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Nested communities of alpine plants on isolated mountains: relative importance of colonization and extinction

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Abstract

Aim This paper seeks to investigate whether alpine floras on isolated mountains in boreal forest show nestedness, and, if that is the case, to determine whether selective extinction or colonization is the likely cause of the observed patterns.

Location Isolated mountains in the boreal coniferous forests of northern Sweden (province of Norrbotten, *c.* 66°N; 18°E). The timberline in the region probably has been 300–400 m above the present some thousands of years before present, potentially covering these mountains.

Methods A data matrix of twenty-seven alpine plant species on twenty-seven isolated mountains was subjected to nested subsets analysis. Extinction probability was assumed to increase with decreasing area, and colonization probability was assumed to decrease with increasing isolation. By sorting the data matrix by these factors and sequentially computing the degree of nestedness, we were able to determine whether the alpine floras were structured mainly by selective extinction or mainly by differential colonization.

Results When ordered by decreasing area the data matrix was significantly more nested than random, but that was not the case when ordered by decreasing isolation. Ordering by maximum altitude also produced significant nestedness.

Main conclusions Contrary to the conventional view that isolated mountains were completely covered with boreal forest some thousands of years ago, the nestedness patterns of alpine plants indicate that many of them survived the forest period on the isolated mountains, probably on cliffs and slopes too steep for the formation of closed forest.

Keywords

Nestedness, palaeoecology, relaxation, Scandes Mountains, species richness, timberline.

INTRODUCTION

Assemblages of species inhabiting a set of islands, real or virtual, are said to be nested when the species in relatively depauperate islands constitute subsets of the species present in richer islands. Under perfect nestedness, each island contains a proper subset of the species assemblages found on richer islands (Atmar & Patterson, 1993). Few data matrices on observed species occurrences on (habitat) islands show perfect nestedness, but most data matrices show some, and

often rather strong, nested subset patterns (Wright & Reeves, 1992; Cook & Quinn, 1995; Wright *et al.*, 1998).

Nested subset patterns must ultimately result from selective extinction, selective colonization, or both. It follows directly from MacArthur & Wilson's (1963, 1967) equilibrium theory that extinction probability increases with decreasing area, and that colonization probability decreases with increasing isolation. Therefore, the approach taken here is to substitute the difficult-to-observe processes of extinction and colonization by the more easily observed area and isolation of the habitat patches. While selective extinction and/or selective colonization must be the ultimate causes of nestedness, it may be significantly influenced by other factors, e.g. nested habitat characteristics (Cook & Quinn,

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1995; Honnay *et al.*, 1999) and facilitated succession (Worthen & Rohde, 1996).

In northern Sweden, the vast boreal forest lie as a broad belt between the Scandes Mountains and the Baltic Sea. Scattered in the forest belt, low mountains protrude through the forest. As habitats for alpine plant species, these mountains are isolated from the coherent mountain range. They may be seen as remnants of the extensive tundra covering the entire Scandinavian Peninsula after the Weichselian glaciation. However, the timberline probably has been 300–400 m above the present some thousands of years before present (Barnekow & Sandgren, 2001), and the isolated mountains may thus have been covered entirely by boreal forest.

The aim of the present study is to investigate whether the floras of alpine plant species on isolated mountains are exhibiting nested subset patterns, and, if that is the case, to determine whether selective extinction or colonization is the likely cause of the observed patterns.

MATERIALS AND METHODS

Study area

The area of investigation is situated in northern Sweden (*c.* 66°N; 18°E) in the province of Norrbotten. The area is relatively level (400–500 m a.s.l), traversed by the deep Skellefte river valley with the great lakes, Hornavan, Uddjaure and Storavan. Scattered throughout the area are isolated mountains rising 300–400 m above the plateau land (Fig. 1). Geologically, they are residuals from the erosion of a previous stratum. The bedrock is predominantly granite and other acidic rocks. Basic volcanic rocks have scattered occurrences. The distance from the isolated mountains to the eastern extensions of the coherent alpine area is 50–100 km (Fig. 1).

