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Published in:
Ecography

DOI:
10.1111/j.0906-7590.2005.04033.x

2005

Citation for published version (APA):
Bruun, H. H., Österdahl, S., Moen, J., & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography*, *28*(1), 81-87. https://doi.org/10.1111/j.0906-7590.2005.04033.x

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ECOGRAPHY 28: 81–87, 2005

Distinct patterns in alpine vegetation around dens of the Arctic fox

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The arctic fox *Alopex lagopus* excavates its dens in gravely ridges and hillocks, and creates a local environment quite distinct from the surrounding tundra or heath landscape. In northern Sweden, the vegetation of 18 dens of the arctic fox was investigated, as well as reference areas off the dens but in geologically and topographically similar locations. The species composition showed considerable differences between den and reference areas, with grasses and forbs occurring more abundantly on the dens, and evergreen dwarf-shrubs occurring more in reference areas. The effect of the foxes' activities is thought to be either through mechanical soil disturbance, or through nutrient enrichment via scats, urine, and carcasses. This was expected to result in differences in plant traits with key functional roles in resource acquisition and regeneration, when comparing dens with reference areas. We hypothesised that the community mean of specific leaf area (SLA) would differ if nutrient enrichment was the more important effect, and that seed weight, inversely proportional to seed number per ramet and hence dispersal ability, would differ if soil disturbance was the more important effect. Specific leaf area showed a significant difference, indicating nutrient enrichment to be the most important effect of the arctic fox on the vegetation on its dens. Arctic foxes act as ecosystems engineers on a small scale, maintaining niches for relatively short-lived nutrient demanding species on their dens in spite of the dominance of long-lived ericaceous dwarf-shrubs in the landscape matrix. Thus, foxes contribute to the maintenance of species richness on the landscape level.

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In many ecosystems of the world, the activities of animals create small distinct patches of environment quite different from the surroundings, most often as disturbances. Small-scale disturbances may have profound influence on vegetation dynamics (Watt 1947, Hobbs and Mooney 1995, Wiegand et al. 1997) and local plant species richness (Platt 1975, Gigon and Leutert 1996). These are non-trophic interactions, unlike most plant-animal interactions, and the phenomenon has been coined physical ecosystem engineering (Jones et al. 1994, 1997). The impact of digging mammals may go through disturbance of foliage and soil or through the redistribution of nutrients. In addition, mammals may act as agents of dispersal of plant propagules. This is also the case for the arctic fox (Graae et al. 2004).

Dens of the arctic fox have been described as lush green in an otherwise brownish landscape of tundra or alpine heathland from many arctic regions, e.g. Scandinavia (Dalerum et al. 2002), Greenland (Nielsen et al. 1994), Alaska (Chesemore 1969, Garrott et al. 1983), and Canada (Smits et al. 1988, Smith et al. 1992, Anthony 1996). However, all these studies have

Accepted 30 July 2004

ISSN 0906-7590

described the dens from the point of view of the fox or of the investigator trying to identify dens at the maximum possible distance. In this paper we consider fox dens as a distinct habitat for vascular plants in arctic and alpine landscapes.

The dens are distributed as islands in a more or less regular pattern due to the territoriality of the foxes. The dens are subjected to heavy disturbance due to the burrowing and the general "traffic" of foxes, and they receive nutrient input from the surroundings via scats and urine and remains from carcasses of prey items (reindeer, lemmings etc.) left by the foxes. It is not known if the fox dens hold higher or lower small-scale species richness than the surroundings, or whether the plant species inhabiting the dens only occur there. The relative importance of disturbance and nutrient enrichment on the vegetation is not known. These factors are very difficult to estimate directly, so we take the indirect approach of seeking a differential distribution of plant traits related to ecological function in resource economy and colonisation. Specific leaf area (SLA, leaf area per unit dry mass) is an easy-to-measure trait that is positively related to mass-based net photosynthetic capacity and mass-based leaf nitrogen and negatively related to leaf life-span (Reich et al. 1997). Species' mean seed weight is inversely proportional to mean seed number per individual or ramet (given equal reproductive effort) due to a trade-off (Harper et al. 1970), and seed number is positively related to the probability that a seed of the species will arrive at any given point in the landscape. Disturbance will create gaps in the vegetation where recruitment from seed bank or seed rain can take place. Therefore, species with relatively small seeds should be superior colonisers of gaps in the vegetation. We hypothesize that, if nutrient enrichment is more important, a larger difference in mean SLA should be expected, with the plant community on fox dens having a higher mean SLA. Conversely, if disturbance is more important, a larger difference in mean seed weight should be expected, with plant species on dens having lighter seeds. Both hypotheses are based on the well-supported notion that within-species variation is at least an order of magnitude smaller than between-species variation. Lastly, we seek to answer the question if a difference between indicator species for fox dens versus surroundings is explicable in terms of a wider range of plant traits along with SLA and seed weight. The regional distribution of the species is included with this set of traits.

