Autosuccession in alpine vegetation: testing the concept on an altitudinal bioclimatic gradient, Jotunheimen, southern Norway

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ABSTRACT

Specific tests of autosuccession (equivalent to non-replacement change in species composition) are made, in which pioneer communities on roadside verges and areas of patterned ground disturbed by cryoturbation are compared with mature communities on a bioclimatic gradient from sub-alpine woodland (850 m a.s.l) to high-alpine fjellfield (2200 m a.s.l). Autosuccession is quantified for the first time using community similarity coefficients and indices of pioneer persistence and importance, which measure nominal- or ordinal-scale differences in species composition between 65 paired pioneer and mature communities. Linear relationships to altitude, with coefficient and index values of ~90–100% in the upper part of the high-alpine belt to ~10–20% in the sub-alpine zone, indicate a continuum from autosuccession to relay succession (the latter characterised by high species turnover and replacement change). Values based on ordinal-scale data are generally ~10% lower than those based on nominal-scale data and use of pioneer sites from roadside verges result in a ~20% offset relative to pioneer sites from sorted circles (the latter comparison reflecting the effect of substrate differences). Autosuccession appears to be characteristic only at altitudes >2000 m a.s.l. in the upper high-alpine zone. Replacement change increases in importance as a constituent of mixed-mode succession through the conventional mid- and low-alpine belts. Spatial variation in the nature of primary succession along the bioclimatic gradient supports a geo-ecological model of succession with predominantly allogenic controls (climatic stress and high levels of substrate disturbance by cryoturbation) at high altitudes and increasing autogenic controls (biological interactions and substrate stability) at lower altitudes.

Key words: autosuccession, relay floristics, alpine vegetation, altitudinal zonation, community similarity coefficients, pioneer persistence index, plant succession models

1. Introduction

Autosuccession is one of the many conceptual models of succession that have been proposed to understand species composition during vegetation change (Connell and

Slatyer, 1977; Pickett et al., 1987; Glenn-Lewin et al., 1992; Matthews, 1992; Walker and del Moral, 2003; Gratzer et al., 2004; Keane et al., 2004; Cutler et al., 2008; Meiners et al., 2015). The term autosuccession was introduced by Cornelius H. Muller in the context of desert vegetation in the southwestern USA (Muller, 1940) and later applied by him to Scandinavian alpine vegetation (Muller, 1952). He defined autosuccession as succession in its simplest form: 'succession consisting of a single stage, in which the pioneer and climax species are the same' (Muller, 1952, p. 296). As such, it would appear to be an appropriate model in extreme or severe environments with a limited species pool.

Muller (1952) differentiated 'autosuccession' from 'secondary succession' in which seriously disturbed areas of vegetation consist wholly or in part of species belonging to a community that differs from the original. If, during vegetation change, one element of the original community depends on the prior establishment of another element of that community, he termed this 'selective autosuccession'. That is, the same species are involved in both the original community and the colonising community but the order in which they colonise differs systematically. 'Non-selective autosuccession' ('true autosuccession') contrasts with this in that there is no difference between the early colonising species and those that establish later. Based on qualitative observations of vegetation in northern Sweden that had been disturbed by frost action, wind erosion and turf removal, he concluded that secondary succession (characterised by species replacement) is exhibited by vegetation in the low-alpine belt and that autosuccession (sometimes selective) occurs in the mid-alpine belt, while non-selective autosuccession characterises the high-alpine belt.

Since then, research on autosuccession has been neglected, although it is similar to 'direct regeneration' or 'direct succession', terms introduced by Hanes (1971) and Whittaker and Levin (1977; see also Miles, 1987), respectively. Indeed, it is widely perceived as the fast recovery process that characterises secondary succession in Mediterranean-type vegetation immediately following fires (Trabaud, 1994; Rodrigo et al., 2004; Buhk et al.,2006). Direct regeneration and autosuccession are also seen as appropriate terms for secondary succession in the paramo of the high tropical Andes (Sarmiento et al., 2003) and the rapid recovery of various types of lowland tropical vegetation following hurricane damage or other disturbances (Vandermeer et al., 1995; Mueller-Dombois, 2008; Mueller-Dombois and Jacobi, 2016).