The climate is cold temperate, with a January mean of −13 °C and a July mean of +14 °C in the town of Arjeplog. The mean annual precipitation is 500–600 mm, with a summer maximum. The climate is generally correlated with altitude, but strongly modified by local topography. During the spring, the snow cover melts earlier in the isolated mountains than in the coherent alpine area. Snow patches may persist until late July providing for ephemeral streams. Persistent brooks are absent from the isolated mountains because of their small catchment areas. The timberline is usually formed by mountain birch (*Betula pubescens* ssp. *tortuosa*) and rarely by scots pine (*Pinus sylvestris*). The isolated mountains are regularly grazed by reindeer during summer time. These are mostly domestic forest reindeer escaping insect harassment on warm summer days by ascending from the forest preferred for grazing to the more windy alpine areas.

The altitude of the isolated mountains ranges between 710 and 856 m a.s.l. The present day timberline lies between 575 and 700 m a.s.l., higher at south-facing slopes than at north-facing. Its situation is determined by an interaction of climate, local topography and reindeer grazing in combination (Oksanen *et al.*, 1995; Hofgaard, 1997).
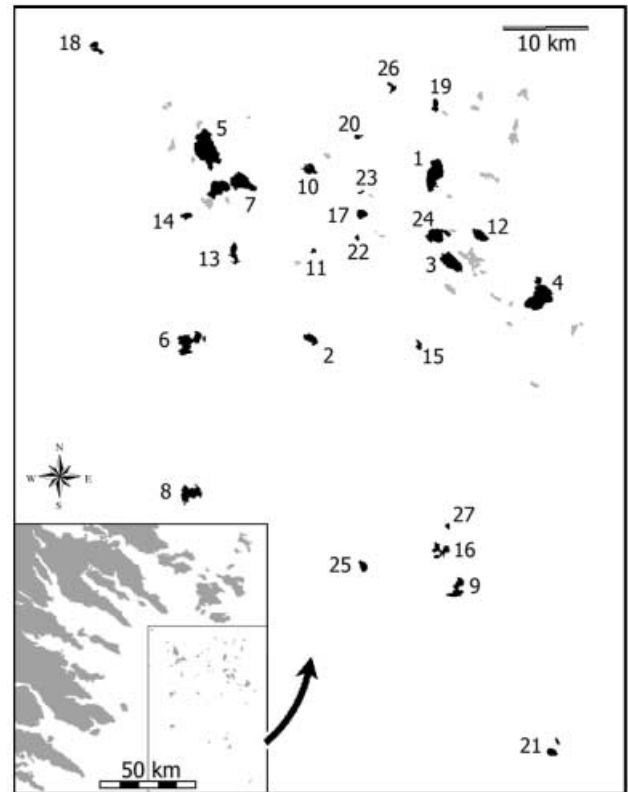
Figure 1 The spatial distribution of the studied (black) and other (grey) isolated mountains. Numbers refer to Tables 1 and 2. Inset is the situation of the study area in relation to the coherent alpine area in the Scandes Mountains.

According to megafossil studies (Kullman & Kjällgren, 2000), scots pine attained its highest upper limit of occurrence in the northern Scandes, about 500 m above the present, in the early Holocene (10,700 cal BP). On the contrary, the limit of mountain birch continued to increase until 3200 cal BP, and then decreased to its present level in the late Holocene (Barnekow & Sandgren, 2001). At its maximum it was *c.* 300–400 m above the present. No detailed knowledge is available for the isolated mountains, but it may be that all of them were covered by forest during the maximum. However, the timberline is to some extent governed by local topography of the isolated mountains. They often have steep sides towards the forest, sometimes too steep to hold a soil cover.