The aim of the present paper is to investigate the differences between dens of arctic fox and comparable areas in the surroundings in terms of 1) vegetation species richness and species composition, 2) functional traits related to disturbance or fertility, 3) a wider set of plant traits and species' regional distribution.

Study area

In the Vindelfjällen Nature Reserve in northern Sweden (66°10′N, 16°10′E) 18 dens of arctic fox were investigated. The landscape matrix is a low-alpine (750–1611 m a.s.l.) mountain tundra without permafrost. The vegetation is dominated by dwarf shrubs, with co-dominance of lichens in drier places and by bryophytes and Cyperaceae in wetter places. The summers are short with snowmelt in June and the first new snow in September. The whole area is relatively level. Eskers, kames and other hilly deposits of glacial or glaciofluvial origin occur frequently (Ulfstedt 1977). Dalerum et al. (2002) surveyed site characteristics and breeding frequency of foxes over a 16-yr period for all 77 dens in the area. They found that the arctic fox in the area preferred glaciofluvial ridges and terraces consisting of sorted sand for denning, and that dens were more widely spaced than random. The Fennoscandian arctic fox has decreased in population size over the last century. Therefore, most of the dens in the area are uninhabited, and, at many den sites, the area used for burrowing has decreased. All dens in this study were uninhabited in the year of investigation, 2001. The time since the last habitation for the studied dens varied between one and 14 or more years.

Methods

Vegetation sampling

At each fox den, the part affected by the most recent habitation was delimited by visual inspection (intact tunnels, freshly dug-up soil). The largest possible rectangle was inscribed in the delimited area (average 168 ± 95 m^2). A reference area was selected as close to the den as possible, with approximately the same elevation, slope and aspect (to minimise differences in wind exposure, and hence snow cover during winter and spring, and in soil drainage). A rectangle of approximately the same size as that on the den was placed. Most often it was easier to vary the size of the reference plot than that of the den plot, but in a few instances a slope on a den was excluded because a slope with a similar aspect was not available in the near surroundings. Because of the shrinking population size of the arctic fox, most dens had a more recently inhabited core area and marginal parts with collapsed tunnels. Marginal areas were excluded from both den and reference plots. Because of the topography, both den and reference plots include a gradient in wind exposition, snow cover and water regime. Within each plot, 20 quadrates of 15×15 cm were placed at random, and the presence of all vascular plant species were recorded. For estimation of SLA of all species encountered (Table 1), ten undamaged mature leaves, developed in

Table 1. The species found on the arctic fox dens and in the reference plots and their frequency (Freq) over all plots (n = 36), indicator values (IV-max) and associated p-values, the relative abundance and relative frequency (separated by a slash) for den and reference plots respectively, mean seed weight (mg) with source, SLA (cm^2/g), and growth form (f = forbs, g = graminoids, dd = deciduous dwarf shrubs, ed = evergreen dwarf shrubs). Sources for seed weight 1) own measurements, 2) Porsild (1920), 3) Grime et al. (1988), and 4) Johansson et al. (1997).

