC's focusing on different types of contrasts. *Hypothesis 1*, the overall gap effect, is tested by a PRC comparing gaps to controls. *Hypothesis 2* is tested by partialling out the overall gap effect, and then coding the gaps in the three successional stages as different 'treatments'. Additionally, three separate analyses were performed to compare overall effects and species responses between the three successional stages. *Hypothesis 3* concerns the differences between large ( $625\text{cm}^2$ ) and small ( $39\text{cm}^2$ ) gaps. Statistically valid comparisons can only be made using sample plots of similar size, however, so this effect is tested by contrasting small gaps with the central plot in large gaps (Figure 1). Size effects are tested for each stage

Testing the effect of	Data Set	Data Stages	Contrast		n	PRC Axis 1			Significance of the difference at each census (p(999))							
			A	B		Variance	F-value	p(999)	A-97	S-98	A-98	S-99	A-99	S-00	A-00	
Gap vs. control	I	All	Gap	Control	756	12.16	99.2	<0.001	0.472	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Successional stages	I	All	Gap*Stage	Control*	756	5.81	7.8	<0.001	**							
	I	0, 10 Years	Gap*Stage	Control*	504	3.48	22.4	<0.001	0.468	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	I	10, 40 Years	Gap*Stage	Control*	504	9.37	66.7	<0.001	0.323	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	I	0, 40 Years	Gap*Stage	Control*	504	6.79	27.8	<0.001	0.774	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Large vs. small gaps	II	All	Small gap	Center	756	2.55	18.6	<0.001	0.337	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	II	0 Years	Small gap	Center	252	5.18	12.6	<0.001	0.307	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	II	10 Years	Small gap	Center	252	6.04	15.0	<0.001	0.023	<0.001	<0.001	<0.001	0.002	<0.001	<0.001	<0.001
	II	40 Years	Small gap	Center	252	6.40	15.8	0.054	0.877	0.008	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Centre vs. edge within large gaps	II	All	Corner	Center	756	0.53	3.6	0.068	0.923	0.745	0.429	0.805	0.049	0.116	0.115	
	II	0 Years	Corner	Center	252	0.89	2.1	0.694	0.945	0.843	0.052	0.987	0.386	0.658	0.569	
	II	10 Years	Corner	Center	252	1.79	4.1	0.030	0.615	0.250	0.511	0.807	0.051	0.034	0.196	
	II	10 Years	Corner	Side	252	1.14	2.5	0.464	0.278	0.498	0.965	0.939	0.184	0.696	0.550	
	II	10 Years	Side	Center	252	1.03	2.3	0.531	0.987	0.053	0.363	0.961	0.396	0.072	0.859	
	II	40 Years	Corner	Center	252	1.86	4.5	0.174	0.775	0.287	0.735	0.377	0.269	0.009	0.143	

\* Overall gap effect partialled out

\*\* time-specific tests are not relevant

**Table 1.** Summary of the PRC analyses carried out to test for overall gaps effect, stage-specific gap effects, gap size effects, and edge effects in successional grasslands. Data entries are in % variance explained. Plot sizes, data sets, and ‘contrasts’ define the data used for each analysis. The ‘contrasts’ describe the model for the PRC’s, where B is coded as ‘reference’ and A is coded as ‘treatment’. N gives the total number of vegetation samples used in the analysis. The differences between A and B are judged (1) by tests of the overall significance of the first PRC axis, and (2) by tests of each individual sampling date. A = autumn S = spring.

individually. *Hypothesis 4*, edge effects, is tested by comparing different subplots within large gaps. ‘Central’ subplots (no vegetated edges) are first tested against ‘corner’ subplots (two vegetated edges). If these are significantly different then the ‘central’ and ‘corner’ subplots are both tested against a ‘side’ subplot with one vegetated edge (Fig. 1). Variation between blocks was partialled out in all PRC analyses and 999 permutations within blocks were performed for all tests. Hypotheses 1 and 2 are tested on Dataset I, the separate analyses on successional stages and tests of hypotheses 3 and 4 are performed on Dataset II.

The PRC’s focus on the floristic variability found within blocks and within sampling dates. In order to get an overview of the total compositional variability, a series of ordinations were performed on Dataset I. (Partial) canonical correspondence analyses (CCAs) were used, as preliminary analyses suggested that unimodal-based methods were most appropriate for analyses on the full variability in the data. All statistical analyses are performed using the software package CANOCO 4 (ter Braak & Šmilauer 1998) and the diagrams are drawn in Sigma Plot version 5 (SPSS 1999).

## Results

Over the four-year study, 86 taxa of higher plants appeared in the plots (Table 3). A large majority, 77 of the taxa, occurs both in gaps and controls, and only one species, *Veronica serpyllifolia*, is relatively common in gaps while never being encountered in controls. The overall treatment effects in these experiments can therefore largely be attributed to differences in relative abundance between gaps and controls, rather than strict microsite selectivity in specialist ‘gap’ and ‘closed

vegetation’ species. The partial CCA analyses show that 54.1% of the total variance in the data is found within experimental blocks. At this scale, the trajectories of gaps through time can account for 11.1% of the total variance, whereas the trajectories of controls remain near constant and can only account for 1.0%. The remaining 44.9% of the total floristic variation is found between the 18 experimental blocks. Here, 23% can be accounted for by successional stages, 6.7% is found between the ‘replicate’ farms within stages, while the remaining 15.2% is found between blocks within farms. In 1998, 1562 recruits were individually recorded in small gaps and the ‘central’, ‘side’, and ‘corner’ subplots within large gaps, corresponding to a mean density of 1851 m<sup>-2</sup>year<sup>-1</sup>. Overall, 77% of these recruits were of seedling origin, but the relative abundance of seedlings and vegetative recruits differed greatly between species ( $f_{seed}$  values, Table 3).

## TESTING THE FOUR HYPOTHESES ABOUT GAP REVEGETATION

The effects of gaps, successional stages, sizes, and edges were tested in a series of PRC’s focusing on differences between contrasts (gap vs. control, differences in gap revegetation trends for successional stages, large vs. small gaps, ‘centre’ vs. ‘side’ vs. ‘corner’ within large gaps) at the scales (625 cm<sup>2</sup>, 39 cm<sup>2</sup>) relevant for each of the four hypotheses (Table 1). For simplicity, separate diagrams are not constructed for each of the 15 individual contrasts evaluated (Table 1); instead a general diagram including all evaluated effects is constructed for Dataset I (Figure 2, Table 2) and for each successional stage separately for Dataset II (Figure 3, Table 2).