Data retrieval

The occurrences of alpine plant species on the isolated mountains (Table 2) were investigated by Wistrand (1962). He defined alpine species as those with their main distribution above the timberline, and for which a reduction in abundance is noticeable just below that limit. Many of these may occur more or less frequently in the subalpine mountain birch forest.

Polygons representing alpine area were extracted from a digital land cover map (Lantmäteriet, 1 : 50,000). In a Geographical Information System environment (ArcView 3.0a; ESRI, Redlands, CA) the areas of the isolated mountains were estimated, and also the distances to other alpine areas. The nearest edge distance from each isolated mountain to all other isolated mountains (whether investigated or not) and to the coherent mountain range was estimated using the script DistByID written by Jeff Jenness. Isolation was computed using a slightly modified version of the formula proposed by Hanski *et al.* (1994):

$$I_i = -\left[\sum_j^m \exp(-d_{ij}) \times \log_e(A_j)\right] \quad (1)$$

where d_{ij} is edge distance (km) from the focal mountain i to mountains j to m, and A_j is alpine area (ha). Both archipelago-internal (from other isolated mountains) and external isolation (from the coherent mountain range) were computed. The reason for the modification of the formula for isolation was the difference between one-species metapopulation models – for which the formula was written – and species richness models. It is reasonable to expect a bending-off relationship between area and species richness (Arrhenius, 1921; Rosenzweig, 1995). Indeed, a linear regression of species richness on log area had a much better fit than one on untransformed area.

The maximum altitude of each mountain was read from maps (Lantmäteriet, 1 : 50,000). The intercorrelation among the geographical variables was explored by linear correlation (Pearson's product moment). The attributes of the twenty-seven isolated mountains are presented in Table 1.

Measurement of nestedness

Nestedness was estimated by three different metrics, the number of 'gaps' (Patterson & Atmar, 1986; Lomolino, 1996), 'discrepancies' (Brualdi & Sanderson, 1999; Jonsson, 2001) and the matrix temperature (Atmar & Patterson, 1993). Matrix temperature, T, a concept derived from thermodynamics, is defined as the percentage actual total unexpectedness in relation to the maximum total unexpectedness. The presence of the most ubiquitous species in the richest island is considered most expected, and likewise the presence of the rarest species in the poorest island is considered least expected. Therefore, unexpectedness is measured along a line running parallel to the skew diagonal. Total unexpectedness is the sum of local unexpectedness normalized over both islands and species to make matrix temperatures comparable among matrices of different size and fill (see Atmar & Patterson, 1993 for details).

Table 1 The attributes of the twenty-seven isolated mountains in northern Sweden. Isolation was estimated in arbitrary units and is given as mere rank

S. no.	Names of isolated mountains	Alpine area (ha)	Altitude (m a.s.l.)	Internal isolation	External isolation
1	Bårggo	43.17	856	7	8
2	Gáldesbuovdda	10.55	800	17	20
3	Lulep Tjåhkålis	29.67	784	3	19
4	Stor-Ståkke	55.21	787	6	21
5	Allebuovdda	74.18	784	11	10
6	Áhkális	33.75	827	2	7
7	Nuorttabuovdda-Årjelbuovdda	63.91	805	1	6
8	Uljabuouda	24.19	784	12	26
9	Lulep Stårbatjvárre	16.45	775	13	11
10	Hássávárre	11.15	745	26	18
11	Måffe	1.88	780	8	14
12	Nammatis	13.89	789	15	4
13	Lulep Iksják	11.21	801	16	9
14	Alep Iksják	5.75	778	5	16
15	Tjuorre	3.65	743	25	22
16	Jellep Stårbatjvárre	10.54	720	27	5
17	Båhttsábuovdda	8.35	723	19	2
18	Árdnasvárre	7.77	786	10	13
19	Gállábuovdda	6.83	780	9	3
20	Ajlesvárre	2.52	745	14	24
21	Tjipko-Tjuorre	8.51	740	21	12
22	Tjähpsåjvve-Svartberget	1.73	741	18	27
23	Såmmarvárre	1.10	748	22	17
24	Alep Tjåhkålis	25.18	782	4	15
25	Välbmabuolda	6.79	710	20	23
26	Suhpevárre	4.53	715	24	25
27	Kuottavárre	1.96	730	23	1