	Freq	IV-max	p	Fox den	Reference	Seed weight (mg)	SLA (cm^2/g)	growth form
Rumex acetosa ssp. *acetosa*	27	93.7	<0.001	**94/100**	6/50	1.286^1	348.6	F
Poa alpigena	17	88.4	<0.001	**99/89**	1/6	0.250^3	191.0	g
Carex bigelowii	36	62.7	<0.001	**63/100**	37/100	0.695^1	388.1	g
Cerastium alpinum	10	46.6	0.003	**93/50**	7/6	0.331^2	402.0	f
Anthoxanthum odoratum	15	45	0.037	**74/61**	26/22	0.615^1	347.2	g
Silene dioica	8	44.4	0.001	**100/44**	0/0	0.91^1	415.4	f
Carex vaginata	9	42.7	0.006	**96/44**	4/6	3.675^1	–	g
Stellaria borealis	6	33.3	0.015	**100/33**	0/0	0.147^2	–	f
Agrostis capillaris	7	32.4	0.028	**97/33**	3/6	0.06^3	758.8	g
Festuca ovina	34	55.8	0.185	63/89	37/100	0.35^3	192.9	g
Trientalis europaea	30	42.7	0.924	48/89	52/78	0.559^1	410.2	f
Solidago virgaurea	17	30.9	0.465	44/39	56/56	0.740^1	228.0	f
Calamagrostis purpurea	7	24.6	0.094	89/28	11/11	–	–	g
Omalotheca supina	4	22.2	0.111	0/0	100/22	0.108^1	–	f
Sibbaldia procumbens	4	22.2	0.104	0/0	100/22	0.552^1	246.6	f
Polygonum viviparum	5	21.5	0.225	3/6	97/22	1.559^1	202.0	f
Arctostaphylos alpinus	3	16.7	0.216	0/0	100/17	2.404^1	115.8	dd
Cassiope hypnoides	3	16.7	0.223	0/0	100/17	0.013^1	200.0	ed
Carex curta	7	14.4	0.58	35/17	65/22	0.130^2	268.6	g
Carex lachenalii	5	11.9	0.77	71/17	29/11	0.424^1	–	g
Equisetum arvense	4	11.1	0.603	33/6	67/17	–	–	f
Omalotheca norvegica	2	11.1	0.492	0/0	100/11	0.092^1	–	f
Thalictrum alpinum	2	11.1	0.499	0/0	100/11	0.857^1	222.2	f
Viola biflora	6	10	0.931	45/22	55/11	0.740^1	539.4	f
Rubus chamaemorus	8	8.8	0.999	26/33	74/11	7.60^4	203.0	f
Ranunculus acris	5	8.7	0.812	39/22	61/6	1.481^1	466.0	f
Deschampsia cespitosa	1	5.6	0.999	100/6	0/0	0.250^3	–	g
Epilobium angustifolium	1	5.6	0.999	100/6	0/0	0.050^3	270.5	f
Juniperus communis	1	5.6	0.999	0/0	100/6	5.513^1	–	ed
Luzula multiflora	1	5.6	0.999	0/0	100/6	0.415^1	295.5	g
Luzula spicata	1	5.6	0.999	0/0	100/6	0.405^1	–	g
Lychnis alpina	1	5.6	0.999	0/0	100/6	0.085^1	215.6	f
Petasites frigidus	1	5.6	0.999	100/6	0/0	–	286.8	f
Phleum alpinum	1	5.6	0.999	0/0	100/6	0.533^1	–	g
Pyrola sp.	1	5.6	0.999	0/0	100/6	0.001^2	–	f
Ranunculus nivalis	1	5.6	0.999	100/6	0/0	0.443^2	–	f
Veronica alpina	1	5.6	0.999	0/0	100/6	0.051^1	235.6	f
Equisetum sylvaticum	2	4.2	0.999	75/6	25/6	–	–	f
Euphrasia frigida	2	3.7	0.999	33/6	67/6	0.169^1	320.0	f
Vaccinium vitis-idaea	28	88.2	<0.001	12/56	**88/100**	0.236^1	56.5	ed
Vaccinium myrtillus	17	87.2	<0.001	2/6	**98/89**	0.201^1	212.6	dd
Empetrum nigrum ssp. *hermaphroditum*	16	82.6	<0.001	1/6	**99/83**	1.543^2	134.6	ed
Juncus trifidus	16	81.7	<0.001	2/6	**98/83**	0.122^1	168.4	g
Hieracium sect. *Alpina*	14	77.8	<0.001	0/0	**100/78**	1.014^1	312.7	f
Salix herbacea	17	74.6	<0.001	4/17	**96/78**	0.145^1	378.8	dd
Deschampsia flexuosa	23	68.6	0.002	18/44	**82/83**	0.430^3	213.5	g
Vaccinium uliginosum	9	50	0.001	0/0	**100/50**	0.222^1	144.8	dd
Betula nana	7	38.9	0.006	0/0	**100/39**	0.267^1	162.2	dd
Diphasium alpinum	5	27.8	0.038	0/0	**100/28**	–	126.3	ed
Phyllodoce caerulea	5	27.8	0.049	0/0	**100/28**	0.012^1	120.9	ed