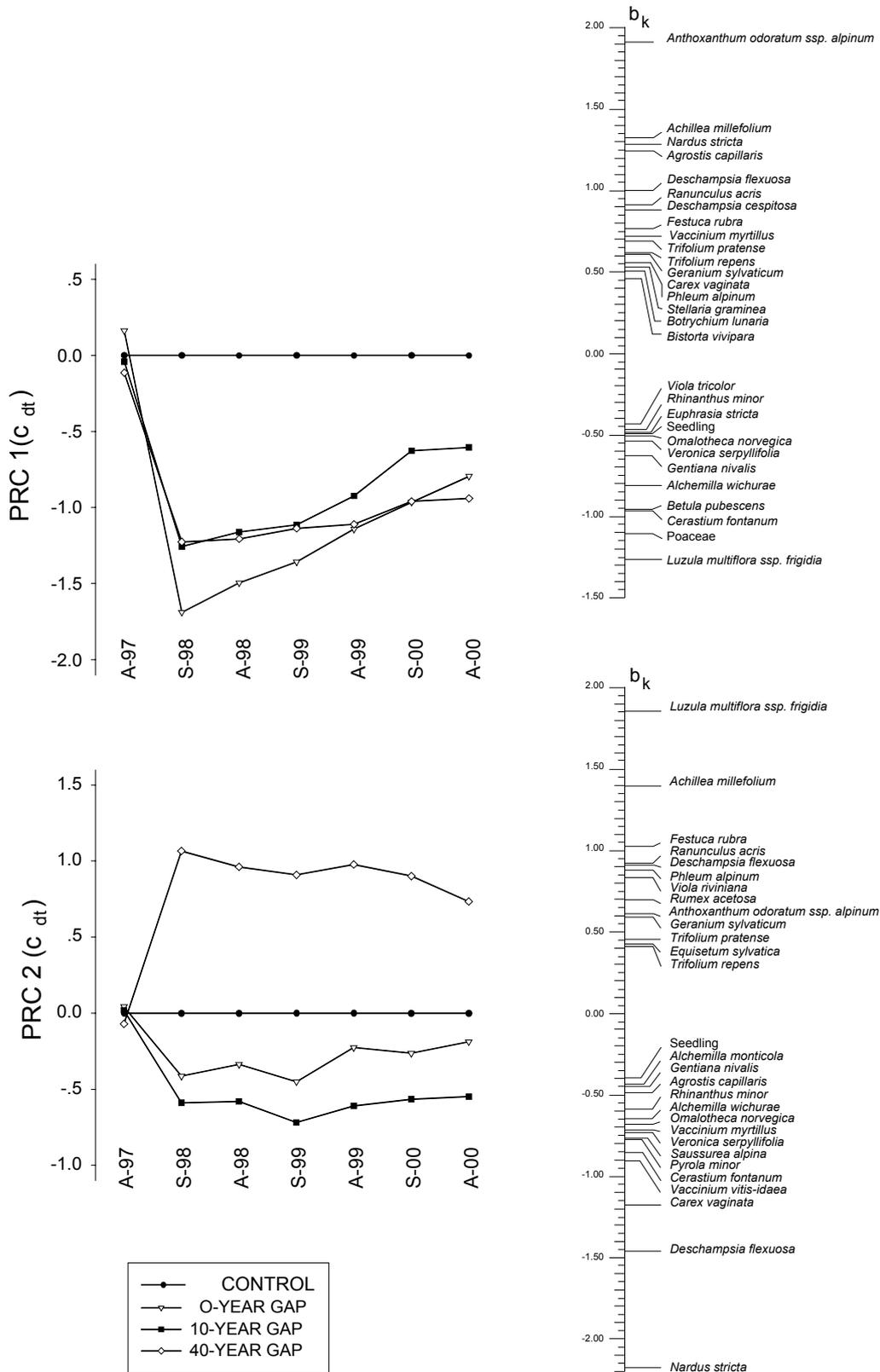
Data	Set of variables	Variance explained		Variance accounted for by			
		Unique	Total	PRC axis 1		PRC axis 2	
					p(999)		p(999)
Dataset I (25*25 cm <sup>2</sup> , n=756)	Time	6.3	6.3				
	Gap*Time	15.4	21.6	13.8	<.001	1.3	<0.001
	Gap*Successional Stage*Time	10.2	31.8	14.1	<.001	5.7	<0.001
Successional stage 1 Dataset II (6.25*6.25 cm <sup>2</sup> , n = 630)	Time	4.6	4.6				
	Gap*Time	4.2	8.8	3.0	<.001	0.7	<0.001
	Gap size*Time	4.4	13.2	4.0	<.001	2.3	<0.001
	Number of edges*Time	1.8	14.9	4.1	<.001	2.4	<0.001
Successional stage 2 Dataset II (6.25*6.25 cm <sup>2</sup> , n = 630)	Time	4.9	4.9				
	Gap*Time	4.5	9.4	3.6	<.001	0.3	0.010
	Gap size*Time	5.5	14.9	4.7	<.001	3.2	<0.001
	Number of edges*Time	1.6	16.6	5.0	<.001	3.2	<0.001
Successional stage 3 Dataset II (6.25*6.25 cm <sup>2</sup> , n = 630)	Time	5.6	5.6				
	Gap*Time	6.6	12.2	5.8	<.001	0.4	0.011
	Gap size*Time	3.3	15.5	6.1	<.001	2.3	<0.001
	Number of edges*Time	1.7	17.3	6.3	<.001	2.5	<0.001

**Table 2.** Summary of PRC's showing how the variance accounted for increases when more detailed explanatory variables are included in the models, and how much of this explained variance that is represented on the two first PRC axes. Data are in % variance explained. The effects of gaps and successional stage are investigated on large (625 cm<sup>2</sup>) gaps and controls (Dataset I). Gap, edge, and size effects are investigated on small (39 cm<sup>2</sup>) plots within large gaps, small gaps, and small controls (Dataset II). N gives the total number of vegetation samples used in each analysis. The full model PRCs on Dataset I and for each successional stage on Dataset II are shown in Figure 3 and 4, respectively.