The method of Patterson & Atmar (1986) counts down through each species column (see Fig. 1) the number of absences followed by a presence, the so called gaps or 'errors'. Given perfect nestedness this number is zero. The rows of the matrix, representing sites, were ordered by species richness, site area and isolation, respectively (Lomolino, 1996). The number of gaps in the ordered matrix was then compared with the mean number of deviances in 9999 matrices where the variable of interest, e.g. area, was assigned to sites at random. The deviance from perfect nestedness was assessed in units of standard deviation of the mean number of errors in the randomized matrices. In the case of species richness, several mountains had the same value. Groups with tied values were therefore ordered internally by decreasing area before the number of gaps was estimated.

The method of Brualdi & Sanderson (1999) counts 'discrepancies', i.e. in a matrix ordered as above the number of occurrences that need to be shifted to the left or upwards to obtain perfect nestedness. The deviance from perfect nestedness was assessed by the RANDNEST null model (Jonsson, 2001) with 100 randomizations, and expressed in units of standard deviation of the mean number of 'discrepancies' in the randomized matrices.

The values of T were computed using the Nestedness Temperature Calculator (Atmar & Patterson, 1995) and tested for deviation from randomness under a null model of equiprobable occurrences (R00 of Wright et al., 1998). Nomenclature follows Flora Europaea (Tutin et al., 1964–80).

RESULTS

Log_e of alpine area of the isolated mountains was strongly positively correlated with log_e of the maximum altitude ($r = 0.755$; $P < 0.0001$) and negatively with internal isolation ($r = -0.879$; $P < 0.0001$). From this also follows a strong negative correlation between log_e altitude and internal isolation ($r = -0.771$; $P < 0.0001$). External isolation was not correlated with the other variables.

The data matrix exhibited quite strong nestedness. The matrix temperature was 19.12°, which is highly significant under the R00 null model ($P < 0.001$). The number of 'discrepancies' was forty-eight, which was 4.88 standard deviation units from the mean of 100 randomized matrices, and highly significant under the RANDNEST null model ($P < 0.001$). Using Lomolino's method, the richness-ordered matrix yielded significantly stronger nestedness than expected under randomness (Table 3). Sorting the data matrix by area and by altitude produced significantly nested patterns, whereas sorting by isolation did not (Table 3). This indicates that species richness patterns are best explained as a result of selective extinction rather than differential colonization.

DISCUSSION

The richness of alpine vascular plant species on isolated mountains in northern Sweden showed rather strong nested subset patterns. This was independently shown by three contrasting methods to assess the strength of nestedness. A pattern similar to the present was found by Patterson & Atmar (1986) for montane rodents on 'sky islands' in the Great Basin of North America. These authors concluded that the montane rodent species had extended their distribution downwards during the last glaciation resulting in more coherent ranges, and that selective extinction had occurred as species retracted into smaller and more isolated mountain peak ranges. However, they did not test if differential colonization could be responsible for the observed pattern.

The nested subset patterns of alpine vascular plant species on isolated mountains in northern Sweden seem to be governed mainly by extinction. This means that alpine plant species probably survived the mid-Holocene forest period in situ. This observation does not conform well to the commonly held view that the isolated mountains were completely covered with boreal forest some thousands of years ago. The vertical extension from timberline to the summit of all investigated isolated mountains is much smaller than the mid-Holocene limit 300–400 m above the present as indicated by Barnekow & Sandgren (2001).