The term autosuccession has rarely been used in the context of primary succession (but see Longton, 1988; Grulke, 1995; Kappen and Schroeter, 2002). However, Matthews (1979, 1992) and Robbins and Matthews (2010) referred explicitly to the concept in accounting for the differences between primary successional pathways on glacier forelands in southern Norway. They concluded, in agreement with Muller's original work (Muller, 1952), that selective autosuccession occurs in the mid-alpine belt and that non-selective autosuccession may characterise the more severe environmental conditions of the high-alpine belt. In addition, Svoboda and Henry (1987) recognized two related types of primary succession – termed 'directional-nonreplacement succession' and 'nondirectional-nonreplacement succession' – which they regarded as characteristic of polar semideserts and polar deserts, respectively (see also Jones and Henry, 2003). In his review of successional models in the context of glacier forelands, Matthews (1992) pointed out that Svoboda and Henry's concepts are essentially equivalent to selective and non-selective autosuccession respectively, and linked all four concepts to the severity of the physical environment in a geo-ecological model of primary succession.

The aim of the present paper is to explore further the concept of autosuccession with three specific objectives:

(1) to quantify autosuccession for the first time in any environment;
(2) to test the concept rigorously in the context of primary succession along a bioclimatic altitudinal gradient in southern Norway extending from below the treeline in the subalpine zone to high-alpine fjellfield; and
(3) to assess the implications of the results and the relevance of autosuccession for geo-ecological models of vegetation succession.

2. Study sites

The study was carried out in the Galdhøpiggen massif of northeastern Jotunheimen centred on the plateau area of Juvflye (Fig. 1). Specific sites were located close to the road from Galdesanden in Bøverdalen to Juvvasshytta and, at higher altitudes, on the flanks of Galdhøe, one of the highest mountain peaks in southern Norway. A detailed (1:50,000) map of the plant communities in the area (NIJOS, 1991), enabled conventional altitudinal divisions of the mature vegetation to be defined relatively precisely as follows:

- Sub-alpine zone: ~850–1025 m a.s.l., mainly mountain birch (*Betula pubescens*) woodland mixed with areas of meadowland and stands of Scots pine (*Pinus sylvestris*). Tall herbs (e.g. monk's hood, *Aconitum septentrionale*), ferns (e.g. *Gymnocarpium dryopteris*) and dwarf shrubs (as in the low-alpine belt) dominate the understorey and gaps in the tree canopy.
- Low-alpine belt: above the tree line at ~1025–1350 m a.s.l., mainly dwarf-shrub heath. Dwarf birch (*Betula nana*), juniper (*Juniperus communis*) crowberry (*Empetrum hermaphroditum*), bilberry (*Vaccinium myrtillus*) and northern willow (*Salix glauca*) are typical dominant species. Numerous herbs (e.g. *Trientalis europea*, *Potentilla crantzii* and *Solidago virgaurea*) are present beneath the shrub canopy.
- Mid-alpine belt: ~1375–1600 m a.s.l., mainly grass- and lichen-heath and extensive areas of late-snowbed communities. The heaths are typically dominated by stiff sedge (*Carex bigelowii*), mat grass (*Nardus sticta*) and a variety of lichens (especially *Cetraria* spp. and *Cladonia* spp.); the late-snowbed communities by least willow (*Salix herbacea*). Other shrubs, e.g. *Empetrum hermaphroditum*, blue mountain heath (*Phyllodoce caerulea*), cowberry (*Vaccinium vitis-idaea*) and creeping azalea (*Loiseleuria procumbens*) occasionally occur in the lower part of the belt.
- High-alpine belt: ~1600–2200 m a.s.l., mainly boulder-rich fjellfield with a discontinuous vegetation cover and extensive semi-permanent snowbeds. A relatively small number of lichens (e.g. *Cetraria nivalis, Stereocaulon alpinum, Alectoria ochroleuca* and *Thamnolia vermicularis*), mosses (e.g. *Racomitrium canescens*), grasses and graminoids (e.g. *Poa alpina, Trisetum*

spicatum and *Luzula arcuata*), and forbs (e.g. *Saxifraga* spp. and *Ranunculus glacialis*) occur as isolated individuals or in small patches.

These altitudinal boundaries are relatively low on this generally north-facing aspect compared to other parts of Jotunheimen, where the tree line (sub-alpine/low-alpine transition) may rise above 1200 m a.s.l. and the lower and upper boundaries of the mid-alpine belt may be as high as ~1500 and 1800 m a.s.l., respectively (Moen, 1999). Examples of the alpine vegetation, and their landscape setting, are shown in Fig. 2A–C. Within each belt there is a mosaic of plant communities controlled largely by interactions between topography, the distribution of snow, microclimate and drainage conditions (Dahl, 1956, 1986; Gjærevoll, 1956; Moen, 1999; Löffler, 2003, 2007; Löffler and Finch, 2005). Although climate, particularly the thermal climate, is the main environmental control on the altitudinal zonation of the vegetation, the tree line and the subalpine zone are less easily defined due to the effects of human-induced disturbances, particularly forest clearance and grazing by cattle, sheep and goats. Furthermore, relatively small individuals of *Betula pubescens* growing up to about 1050 m a.s.l. indicate that trees may be currently invading the lowermost part of the low-alpine zone.