*Hypothesis 1: The composition of the vegetation that develops in bare-ground gaps is different from the surrounding grassland.* Differences between gaps and controls through time can account for 21.6% of the within-plot variance (Table 2). The effect is highly significant, both overall and for all sampling dates except from the baseline (pre-treatment) census (Table 1). The diagram (Fig. 2) shows that the species composition was dramatically changed by gap creation, that gaps are becoming more similar to controls with time, and that the process is relatively slow as gaps are still significantly different from controls three years later (Fig 2 PRC axis 1, Table 1). The predicted changes in abundance based on PRC 1 scores are a 20% decrease in mean abundance in gaps relative to the controls for species with high positive  $b_k$  values, and a 10% increase in mean abundance for species with high negative  $b_k$  values at the first sampling date after gaps were created (Fig. 2). Gap increasers include ruderals such as *Cerastium fontanum*, *Veronica serpyllifolia*, and *Viola tricolor*, grassland herbs such as *Alchemilla wickuriae*, *Euphrasia stricta*, *Luzula frigida*, *Omalotheca norvegica*, and *Rhinanthus minor*, and alpine species such as *Bistorta vivipara* and *Gentiana nivalis*. Overall, species with high seedling recruitment are more likely to colonize gaps than vegetatively recruiting species (Pearson's correlation coefficient between  $b_k$  and  $f_{seed}$ :  $r_p = -0.54$ ,  $n=63$ ,  $p<0.001$ ), and rare species tend to increase in relative importance in gaps ( $b_k$  and number of occurrences in the data:  $r_p = 0.46$ ,  $n=86$ ,  $p<0.001$ ,  $r_p=0.66$ ,  $0.72$ , and  $0.82$  per successional stage,  $p<0.001$ ).

*Hypothesis 2: In grasslands undergoing secondary succession, the overall compositional effect of gaps increases over time, and the identity of gap regenerators changes.* A PRC model that allows for different gap effects in the three successional stages increases the explained variance with 10.2% relative to a model with a single gap revegetation trend only (Table 2), and gaps in all three successional stages are significantly different (Table 1). The 40-year gaps appear most floristically distinct (Table 1, Fig. 2, PRC 2), and the succession towards the composition of the controls (the slope of the PRC curve through time) is slightly slower here (Fig. 2, PRC 1). This result agrees with the first part of hypothesis 2.

The gap effect increases considerably during succession, with 8.8% of the compositional variance in dataset II being accounted for by revegetation trends in the 0-year grasslands, 9.4% in 10-year grasslands, and 12.2% in 40-year grasslands (Table 2). Overall, 74% of the species are affected by gaps, positively or negatively, in at least one of the stages, but the responses of individual species are generally not consistent along the successional sequence (Table 3, Fig. 3). There is a general tendency for species that are gap-dependent in early-successional grasslands to decrease in abundance or disappear in the later stages (Correlation between  $b_k$  in 0-year grasslands and relative change in abundance between 0 and 40 years:  $r_p = -0.46$ ,  $n=32$ ,  $p<0.01$ ). This typically affects open-vegetation grassland species, such as *Alchemilla wickuriae*, *Euphrasia stricta*, *Gentiana*



**Figure 2.** PRC diagram and species weights ( $b_k$ ) showing the overall impact of gaps, and differential gap effects between the three successional stages, on the floristic composition in the large (625 cm<sup>2</sup>) gaps and controls. PRC axes 1 and 2 (Table 2) are shown. Only species with relatively strong responses - with weights outside the [-0.4, 0.4] range - are shown for each axis. The significance of the overall effect and the significance of the difference between gaps and controls at each individual census are given in Table 1. These diagrams present the overall patterns in the data; diagrams from analyses per stage are presented for the small-plot data only (see Figure 3). A = autumn S = spring.

*nivalis*, and *Sagina procumbens*, which occur predominantly in 0-year gaps, and *Alchemilla monticola*, *Galium boreale*, *Omalotheca norvegica*, *Botrychium lunaria*, *Rhinanthus minor*, *Trollius europaeus*, and *Cerastium fontanum*, which are also found in 10-year gaps, but are absent from the 40-year successional stage. The species that occur throughout, including *Bistorta vivipara*, *Luzula frigida*, *Rumex acetosella*, and *Trifolium repens*, tend to become more gap-dependent during succession (i.e.  $b_k$  values decrease, Table 3). These differences between stages agree with the second part of hypothesis 2.

*Hypothesis 3: Gaps of different sizes are filled with different assemblages of species.* Allowing for differential effects of large and small gaps increases the explained variance by 3.3 – 5.5% within stages (Table 2). The size effect is highly significant in the 0 and 10-year stages, but marginally insignificant ( $p = 0.054$ ) in the 40-year successional stage (Table 1). The sequential tests performed for each point in time shows that significant differences between small and large gaps appear the first year after treatment, and persist through the study period. The diagram (Fig. 3) indicates that the differences between large and small gaps in the 0 and 10-year successional stages accelerate through time, because the small gaps do not follow the successional change of the larger gaps towards the composition of controls later on (Fig. 3). In these two successional stages PRC axis 2 further differentiates large gaps from small gaps and controls, indicating that the difference is caused by a subset of the gap species that are not able to regenerate successfully in small gaps (Table 3). A majority of the gap-regenerators occur preferentially in large gaps, but a group of species, including *Botrychium lunaria*, *Trollius europaeus*, *Galium boreale*, and *Omalotheca supina*, appear consistently in small gaps (i.e. their  $b_k$  values are negative on PRC 1 and positive on PRC 2). Therefore, hypothesis 3 is upheld.