Alpine species can to a certain extent live in the mountain birch forest that may have covered some of the isolated mountains in the mid-Holocene. They may also occur elsewhere, e.g. scree slopes (Wistrand, 1981), and along brooks and rivers (Heikkinen & Neuvonen, 1997; Bruun et al., in press). Alpine species may thus have survived the mid-Holocene forest period predominantly in slopes too steep to support trees or at least closed forest. Of the species in Table 2, at least Lychnis alpina, Cerastium alpinum, Carex atrata and Saxifraga nivalis are known to occur on cliffs and scree slopes, both in fringes of the Scandes Mountains and as outposts in the boreal forests of the studied region (Lundqvist, 1968). In their ranges above the timberline, most of the alpine species in Table 2 usually occur in quite dry sites and rather sparse vegetation cover. It is, however, not possible to say whether this is attributable to present-day environment (isolated mountains having mostly dry soils) or to species originating from steep, and thus excessively drained, slopes.

The alternative hypothesis, that selective immigration was the main responsible factor behind the nested subset patterns, was not supported, although sorting the incidence matrix by internal isolation only produced a few more 'gaps' than did sorting by area or altitude (Table 3). However, if the nestedness were created by immigration, we would expect immigration from the Scandes Mountains 'mainland' 50–100 km away to be more important than migration among the isolated mountains up to 90 km apart, and therefore external isolation to be more important than internal. That was clearly not the case. Still, we do not want to exclude completely that immigration has contributed to the observed pattern, just to a lesser degree than extinction. Everything else being equal, larger mountains have a higher probability of being hit by plant propagules, and larger mountains may disproportionately attract seed dispersal vectors such as birds or mammals, in particular reindeer.

Table 2 The data matrix of twenty-seven alpine species on twenty-seven isolated mountains. The matrix is ordered by decreasing species richness of mountains, and by decreasing frequency of species. Species names are abbreviated as follows: **Lois pro**, *Loiseleuria procumbens*; **Diph alp**, *Diphasium alpinum*; **Arct alp**, *Arctostaphylos alpinus*; **Junc tri**, *Juncus trifidus*; **Phyl cae**, *Phyllodoce caerulea*; **Sali her**, *Salix herbacea*; **Lz spica**, *Luzula spicata*; **Hier Alp**, *Hieracium alpinum*; **Diap lap**, *Diapensia lapponica*; **Epil ana**, *Epilobium anagallidifolium*; **Athy dis**, *Athyrium distentifolium*; **Cx bigel**, *Carex bigelowii*; **Omal sup**, *Omalotheca supina*; **Pedi lap**, *Pedicularis lapponica*; **Sibb pro**, *Sibbaldia procumbens*; **Lych alp**, *Lychnis alpina*; **Lz arcua**, *Luzula arcuata*; **Ante alp**, *Antennaria alpina*; **Card bel**, *Cardamine bellidifolia*; **Cera alp**, *Cerastium alpinum*; **Cass hyp**, *Cassiope hypnoides*; **Cx atrat**, *Carex atrata*; **Cx lache**, *Carex lachenalii*; **Oxyr dig**, *Oxyria digyna*; **Saxi niv**, *Saxifraga nivalis*; **Tris spi**, *Trisetum spicatum*; **Vahl atr**, *Vahlodea atropurpurea*