full light, were collected from ten ramets at one site (typically the first time a species was encountered). They were kept in sealed plastic bags at ambient temperature for up to five days, then at 5°C for another few days. In the lab they were scanned, the areas estimated with ImageTool ver. 2.0. Only leaf laminas were used, excluding petioles or sheaths. Leaf samples were then air dried, and finally dried at 50°C for 24 h before weighing. Some of the less common species were missed in the leaf sampling (see Table 1). Only a few species had ripe seeds during the investigation period. Therefore, seed mass data from a different Swedish mountain area (Mount Helags) were used (Bruun unpubl.). Seeds were stored in paper envelopes at room temperature and ambient moisture for two-four weeks, and subsequently 10 randomly selected seeds were weighed individually on a Mettler MT5 balance (nominal accuracy 0.001 mg). For convenience, the term "seed" will be used throughout to encompass also achenes and similar small indehiscent fruits. For a few species, data on seed mass were retrieved from literature sources (see Table 1).

Information about growth form (dwarf shrub, graminoid, and forb), leaf longevity, plant height (mean of minimum and maximum), and elevation of highest occurrence in the Scandes mountains was retrieved from Lid (1985). Information on flowering phenology (mean between earliest and latest month) was obtained from Mossberg et al. (1994). Data on the type of clonal propagation was retrieved from the database CloPla1 (Klimeš et al. 1997), and re-categorised into a binary variable ("rhizomatousness") as long (>10 cm) and short stolons/rhizomes. Information on species' distribution was obtained at three geographic scales. The number of mapping districts (more or less corresponding to countries) from which the species was known in Flora Europaea (Tutin et al. 1964–1980) was counted. From an on-going flora survey (Jonsson pers. comm.) information about the number of 5×5 km quadrates in which the species are known to occur was obtained from two nested geographical regions in which the investigation area is embedded, one smaller (Sorsele parish, 7493 km^2) and one larger (Västerbotten province, 59 194 km^2). Nomenclature follows Flora Europaea (Tutin et al. 1964–1980).

Data analysis

The difference in total species number, and in the number of dwarf shrub, graminoid and forb species separately, between den and reference plots was tested by sign tests (Sokal and Rohlf 1995). The question whether any plant species seem to prefer or avoid the fox dens was investigated by Indicator Species Analysis (Dufrêne and Legendre 1997) with den/reference plot as a binary classification. To answer the question if mean SLA was higher and/or seed weight was lower on den plots as compared to reference plots, weighted averages (species frequencies as weights) for each plot were compared and tested by paired-sample t-test (one-tailed). Finally, a stepwise discriminant analysis was used to model which species traits best explained the distinction between indicator species for den and reference plots (two-tailed test).

Results

Considerable differences in vegetation composition between den and reference plots were found. Little difference in the vegetation in relation to time since last habitation of dens (1–14 yr) was found, and it was orders of magnitude smaller than the difference between den and reference plots (data not shown). Therefore, the aspect of den succession after fox abandonment was not considered any further.