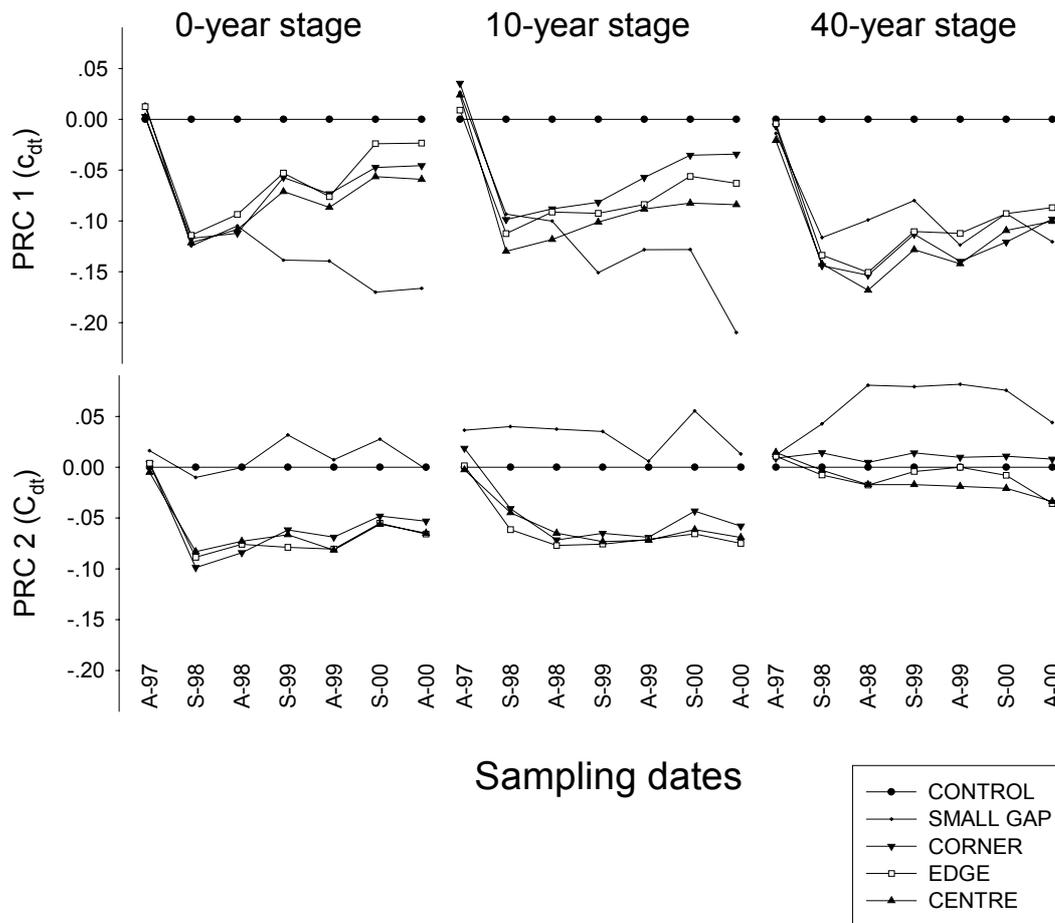
*Hypothesis 4: Within relatively large gaps edge effects will operate, so that the centre and periphery will be colonised by different species.* Significant edge effects appear in the mid-successional stage ( $p = 0.03$ , Table 1), but the effects are relatively weak, adding only 1.6% to the explained variance (Table 2). The sequential tests suggest that edge effects set in relatively late, as significant differences between corners and centres do not appear until two years after the experiments were initiated. On the diagram, the trajectories of the different subplots within large gaps in the 10-year stage through time appear distinct and parallel, ‘corners’ approach the controls first, followed by ‘sides’, while the ‘centres’ differ most strongly from the closed vegetation (PRC 1, Fig. 3). This

suggests that these edge effects may be ecologically interpretable despite the weak overall compositional response. Hypothesis 4 is therefore corroborated, but only in the 10-year successional stage.

## Discussion

### OVERALL EFFECTS, TEMPORAL TRENDS, AND COLONISATION MODES

The obvious effect of fine-scale disturbances is to decrease the dominance of persistent long-lived species, thereby providing better availability of light, nutrients, and space for recruits. The initial colonisation of bare ground reflects the local availability of propagules, and hence there is a general tendency for species that are common in the established vegetation to also become the most successful gap colonisers (see also Reader & Buck 1990, Rusch & van der Maarel 1992, Arnthórsdóttir 1994, Bullock *et al.* 1995, Rogers & Hartnett 2001). This is reflected in the relationship between abundance in closed vegetation and gaps in these grasslands (Dataset I:  $r_p=0.89$ ,  $n=66$ ,  $p<0.001$ , Dataset II:  $r_p=0.58$  to  $0.88$ ,  $n=15$  to  $39$ ,  $p<0.05$  in all cases). Within this overall constraint, however, the species composition that develops within gaps differs from the closed vegetation controls in strong, significant, and very persistent ways (Tables 1 & 2, Figs. 2 & 3). The time it takes for gaps to become indistinguishable from undisturbed patches of vegetation may range from a few weeks or months (Arnthórsdóttir 1994, Bell *et al.* 1999) to decades (Martinez-Tuarez *et al.* 1997), depending on site factors such as climate and productivity, biological traits of the colonising species, and the size and severity of the disturbance. Actual revegetation trajectories and rates in subalpine grasslands have not been documented previously, but in vegetation types that are comparable with respect to productivity, such as unproductive grassland (Goldberg & Gross 1988, Kotanen 1997a, b), the ground layer of boreal forests (Rydgren *et al.* 1998), and dwarf-shrub heaths (Britton *et al.* 2000), gap effects can typically be distinguished for less than five years. In comparison, the trends in this study appear relatively slow (Fig. 2). The overall compositional responses are remarkably consistent across data sets and scales of study, with estimated species responses ( $b_k$  values) implying a ca. 20% increase in the number of small-plot occurrences in the most strongly gap-dependent species, and a ca. 20% decrease in the most characteristic closed-sward species the first year after disturbance (Fig. 2, Table 3). Consequently, the species in these grasslands do not have absolute gap or closed-sward requirements, but exhibit a range of responses ranging from positive via neutral to negative. This



**Figure 3.** PRC diagrams showing the impact of gaps, gap size, and edge effects on the floristic composition in small plots (39 cm<sup>2</sup>) within large and small gaps and controls in the three successional stages (Table 2). The significance of the PRC diagrams are given in Table 2, the significance of differences between individual contrasts through time are given in Table 1, and species scores ( $b_k$ ) for all species on the different PRC's are given in Table 3. These diagrams present the main patterns within successional stages, separate diagrams from analyses of individual contrasts (Table 1) are not presented. A = autumn S = spring.

supports the view that gap responses should be seen as a continuum rather than on-off traits (Hubbell *et al.* 1999, Bullock 2000).