S. No	Names isolated mountains	Lois pro	Diph alp	Arct alp	Junc tri	Phyl cae	Sali her	Lz spica	Hier Alp	Diap lap	Epil ana	Athy dis	Cx bigel	Omal sup	Pedi lap	Sibb pro	Lych alp	Lz arcua	Ante alp	Card bel	Cera alp	Cass hyp	Cx atrat	Cx lache	Oxyr dig	Saxi niv	Tris spi	Vahl atr	
1	Bårggo	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1		1				1					18
2	Gáldesbuovdda	1	1	1		1	1	1	1	1			1	1	1	1	1		1		1		1		1				17
3	Lulep Tjåhkålis	1	1	1		1	1	1	1	1			1	1	1	1			1	1						1	1		16
4	Stor-Ståkke	1	1	1	1		1	1	1		1	1	1	1	1	1						1							14
5	Allebuovdda	1	1	1	1		1	1	1		1	1	1	1	1	1													13
6	Áhkális	1	1	1	1		1	1	1	1			1	1	1	1		1											13
7	Nuorttabuovdda-Árjelbuovdda	1	1	1	1		1	1	1		1	1		1	1													1	12
8	Uljabuouda	1	1	1	1		1	1	1		1	1	1																10
9	Lulep Stårbatjvárre	1	1	1	1	1		1	1	1							1				1								10
10	Hássávárre	1	1	1	1	1		1	1		1	1	1																10
11	Måffe	1	1	1	1	1		1	1		1	1						1											10
12	Nammatis	1	1	1	1	1		1	1		1	1																	9
13	Lulep Iksjåk	1	1	1	1	1		1	1		1	1																	9
14	Alep Iksjåk	1	1	1	1	1	1		1	1	1																		9
15	Tjuorre	1	1	1	1	1	1		1	1	1																		9
16	Jellep Stårbatjvárre	1	1	1	1	1	1		1	1																			8
17	Båhtsåbuovdda	1	1	1	1	1	1		1	1																			8
18	Årdnasvárre	1	1	1	1	1	1	1		1																			8
19	Gållåbuovdda	1	1	1	1	1	1	1		1																			8
20	Ajlesvárre	1	1	1	1	1	1	1		1																			8
21	Tjipko-Tjuorre	1	1	1	1	1	1	1																					7
22	Tjåhpsåjvve-Svartberget	1	1	1	1	1	1	1																					7
23	Sånmarvárre	1	1	1	1	1	1	1																					7
24	Alep Tjåhkålis	1	1	1	1	1	1																						6
25	Vålbmabuolda	1	1	1	1	1	1																						6
26	Sulhpevárre	1	1	1	1	1																							5
27	Kuottavárre	1	1	1	1	1																							5
		27	27	26	25	22	20	19	17	12	11	9	8	7	7	6	3	3	2	2	2	1	1	1	1	1	1	1	

Table 3 Deviation from randomness when the data matrix is ordered by species richness, patch area and isolation, using Lomolino's method. The deviation (SD units) is given as the difference between the mean number of errors in 9999 randomized matrices and the observed number of errors, divided by the standard deviation over randomizations. The *P*-values are two-sided

	Species richness	Alpine area	Altitude	Internal isolation	External isolation
No. errors	61	70	69	72	75
SD units	3.91	2.20	2.39	1.82	1.24
P-value	0.0002	0.021	0.014	0.052	0.127

Pollen stratigraphic data from the isolated mountains, or from lakes nearby, could potentially corroborate or contradict the interpretation of present-day patterns made here. Unfortunately, no such studies exist to our knowledge. The isolated mountains do neither have lakes nor permanent watercourses. Moreover, the alpine vegetation on isolated mountains has a very low pollen productivity compared with the coniferous boreal forest in which they are embedded (Birks & Birks, 2000). Therefore, they are likely to go undetected in regional pollen diagrams.

Altitude seems to be of equal importance as area. These two factors are to some extent dependent on each other – a higher peak usually also implies a larger alpine area, as shown by the correlation. Altitude may be interpreted as indicating a higher probability of alpine species survival during the forest period, or as indicating higher present-day habitat heterogeneity. However, the largest isolated mountains (Allebouvdda and Nuorttabuovdda-Årjelbuovdda) are comparatively low and with flat slopes. They also have disproportionately depauperate floras. Moreover, the species with fewest occurrences (Table 2), but not necessarily those contributing the least to nestedness, seem mainly to be species with a middle- to high-alpine main distribution, e.g. *Oxyria digyna*, *Trisetum spicatum* and *Vahlodea atropurpurea*.

In conclusion, alpine plant species probably survived the mid-Holocene forest period on the isolated mountains, especially those with high peaks and/or steep slopes.

ACKNOWLEDGMENTS

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BIOSKETCHES

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