The total species richness was higher on the reference plots than on the den plots, on average by 3.5 species (Table 2). The same was the case for dwarf shrubs, whereas no significant difference was detected for graminoids or forbs (Table 2).

Of the 51 species, 9 were significant indicators of fox den vegetation, and 11 were significant indicators of the reference vegetation (Table 1). Despite the fact that only dwarf shrubs showed a consistently higher species richness on reference plots, all three growth forms were almost equally well represented among the indicator species. However, eight out of 11 indicator species for reference plots were dwarf shrubs, while all nine indicator species for dens were graminoids or forbs. Most species exhibited a strong difference between den and reference plots in both relative abundance (mean abundance in plots within the group over mean abundance in all plots) and relative frequency (number of inhabited plots within the group over the total number of inhabited plots). However, one species, *Carex bigelowii*, was present in all plots examined, but with significantly higher abundance (frequency in subplots) on den plots. The least common significant indicator species occurred in five plots. Excluding species with less than five occurrences, because they could not possibly be indicative of anything due to scarcity, ten species remained with occurrences roughly evenly distributed among den and reference plots. The most frequent of these apparently indifferent species were *Festuca ovina*, *Solidago virgaurea*, and *Trientalis europaea*.

A significantly higher weighted average of SLA was found on the den plots as compared to the reference plots (Fig. 1), both when tested over all species ($p<0.0001$) and when tested for significant indicator species only ($p<0.0001$). On the contrary, no significant difference in weighted average of seed mass was found, neither for all species ($p=0.058$) nor for the subset of significant indicators ($p=0.31$). The average seed mass was in fact higher on reference plots, but the variation around the mean was very large and overlapping with the range of mean seed mass for den plots (Fig. 1).

The species traits (including regional abundance) superior in discrimination between indicator species for den plots vs reference plots were the "rhizomatousness" and growth form (dwarf shrub vs forbs and graminoids) (Table 3), but a model based on SLA and growth form had exactly the same accuracy of prediction (not shown).

Table 2. The average total species number in den and reference plots ($n=18$ for each), as well as average numbers of dwarf shrubs, graminoids, and forbs. Differences are tested by sign tests.

	Dwarf shrubs	Graminoids	Forbs	Total
Fox den plot	0.8	5.3	4.7	10.8
Reference plot	5.3	4.7	4.3	14.3
p	<0.00001	0.16	0.18	0.012

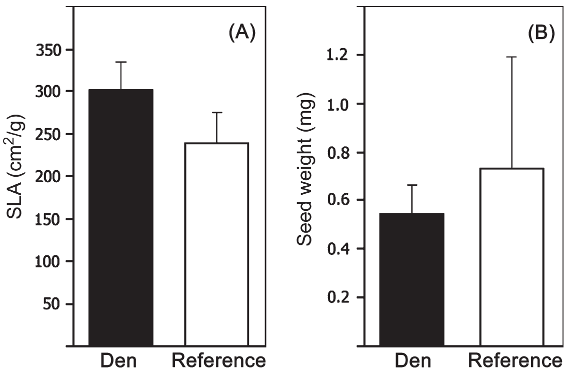

Fig. 1. Difference in (A) specific leaf area (SLA) and (B) seed weight (weighted averages over all species) between den and reference plots. SLA was significantly different ($p < 0.0001$; paired-sample t-test), whereas seed weight was not. Error bars show standard deviations.

The discriminant model was able to correctly classify (Wilk's lambda = 0.303; DF = 2; $p < 0.001$) all nine indicator species for den plots, and eight of the eleven indicator species for reference plots (Table 4). However, the three non-chamaephyte indicator species for reference plots were misclassified, i.e. *Deschampsia flexuosa*, *Hieracium* sect. *Alpina*, and *Juncus trifidus*.