Gap increasers tend to colonise gaps from seeds rather than from clonal ingrowths ( $f_{\text{seed}}$  values, Table 3), and seedlings make up 77% of all first-year recruits. This is comparable to, for example, the 83% reported from alvar grasslands in Sweden (Rusch & van der Maarel 1992), and contrasts with the predominantly clonal recruitment reported from gaps within perennial grasslands elsewhere (Rapp & Rabinowitz 1985, Coffin & Lauenroth 1989, Milberg 1993, Arnthórsdóttir 1994, Kotanen 1997b). This may relate to the low productivity and slow dynamics of this system: gaps in subalpine perennial grassland, once created, are open to recruitment for extended periods of time. A mechanism that could contribute to the high colonisation success of seedlings, both in absolute numbers and relative to clonal ingrowths, is the very specific germination requirements found in

many grassland species (Grime *et al.* 1981, Baskin & Baskin 1998). Such responses may function to inhibit germination of a subset of the species in closed vegetation, resulting in higher overall germination rates as well as differences in the relative abundance of species in gaps (Hutchings & Booth 1996, Vandvik & Elven 2002). Once germinated, seedlings cannot rely on support or provision from the maternal plant during establishment, and competitive effects of established plants in a closed vegetation sward should therefore be more deleterious for seedlings than for clonal recruits. The overall compositional difference between gaps and controls may thus reflect the added effect of higher seed germination on bare ground and a relatively higher probability for survival and successful establishment of the seedlings that do appear here. The trend for locally rare species to increase in relative importance in gaps agrees with the findings of Lavorel *et al.* (1994), and suggests a mechanism by which gap