Mean annual air temperature (MAAT) at Juvvasshøe (1894 m) was –3.5 °C for the period AD 2000–2014 according to the Norwegian eKlima database (http://www.re3data.org/repository/r3d100011719), while 800–1000 mm is the estimated mean annual precipitation (MAP) for the Galdhøpiggan massif, including Juvflye (Isaksen et al., 2011). Furthermore, Ødegård et al. (1992) estimated the MAAT to be –2.6 °C at 1500 m and –6.4 °C at 2200 m a.s.l. Application of a temperature lapse rate of 0.6 °C per 100 m rise in altitude, suggests a MAAT of about +0.4 °C at 1025 m a.s.l. (the approximate height of the tree line) and +1.3 °C at 850 m a.s.l. (the lowest altitude investigated in this study).

These values of MAAT are consistent with the existence of permafrost in the higher parts of the study area, with an active layer thickness of ~1.5-2.5 m for central Juvflye, and a lower altitudinal limit of discontinuous permafrost at ~1450 m a.s.l. (Ødegård et al., 1992, 1996; Isaksen et al., 2002, 2011; Harris et al., 2009; Farbrot et al., 2009; Lilleøren et al., 2012; Ginås et al., 2017). Most of the high-alpine belt is therefore characterised by boulder field underlain by permafrost, with extensive areas of periglacial patterned ground (Washburn, 1956; Ballantyne, 2018; French, 2018). The patterned ground consists of sorted circles (typical diameters, 3–6 m) on relatively flat plateau areas, which merge into sorted stripes on gently sloping terrain (Ødegård et al., 1987, 1988; Winkler et al., 2016).

Regional deglaciation occurred in Jotunheimen during the Preboreal chronozone, at least ~10,000 years ago (Lie et al., 2004; Matthews and Dresser, 2008; Nesje, 2009; Velle et al., 2010; Stroeven et al., 2016). This left a substrate predominantly of till, which is derived from the local bedrock, pyroxene-granulite gneiss (Lutro and Tveten, 1996) in which the patterned ground developed rapidly and then stabilized by 8000-7000 years ago (Winkler et al., 2016). Stabilization of the patterned ground in this sense refers to the large clasts being wedged together in the troughs or gutters that surround the sorted circles (thus rendering them essentially relict landforms). Local glaciers appear to have melted away during the Holocene Thermal Maximum but regenerated during neoglaciation, certainly by about 6000 years ago (Matthews and Dresser, 2008), possibly earlier (Ødegård et al., 2017). Further glacier expansion occurred following climatic deterioration in the late Holocene, culminating in the Little Ice Age glacier maximum of the eighteenth century (Matthews, 2005; Matthews and Dresser, 2008; Matthews et al., 2014). However, despite lowering of the altitudinal limits of permafrost, there is no evidence to support reactivation of the patterned ground during late-Holocene climatic deterioration or the Little Ice Age (Winkler et al., 2016).

3. Methodology

3.1 Field sampling

Testing the autosuccession concept involved comparing pioneer vegetation with closely adjacent mature (‘climax’) vegetation at paired sites (representing dependent samples). The 65 site-pairs were located at 25 m altitudinal intervals along transects from 850 m a.s.l. to 2200 m a.s.l. (Fig. 1). Transects had a predominantly northerly aspect. However, a minority of site-pairs were located on southeasterly-facing slopes of Galdhøe and on the plateau area of Juvflye. An overlap of five site-pairs between transects ensured that the effect of this difference in slope aspect could be assessed.

At each site, quadrats were used to obtain a representative sample of the vegetation (based on the minimal area principle applied to the mature vegetation; Kent, 2012). Equivalent areas (4 m^2) were sampled from the pioneer vegetation and the closely adjacent mature vegetation in each site pair (e.g. Fig. 3A-D). However, the quadrat size used for the pioneer vegetation differed from that used for the mature vegetation (see below). Percentage cover of each species was estimated subjectively as the area of each quadrat occupied by the above-ground parts of each species on a scale of 0-100% at 5% intervals; with additional subdivision of the 0-5% interval to the nearest 1% and species occupying <1% recorded as 1%. Site cover values were obtained by cumulating the cover values of the individual quadrats.