Discussion

Several species discriminated between dens of the arctic fox and the surroundings. These species constituted a clear-cut selection based on functional plant traits. Tough-leafed dwarf-shrubs, evergreen or deciduous, found abundantly in the alpine heath (including the reference plots), were virtually absent from the fox dens. In contrast, soft-leafed forbs and graminoids were abundant on the dens. Most species occurring on the dens also occur elsewhere in the alpine landscape, mainly on other site subjected to physical disturbance (by frost or solifluction) or slight nutrient enrichment (by mobile soil-water), such as snow-bed margins. Only *Agrostis capillaris* is rare above the timberline, but relatively common on open ground in the lowland. The difference in species composition encountered in this study is much larger than that found previously in Alaska and Greenland. Anthony (1996) found only one graminoid (*Carex rariflora*) to occur more frequently and one dwarf shrub (*Empetrum nigrum* ssp. *hermaphroditum*) to occur less frequently on dens than in reference plots. Nielsen et al. (1994) found one dwarf shrub (*Salix glauca*), two forbs (*Stellaria longipes* and *Equisetum arvense*), and one graminoid (*Poa arctica*) to occur more frequently on dens than in the surroundings, and further one forb (*Polygonum viviparum*) to occur less frequently. Thus, it seems that the pool of species favoured by nutrient enrichment and disturbance is larger in the Scandes Mountains than in the Arctic. This could be attributed to a larger influx of propagules of species mainly inhabiting habitats below the timberline. However, the mentioned studies recorded vegetation composition by methods quite different from that employed here, and the results are thus not directly comparable.

Table 3. Stepwise discriminant analysis for separation of den and reference indicator species in terms of their functional attributes. Only significant attributes are shown.

Step	Variable	F	DF	p
1	Dwarf shrub	21.6	18	<0.001
2	Rhizomatousness	19.6	17	<0.001

Abundance-weighted seed mass did not differ between species on vs off dens, whereas abundance-weighted SLA did. Based on our initial hypothesis, we therefore conclude that nutrient enrichment of the dens via scats, urine and carcasses (which were observed frequently in the field) is the main factor responsible for the difference in species composition of the vegetation. The productivity of the low-alpine matrix vegetation, which was represented by the reference plots, is likely to be highly nutrient-limited (Sonesson and Callaghan 1991, Molau and Alatalo 1998), whereas some soil disturbance due to frost is likely to be ubiquitous (Sigafoos 1952, Jonasson and Sköld 1983). Therefore, the behaviour of the arctic fox, which involves both nutrient enrichment and disturbance, has its main effect trough nutrient enrichment. The difference in nutrient availability between den and matrix vegetation may have been amplified by herbivory leading to enhanced nutrient cycling, as live lemmings or lemming droppings were observed at several dens, and reindeer droppings on all dens.

The mechanism for the shift in dominating growth form, from dwarf shrubs with low SLA to graminoids with high SLA, is thought to take place via a reversal of competitive hierarchies with nutrient availability. Low SLA is associated with low photosynthetic capacity, low leaf nitrogen concentration, and long leaf life-span (Karlsson 1992, Reich et al. 1997), and SLA is strongly correlated with potential relative growth rate (Westoby 1998). Hence, dwarf shrubs should be competitively superior in the nitrogen-limited alpine heath, but inferior on the more nitrogen-rich den soil.

Table 4. Separation of the den and reference indicator species according to the discriminant function, the number of species in each group, and the classification error in absolute number of species and in percentages. The model was significant overall (Wilk's lambda = 0.303; $p < 0.001$).

		Predicted group	
	No. spec.	Fox den	Reference
Fox den plot	9	9 (100%)	0 (0%)
Reference plot	11	3 (27%)	8 (73%)