Successional stage	Occurrence (%)			Regenerative mode ( $f_{seed}$ )	PRC 1			PRC 2		
	per stage				Controls - Gaps			Control/Small - Large Gaps		
	0-yr.	10-yr.	40-yr.		0-yr.	10-yr.	40-yr.	0-yr.	10-yr.	40-yr.*
<i>Achillea millefolium</i>	35.6	47.3	4.3	0.60	<b>1.77</b>	<b>1.86</b>	<b>0.61</b>	0.17	0.42	0.12
<i>Agrostis capillaris</i>	62.2	65.7	28.7	0.23	<b>1.19</b>	<b>1.28</b>	<b>0.95</b>	<b>1.28</b>	-0.35	<b>0.57</b>
<i>Alchemilla monticola</i>	17.0	11.6	1.9	1.00	<b>-0.63</b>	<b>-0.80</b>	-0.37	<b>1.05</b>	<b>-1.12</b>	0.04
<i>Alchemilla subcrenata</i>	2.7	1.4	1.3	0.75	<b>-1.50</b>	-0.39	-0.05	<b>1.57</b>	0.33	<b>1.57</b>
<i>Alchemilla wichuriae</i>	12.2	4.4	0.8	1.00	0.19	0.31	-0.19	<b>-1.24</b>	-0.40	-0.22
<i>Anthoxanthum odoratum</i> ssp. <i>alpinum</i>	26.0	24.4	11.4	0.44	<b>1.38</b>	<b>0.88</b>	<b>0.82</b>	<b>1.94</b>	<b>1.77</b>	0.10
<i>Anthriscus sylvestris</i>	1.7	0.6	0.5	1.00	<b>-1.43</b>	<b>-0.91</b>	-0.09	<b>1.25</b>	<b>0.55</b>	<b>0.92</b>
<i>Betula pubescens</i>	6.3	0.2	4.4	1.00	-0.05	0.07	0.08	<b>-1.52</b>	0.05	<b>-0.69</b>
<i>Bistorta vivipara</i>	36.0	19.2	11.7	0.99	<b>1.47</b>	<b>0.93</b>	0.44	-0.16	<b>-0.61</b>	-0.42
<i>Botrychium lunaria</i>	6.2	7.1	1.3		<b>-1.69</b>	<b>-1.95</b>	-0.16	<b>2.27</b>	<b>2.04</b>	<b>1.50</b>
<i>Campanula rotundifolia</i>			3.2	1.00			0.44			-0.42
<i>Carex brunnescens</i>		0.2	0.3			0.04	-0.07		0.14	<b>0.64</b>
<i>Carex vaginata</i>		0.6	0.6	1.00		-0.13	0.31		-0.36	-0.04
<i>Cerastium fontanum</i>	9.7	7.6		1.00	0.19	0.09		<b>-1.45</b>	<b>-1.07</b>	
<i>Deschampsia cespitosa</i>	5.7	12.9	4.6	0.82	<b>-0.94</b>	0.46	0.29	<b>0.99</b>	<b>1.12</b>	<b>-0.52</b>
<i>Deschampsia flexuosa</i>	3.8	1.7	19.2	0.32	-0.30	0.18	<b>1.63</b>	<b>1.06</b>	<b>0.56</b>	0.00
<i>Empetrum hermaphroditum</i>		0.2	0.2			-0.23	-0.02		0.27	-0.29
<i>Equisetum pratense</i>		0.3				-0.01			0.06	
<i>Equisetum sylvaticum</i>	0.2	0.3		1.00	-0.08	0.02		-0.25	-0.32	
<i>Euphrasia stricta</i>	19.2			1.00	<b>0.77</b>			<b>-1.48</b>		
<i>Festuca ovina</i>	7.9	0.6	6.3	1.00	<b>-1.16</b>	0.11	<b>0.53</b>	<b>1.12</b>	-0.32	<b>-0.79</b>
<i>Festuca rubra</i>	14.9	15.7		0.49	<b>1.07</b>	<b>1.03</b>		0.01	<b>0.89</b>	
<i>Gallium boreale</i>	3.5	1.4		0.86	<b>-0.90</b>	<b>-1.19</b>		<b>0.65</b>	<b>1.08</b>	
<i>Gentiana amarella</i>	1.6			1.00	-0.05			0.05		
<i>Gentiana nivalis</i>	4.1			1.00	-0.26			<b>-1.09</b>		
<i>Geranium sylvaticum</i>	3.7	5.2	0.3	1.00	<b>0.71</b>	<b>0.59</b>	0.00	<b>0.68</b>	0.06	-0.19
<i>Hieracium lactucella</i>	0.5	0.3	0.2		0.26	<b>-0.57</b>	-0.14	-0.09	<b>0.53</b>	0.43
<i>Juncus filiformis</i>	0.3	0.6		1.00	0.11	-0.11		-0.31	-0.20	
<i>Juniperus communis</i>			0.2				0.03			-0.08
<i>Leucanthemum vulgare</i>	12.5			0.88	<b>0.76</b>			-0.30		
<i>Leontodon autumnalis</i>	1.7	2.5	0.2	1.00	<b>-1.14</b>	0.12	-0.09	<b>1.29</b>	-0.49	-0.17
<i>Luzula multiflora</i> ssp. <i>frigida</i>	4.9	5.9	20.2	0.98	0.02	-0.18	<b>-1.00</b>	<b>-0.80</b>	<b>-0.80</b>	<b>-1.92</b>
<i>Luzula pilosa</i>	0.5	1.1	5.1	0.97	<b>-0.53</b>	<b>-0.50</b>	-0.19	<b>0.65</b>	<b>0.99</b>	<b>2.86</b>
<i>Nardus stricta</i>	6.5	2.1	29.7	0.61	<b>0.80</b>	<b>0.57</b>	<b>1.74</b>	<b>0.78</b>	0.47	<b>-0.96</b>
<i>Omalotheca norvegica</i>	6.5	12.2	0.2	1.00	0.08	-0.27	-0.02	<b>-0.73</b>	<b>-1.69</b>	0.03
<i>Omalotheca supina</i>	1.0	3.7		1.00	-0.01	<b>-1.48</b>		-0.10	<b>1.81</b>	
<i>Phleum alpinum</i>	2.5	4.1	1.0	0.71	0.42	0.45	<b>0.69</b>	0.11	0.10	-0.21
<i>Phleum pratense</i>	0.6	0.2			-0.41	-0.27		0.37	0.41	
<i>Poa pratensis</i> ssp. <i>alpigena</i>	3.2	6.5		0.65	0.29	0.23		-0.28	0.00	
<i>Poa alpina</i>	3.8	1.0		0.75	0.39	<b>-0.58</b>		0.19	0.48	
<i>Poa glabra</i>	0.8				-0.41			<b>0.88</b>		
Poaceae	1.9	2.2	1.0	0.83	-0.36	-0.37	-0.05	<b>-0.84</b>	-0.37	-0.08
<i>Prunella vulgaris</i>	5.6	0.3	0.3	1.00	0.46	-0.04	-0.01	-0.01	<b>0.50</b>	<b>0.62</b>
<i>Pyrola minor</i>	1.6		0.5		<b>-0.97</b>		0.00	<b>1.16</b>		-0.10
<i>Ranunculus acris</i>	16.2	6.8	0.5	0.98	<b>1.43</b>	<b>1.28</b>	0.11	<b>0.50</b>	<b>0.76</b>	<b>0.50</b>
<i>Ranunculus auricomus</i>	2.4	4.0	0.6	1.00	<b>-1.57</b>	0.25	-0.03	<b>1.42</b>	<b>1.15</b>	<b>0.78</b>
<i>Rhinanthus minor</i>	12.1	16.2		1.00	0.43	<b>0.56</b>		<b>-1.02</b>	<b>-0.59</b>	
<i>Rumex acetosa</i>	4.4	28.9	1.0	0.98	<b>-0.55</b>	<b>0.81</b>	0.43	<b>0.84</b>	0.25	-0.39
<i>Rumex acetosella</i>	6.2	6.8		1.00	0.38	<b>-1.48</b>		<b>-0.74</b>	<b>2.54</b>	
<i>Sagina procumbens</i>	3.3			1.00	<b>-0.64</b>			0.02		
<i>Salix</i> spp.	0.8	0.3		1.00	-0.38	0.08		0.08	-0.21	
<i>Saussurea alpina</i>			0.2				0.02			0.01
Seedling	2.5	3.0	0.8	1.00	<b>-0.66</b>	-0.49	-0.21	0.40	0.34	-0.17
<i>Silene pratensis</i>		0.2		1.00		-0.05			-0.11	
<i>Silene vulgaris</i>	0.2			1.00	-0.02			0.00		
<i>Solidago virgaurea</i>	0.5			1.00	0.03			0.02		
<i>Stellaria graminea</i>	6.5	1.1		1.00	<b>0.72</b>	<b>0.62</b>		0.32	0.25	
<i>Stellaria media</i>	0.3	0.5		1.00	<b>-0.56</b>	-0.25		<b>0.57</b>	0.30	
<i>Taraxacum</i> spp.		0.5				0.00			-0.31	
<i>Trifolium europaeus</i>	1.3			1.00	0.34			-0.30		
<i>Trifolium pratense</i>	9.8			0.83	<b>0.63</b>			0.31		
<i>Trifolium repens</i>	31.0	6.5		0.43	<b>0.54</b>	0.43		<b>0.84</b>	<b>-0.72</b>	
<i>Trollius europaeus</i>	4.8	0.6		1.00	<b>-1.77</b>	<b>-0.68</b>		<b>1.97</b>	<b>0.69</b>	
<i>Vaccinium myrtillus</i>	6.7		4.6	0.71	<b>0.57</b>		0.10	0.30		0.10
<i>Vaccinium vitis-idaea</i>	1.6		5.1	0.43	<b>-0.83</b>		0.36	<b>0.79</b>		<b>0.93</b>
<i>Veronica alpina</i>		0.2	0.5	1.00		-0.03	-0.20		-0.03	<b>0.84</b>
<i>Veronica serpyllifolia</i>	0.5	1.9	0.6	1.00	-0.04	-0.34	-0.10	-0.40	-0.22	<b>1.12</b>
<i>Vicia cracca</i>	5.1	0.3		1.00	0.41	-0.22		-0.48	0.49	
<i>Viola biflora</i>	7.6	5.6	0.6	0.96	0.18	0.48	<b>0.51</b>	0.20	-0.27	-0.25
<i>Viola palustris</i>	1.1	6.0	7.8	0.96	-0.46	-0.39	0.02	0.47	<b>1.15</b>	<b>-1.06</b>
<i>Viola riviniana</i>	1.0	0.6	3.0	1.00	<b>0.53</b>	<b>-0.68</b>	-0.31	0.45	<b>0.82</b>	0.16
<i>Viola tricolor</i>	2.5	0.3		1.00	-0.14	-0.08		0.00	-0.29	
Correlation with 0-year $b_k$						0.61***	0.33*		0.38*	0.33*
Correlation with 10-year $b_k$							0.53**			0.35*
Correlation with $f_{seed}$	-0.52***	-0.53***	-0.63***		-0.30*	-0.44**	-0.68**	-0.37**	-0.13	-0.09
Correlation with % occurrence in controls					0.66***	0.72***	0.82***	0.23	0.19	-0.03
Correlation with % occurrence in large gaps					0.60***	0.42**	0.22	-0.07	-0.23	-0.43*
Correlation with % occurrence in small gaps					0.01	0.13	0.55**	0.54***	0.45***	0.29