The sampling design also took account of two different types of disturbed pioneer vegetation: that growing on the centres of sorted circles (Fig. 4A); and that colonising roadside verges (Fig. 4B). Possible effects of differences between these types of pioneer sites were investigated by comparing the vegetation at five locations of the two site types on the Juvflye transect where they occurred at the same altitude. Occasionally, sorted stripes were used where circles were not available at the requisite altitude. Relict sorted circles and stripes with disturbed centres (e.g. Fig. 2A) exist at altitudes above 1800 m while roadside verges exist below 1850 m a.s.l. The verges were constructed from material excavated locally when the road was asphalted in 2004: thus, they were 12–13 years old when the fieldwork for this study was carried out. In areas of pioneer vegetation, sixteen 0.5 m x 0.5 m quadrats were sampled from the vegetated fringe areas of disturbed patterned ground and/or roadside verges. Small quadrats were necessary because suitable pioneer areas were limited. Verges on the upslope side of the road were avoided as they tend to be fed and sometimes flooded by snow meltwater draining from the hillside and also sometimes receive eroded remnants of mature vegetation and soil from unstable areas upslope.

Most areas of mature vegetation and all sites below 1650 m a.s.l. were on areas without patterned ground (e.g. Fig. 2C). Above 1650 m some areas of mature vegetation were located on those parts of relict patterned ground with a continuous vegetation cover unaffected by disturbed centres (e.g. Fig. 2B). Four 1 m x 1 m quadrats were sampled at each of the mature vegetation sites. Well-drained areas exhibiting the greatest biomass were targeted. Quadrats of this size were small enough to fit both within particular patches of the shrub, graminoid and/or lichen mosaic and the vegetated centres of relict sorted circles. At the same time, 1 m^2 quadrats were large enough to include most of the species present locally while avoiding vegetated areas exhibiting any type of disturbance. The selection of well-drained sites ensured maximum compatibility with the pioneer sites from roadside verges and disturbed circle centres, both of which tend to be relatively well-drained habitats. Boggy areas of mature vegetation were therefore avoided.

3.2 Plant community similarity coefficients

The difference in species composition between the pioneer and mature communities at each pair of sites was measured using two related similarity coefficients. One of these coefficients (S_n) has been widely used in plant community analysis (Mueller-Dombois and Ellenberg, 1974; Jongman et al., 1995; Lepš and Šmilauer, 2003; Kent, 2012); the second coefficient used (S_o) is novel to this study. Both can be expressed as values between 0 and 1 or as percentages. Here, they are expressed as percentages: 100% indicating perfect similarity.

First, Sørensen’s similarity coefficient (S_n), equivalent to the Bray-Curtis similarity coefficient, was used to measure nominal-scale (qualitative) differences between each pair of sites based on the presence or absence of species:

$$S_n = 200c / (a + b) \qquad (1)$$

where, a is the number of species in the pioneer site, b is the number of species in the mature site, and c is the number of species common to both sites. Being based on presence/absence data, equation (1) takes no account of species abundance, gives equal weight to common and rare species, and is closest to measuring community similarity as originally conceived by Muller (1940, 1952) in his definition of autosuccession.

The second similarity coefficient is related to but different from the quantitative version of the Sørensen/Bray-Curtis coefficient (S_i), which uses interval-scale data rather than presence-absence data and measures quantitative community differences based on cover-value scores:

$$S_i = 200C / (A + B) \qquad (2)$$

where, A is the sum of the scores in the pioneer site, B is the sum of the scores in the mature site, and C is the sum of the lesser scores of the species common to both sites. Equation (2) is therefore overwhelmed by differences in species abundance between sparsely vegetated pioneer communities and the dense mature vegetation with consequent major down-weighting of rare species. Although the commonly used S_i coefficient is not used in this study, it is included here to clarify how it differs from the equivalent ordinal-scale similarity coefficient S_o, which we use instead. S_o measures rank-order differences in species composition based on cover values. Derived specifically for this study, this coefficient is based on similar principles to the other coefficients defined above:

$$S_o = 200\gamma / (\alpha + \beta) \qquad (3)$$

where, α is sum of the ranks in the pioneer site, β is the sum of the ranks in the mature site, and γ is the sum of the lesser ranks of the species common to both sites. Use of equation (3) produces a similarity coefficient that is intermediate in character between equations (1) and (2) in terms of the weighting given to species abundance: high cover scores have greater effect than in equation (1) while rare species are more effective than in equation (2). *So* is used in this paper to extend the analysis of autosuccession beyond the presence/absence of species (see discussion below).