In spite of the support for nutrient enrichment as the main cause for the peculiar vegetation on fox dens, disturbance may play a role as well. Nutrient enrichment and disturbance may in fact pull in the same direction. For a number of reasons, the creeping dwarf shrubs may be more sensitive to both soil disturbance and plant tissue destruction than graminoids and perhaps forbs. If the photosynthetic tissue is destroyed by disturbance, the return on investment is much lower than expected, and especially evergreen dwarf shrubs will suffer relatively high losses. Furthermore, all of the dwarf shrub species found tended also to be rhizomatous or stoloniferous. Although all species found were clonal to some extent, the indicator species for reference plots generally had longer rhizomes or stolons than those for den plots. Low SLA alone probably indicates comparatively slow regrowth of rhizomes or stolons destroyed by disturbance. We do not have data for differences in the mechanical properties of rhizomes/stolons of dwarf shrubs vs forbs and grasses, but Jonasson and Callaghan (1992) found that roots of graminoids tolerated a significantly higher breaking strain (a measure of how much a root is deformed by stretching) and a much higher breaking stress before they broke, than did roots of forbs and dwarf shrubs among species from frost heaved ground in the northern Scandes. In addition, soil disturbance by the arctic fox is probably changing abiotic conditions in the alpine heath in several ways apart from increasing nutrient availability (Tardiff and Stanford 1998), e.g. increased soil pH and temperature (Smith et al. 1992).

Why were the graminoids *Deschampsia flexuosa* and *Juncus trifidus*, and the forb *Hieracium* sect. *Alpina* behaving contrary to the expected pattern? *Juncus trifidus* had the lowest SLA value among the graminoids, and it is probably too slow-growing to keep up with the more competitive grasses in the den vegetation. Both *Juncus trifidus* and *Hieracium* sect. *Alpina* were found to avoid frost-heaved soil by Jonasson and Sköld (1983). Nevertheless, the behaviour of these species indicates that one or more important functional traits have not been identified by this study.

Our initial hypothesis regarding seed mass was based on the well-established trade-off between seed mass and seed number given equal reproductive effort (Harper et al. 1970). However, this trade-off may not be particularly strong, especially not the range between 0.1 and 3 mg seed mass (Shipley and Dion 1992). Thus, considerable unpredicted variation in seed number per ramet, and consequently ability to recruit at scattered soil disturbances, must be expected. This may have reduced the probability of finding support for our initial hypothesis on seed mass and disturbance. Our field observations indicated that *Cerastium alpinum* and *Stellaria borealis* were often found on rather fresh soil heaps dug up by arctic foxes. However, the design of our investigation does not let us distinguish between patches with different disturbance intensity within the den plots.

Our estimate of the difference in species composition and trait distribution is likely to be conservative. Firstly, bryophytes and lichens were not included. Lichens constituted a large proportion of the visual vegetation cover on reference plots, but were hardly observed on den plots. Secondly, the proximity of den and reference plots makes floristic similarity due to propagule flow (the "spatial mass effect" of Shmida and Ellner 1984) between the den and reference areas likely, but was necessary in order to minimise confounding effects. Thirdly, we assumed species' traits to have constant values. Previous studies have shown that intraspecific variation in SLA is likely go in the same direction as interspecific variation in the same trait (Kudo et al. 1999, 2001), albeit an order of magnitude smaller. Analysis of traits of all species from den and reference plots separately would thus be likely to increase differences. Our field impression was that single ramets of many species occurring on both den and reference plots, e.g. *Carex bigelowii*, were taller and sturdier on than off fox dens.

The described effect of the arctic fox on the vegetation on its dens is an example of physical ecosystem engineering (Jones et al. 1994, 1997). This effect is imposed on a tiny fraction of the entire landscape. However, since the suite of species inhabiting fox dens is almost completely different from the dominant species in the matrix, landscape-scale species richness is maintained, at least in part, by the arctic fox. In other words, fox dens seem to provide habitat space for relatively short-lived and nutrient demanding species in an ecosystem otherwise dominated by long-lived ericaceous dwarf-shrubs, a phenomenon reported from both similar (Doak and Loso 2003) and different ecosystems (Dean and Milton 1991)

In conclusion, the effect of nutrient enrichment, and less so disturbance, creates structurally and compositionally very distinct vegetation on the dens of the arctic fox, although most species occurring on the dens also occur elsewhere in the alpine landscape.

Acknowledgements – The research was done within the project MountainMISTRA supported by MISTRA – the Swedish Foundation for Strategic Environmental Research.

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