**Table 3.** Species weights ( $b_k$ ) for all species on the PRC's showing how gaps of different sizes, and corner, side, and central subplots within large gaps revegetate within the different successional stages (Table 2, Fig. 3). For all stages, PRC 1 contrasts gaps from controls, and species that occur predominantly in gaps have negative  $b_k$ 's while closed sward species have positive  $b_k$ 's. For the 0-year and 10-year stages, PRC 2 contrasts large gaps (negative  $b_k$ 's) from small gaps and controls (positive  $b_k$ 's). Strong responses ( $b_k$  outside the [-0.4,0.4] range) are shown in bold. The regenerative mode (seed or vegetative) of each individual recruit appearing in the gaps in 1998 was noted, and for all species  $f_{seed}$ , the fraction of recruits originating from seeds, was calculated. Pearson's correlation coefficients between the  $b_k$ s in different successional stages, and between the  $b_k$ s and  $f_{seed}$  are shown at the bottom of the table. Additional species occurring within Dataset I are *Carex nigra*, *Carex ovalis*, *Carex pilulifera*, *Dactylorhiza* spp., *Epilobium anagallidifolium*, *Euphrasia frigida*, *Hieracium pilosella*, *Hieracium sylvaticum*, *Molinia caerulea*, *Melampyrum sylvaticum*, *Myosotis decumbens*, *Poa annua*, *Ranunculus repens*, and *Selaginella selaginoides*.

revegetation can contribute to local survival of infrequent species in these grasslands.

#### GAP SIZE AND EDGE EFFECTS

A large number of empirical and theoretical studies show that large gaps should be more open to seedling recruitment than small gaps. Large gaps are more environmentally different from the closed vegetation than small gaps (Goldberg & Werner 1983, Morgan 1997, Kotanen 1997b, King & Grace 2001), and they generally fill more slowly, thereby providing increased time for colonisation (Bullock *et al.* 1995, Rogers & Hartnett 2001). In habitats where competition from a dense vegetation sward poses the major threat to seedling survival, the number of successfully establishing species will increase with gap size (Grubb 1977, Denslow 1980, Miller 1982, Chambers 1995, Roger & Hartnett 2001, Table 3). But at the same time, gap size also affects the gap environment. The intact vegetation sward functions to ameliorate the environmental variation, so that the diurnal amplitudes in temperature and moisture are larger in gaps than in closed vegetation, and will increase with the size of gaps (Thompson *et al.* 1977). Such differences in environmental variability may form the basis for environmental cueing responses in seeds (Grime *et al.* 1981, Baskin & Baskin 1998), but this also means that the probability of damage by environmental hazards such as drought and frosts increases with gap area. In habitats where both competition and climatic hazards on bare ground may become sufficiently high to pose threats to seedling survival, successful establishment will be predicted to occur in gaps of intermediate sizes. The optimal gap size will vary with species traits such as seed size, dispersal traits, and seedling growth form, and for a given species it should increase with the height and density of the standing vegetation and decrease with the exigencies of gap microclimate. These counteracting effects of gap size on seedling survival may explain some apparently inconsistent responses of subalpine grassland species (Table 3), such as why, for example, *Botrychium lunaria*, *Galium boreale*, and *Trollius europaicus* appear selectively in small gaps. Following de Hullu & Gimingham (1984), a change in preference from small to large gaps along the successional sequence, as observed in, for example, *Alchemilla monticola* and *Leontodon autumnalis*, may be explained by a shift in gap environment and competitive effects as the height and density of the surrounding vegetation increases during succession. Although only two gap sizes were investigated here, this interpretation matches the findings of Williams (1992), who investigated a wider range of gap sizes in drought-prone subalpine perennial grasslands in Australia, and found that optimal gap sizes differed between species. Such gap-size

effects may also contribute to explain one of the most unexpected results of this study, namely that small gaps remain more distinct from controls over time than large gaps (Fig. 3, stages 1 and 2). This contrasts with the findings of a number of other studies (Goldberg & Werner 1983, Ryser 1993, Bullock *et al.* 1995, Morgan 1997, Britton *et al.* 2000). If small and large gaps are colonised by different subsets of species, and if the small-gap specialists are, on average, more persistent, or better able to withstand competition, than large-gap specialists, then slower succession towards the control composition in small gaps will actually be the expected outcome.

According to Kotanen (1997b), the same general differences in microenvironment and vegetation closure should exist in the central area vs. the periphery of large gaps, and the revegetation of centres and edges could therefore be expected to differ in the same ways as large and small gaps. Such a relationship is not found in this study, as edge effects are weaker, appear much later (Table 1), and induce a different compositional response (i.e. relates to a different PRC axis than size effects, Table 2, Fig. 2). As significant differences between subplots do not appear until two years after gaps are created, it may safely be concluded that edge effects do not operate on the initial colonisation or early establishment phases of gap revegetation. This also rules out a centre-to-vegetation edge micro-environmental gradient as a causal factor, because centre and edge environments will become progressively more similar as seedlings and vegetative ramets cover the bare ground. The 33% clonal recruitment into gaps will move in from the edges, and vegetation closure within gaps will therefore progress from the corners to the edges and centres. Competition between recruits will be expected to set in as the vegetation closes, resulting in a temporary divergence in floristic composition until competitive exclusion of the most typical bare-ground species (i.e. species with low  $b_k$  values) has occurred throughout the gap. This prediction fits the experimental results in the mid-successional stage better (Figure 3), suggesting that the edge effects result from within-gap trends in vegetation closure and competitive exclusion, rather than from differential colonisation due to small-scale environmental variability.

#### GAP REGENERATION ALONG THE SUCCESSIONAL SEQUENCE

Although the observed differences in species composition and gap revegetation dynamics between successional stages could potentially be due to factors other than land-use history (e.g. differences in altitude, topography, substrate, moisture or soils), several features suggest that land-use is of overriding importance. First, in the

selection of replicate farms within successional stages great care was taken to avoid any systematic differences in these potentially important factors between stages (Figure 1). Second, local site factors have been shown to be relatively unimportant for the vegetation development at summer farms, partially because summer farms were initially located on similar places in the landscape, and partially because centuries of land-use prior to abandonment functions to homogenise any initial differences (Vandvik & Birks 2002a). Third, the timing of abandonment and other differences in land-use generally relate more to the economy and interests of the individual landowner than to ecologically relevant characteristics (productivity, spatial isolation etc.) of the summer farm (V. Vandvik, *personal observation*). Fourth, abandonment history can account for a very large fraction (more than  $\frac{3}{4}$ ) of the total between-farm floristic variability (CCA results). Overall, it is therefore likely that the effects of land-use history are of overriding importance for the systematic differences in floristic composition and gap responses appearing between successional stages in the study.

A major objective of this study was to investigate whether, and how, revegetation dynamics of fine-scale disturbance in a closed sward change along a successional sequence. The formal tests, performed on dataset I (Table 1), demonstrate that such changes occur in these grasslands. Further, the differential gap responses are relatively strong, as the explained variance increases considerably, from 21.6% to 31.8%, when these responses are allowed for in the PRC's (Table 2). These results imply that for an appreciable fraction of the species in these grasslands, the relationship between abundance in controls and the probability of appearance in bare-ground gaps changes during succession.

One aspect of these changes is a general trend for seed regenerating species to become relatively more dependent on gaps through the successional sequence (correlation between  $f_{\text{seed}}$  and PRC 1 becomes stronger, Table 3). This implies that different processes operate on the vegetative and regenerative phases in the life cycles of these species. Such differences can be illustrated by looking at how the responses of particular species differ between studies focusing on the vegetative and regenerative parts of the plant life cycle. For example, Moen & Oksanen (1988) investigated species responses after protection from grazing in alpine snow-beds, and found that the growth and performance of tall herbs, including *Omalotheca norvegica*, *Trollius europaeus*, and *Bistorta vivipara*, increased when protected from grazers. In contrast, the same three species appear as gap-dependent in this study, and this dependency increases along the successional sequence. This

implies that these species decrease in abundance in the closed vegetation along the 40-year successional sequence, but that recruitment into gaps is comparatively less adversely affected. In an experimental study of the germination and establishment of grassland herbs, successful establishment of *Trollius europaeus* (as for 73% of the investigated species) was effectively inhibited in closed vegetation (Vandvik & Elven 2002). For small-stature grassland herbs (e.g. *Alchemilla wichuriae*, *Botrychium lunaria*, *Cerastium fontanum*, *Euphrasia stricta*, *Gentiana nivalis*, and *Rhinanthus minor*) however, the increase in the height and density of the grassland sward during secondary succession (Morgan 1997, V. Vandvik *unpublished data*) will have a more immediate negative effect on established plants. This is reflected in their decreasing abundance between the 0-year and 10-year stages. The overall abundance of mature plants in the closed sward will again be reflected in the seed rain into gaps. The relative increase in gap dependency of seed regeneration species, however, indicates that the availability of propagules is a less serious limitation for population persistence of grassland herbs during succession than the availability of safe sites for regeneration. This may in part be attributed to the relatively extensive seed banks under these grasslands, containing 66 species, 39 of which also appear in the gap revegetation data, and having a mean density of 2131 seeds per  $\text{m}^2$  (V. Vandvik, *unpublished data*). Once a gap is created, the relatively slow revegetation dynamics of gaps in these grasslands enable short-lived, small-stature species such as *Euphrasia stricta* and *Gentiana nivalis* to establish, grow, and reproduce before the gap closes. Larger gap regenerating species, such as *Trollius europaeus* and *Omalotheca norvegica*, may establish large and competition-resistant individuals.

The changes in local disturbance regimes within these grassland may be seen as a change in the 'environmental sieves' that function to exclude subsets of the species in the regional species pool from local communities (Zobel 1992, 1997). The time-scales involved will increase with the life expectancy of the mature plants, explaining why relatively short-lived species tend to appear only in the 0-year stage in these grasslands while more long-lived species persist in the 10-year grasslands as well. The differences in the local floras of these grasslands, with 28 species disappearing and only 7 new species appearing along the successional sequence (Table 3), indicate that the disturbance regime exerts a strong influence.

#### PRC APPLICATIONS

The PRC methodology was originally developed in ecotoxicology (van den Brink & ter Braak 1997,

1998, 1999, Kedwards *et al.* 1999), and has recently been used in arthropod ecology (Frampton *et al.* 2000, 2001), but it clearly has potential for a much wider application in experimental community ecology. The analysis zooms directly in on the relative difference between treated plots and controls through time, and is most readily applicable for classical BACI (before – after, control – impact) design experiments. However, the general methodology can be used to test other contrasts as well, as exemplified in this study in the tests of large vs. small gaps and corners vs. edges vs. centres within large gaps. An additional advantage is that because of the relatively simple ANOVA-type modelling and the combined overall and sequential testing, the methodology is equally applicable for short and long time-series.

### Conclusions

The results of this study demonstrate that fine-scale disturbances can have considerable effects on the community structure and floristic composition of subalpine perennial grasslands. All the four hypotheses regarding gap effects were upheld, showing that gaps do not exert simple on-off effects: Small and large gaps and edges and centres are colonised by partially distinct assemblages of species, and these overall trends as well as the responses of individual species change during secondary succession. This illustrates how processes operating at different scales may interact (Pickett *et al.* 1987, 1989, Zobel 1992): the disturbance regime, at the scale of the entire grassland, affects the dynamics within individual disturbances occurring in these grasslands. Such detailed experimental studies of fine-scale vegetation dynamics in subalpine vegetation have not been carried out previously. Compared to the results of other studies in grassland, revegetation was slow in small as well as large gaps, and edge effects were weak, suggesting that clonal encroachment and competitive effects are relatively low. Gaps were still significantly different from control vegetation three years after the gaps were established, and the plots would have to be followed longer to determine the actual duration of the effect. This may be attributed to the slow growth rates and short growing seasons in these climates. As the effects of individual gaps are so persistent, a given disturbance regime (i.e. a frequency of gap creation) will have a larger effects here than in more benign climates.

### Acknowledgements

I am greatly indebted to John Birks for his contribution in the design of this study and valuable discussions of the statistical approach, Petr Šmilauer for statistical advice, Beate H. Ingvarsen

for drawing the maps and figures, Baard Olav Skogrand, Heidi Solstad, Kjell-Tore Hansen, and Ann-Kristin Østgård, for field assistance, to the six landowners for permission to set up and maintain the experiments on their land, to Solveig Nygård for letting me use Nygårdsvollen for lodging, and to my parents and in-laws for doing the most important job of all: looking after my two favourite recruits during field seasons. Einar Heegard, Hilary Birks, and Vibekke Vange provided helpful suggestions to earlier versions of this manuscript. The work was supported by the Norwegian Research Council (Grant no. 73758/410).

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