3.3 Indices of pioneer species persistence and importance

Related to the similarity coefficients but measuring different aspects of the similarity between the pioneer and mature communities are the indices of pioneer persistence (*PP*) and pioneer importance (*PI*). These indices were first defined and used in the context of insect and anthropod succession based on nominal scale (presence and absence) data by Vater and Matthews (2015):

$$PP_n = 100c / a \qquad (4)$$

$$PI_n = 100c / b \qquad (5)$$

The PP_n index measures the proportion of the pioneer species that persist through time to form the mature successional stage, whereas the PI_n index measures the proportion of the species at the mature stage that comprise the persistent pioneer element. Both are directly relevant to the original concept of autosuccession and complement *Sn*.

Ordinal-scale equivalents of these indices are also defined and used in the present study as complementary to *So*:

$$PP_o = 100\gamma / \alpha \qquad (6)$$

$$PI_o = 100\gamma / \beta \qquad (7)$$

The PP_o and PI_o indices measure the extent to which the rank order of species is preserved during the transition from pioneer to mature stages. By taking more account of the abundance of species relative to the nominal-scale indices, these ordinal-scale indices are again used to broaden the analysis and further develop autosuccession concepts.

3.4 Analysis of altitudinal variation in coefficients and indices

Altitudinal variation in the values of the similarity coefficients and indices of pioneer persistence and importance was interrogated using direct graphical analysis in relation to the altitudinal gradient combined with statistical techniques of linear regression and correlation (Zar, 1974). In order to assess the validity of including data from different transects in the same analyses, pairwise comparison was carried out of sites with similar altitude on the overlapping portions of the northwest-facing Galdhøe transect (at 1925-2050 m a.s.l.) and the southeast-facing Juvflye transect (at 1750-1850 m a.s.l.), though the available five site-pairs represent a limited sample size. Similarly, the possible effect of differences in pioneer site type (i.e. use of roadside verges or sorted circle centres) was assessed by pairwise comparison of the two types of site where they occurred at the same altitude on the Juvflye transect (five site-pairs). Pairwise comparisons were tested using Student's t tests of dependent means (Matthews, 1991). Differences in the coefficients and indices between conventional altitudinal zones defined independently for the local area (NIJOS, 1991; see above) were tested graphically and statistically using 95% confidence intervals.

4. Results

Values of the two similarity coefficients and the four indices of pioneer persistence and importance on the two transects exhibit high variability between the 65 sites, which is strongly related to altitude and site type (Table 1).

4.1 Comparing different aspects and site types

In relation to the aspect comparisons, none of the similarity coefficients or the indices of pioneer persistence or importance differ significantly according to the Student's t test of dependent means, despite the number of species differing significantly (Table 2). In contrast, the pioneer site-type comparisons consistently result in statistically significant differences at various significance levels (Table 2).

In the light of these comparisons it was considered justifiable to include sites from different transects in the same analysis provided they were of the same site type. In contrast, different pioneer site types should not be included in the same analysis because there is a systematic difference of 20–23% between the site types for the nominal-scale coefficients and indices (S_n, PP_n and PI_n) and 27–31 % between site types using measures based on an ordinal scale (S_o, PP_o and PI_o). Results of further analyses reported below therefore use pioneer sites from either patterned ground (circle sites) or roadside verges (verge sites) but not both.

4.2 Altitudinal patterns in coefficients and indices

The nominal-scale similarity coefficient (S_n) varies from >90% at the highest altitude sites to <20% at the lowest altitudes, with a strong linear gradient of increasing similarity with altitude (Fig.5A). The correlation coefficients show that a significant proportion of the variability in S_n is explained by altitude (64% and 43% for the roadside-verge and sorted-circle sites, respectively). Indeed, S_n attains values of 100% at two sites above 2000 m a.s.l. whereas one site below the tree line at 875 m a.s.l. has a value of only 5%. The offset of at least 20% similarity between the gradients based on verges and circles is clearly seen in this figure: S_n values of ~50% characterise roadside-verge sites at 1800 m a.s.l. whereas sorted-circle sites at the same altitude attain values around 70%.

Large differences are also shown between the mean similarity values characteristic of contiguous conventional altitudinal zones or belts. Although these differences are not always statistically significant according to the degree of overlap exhibited by the confidence intervals shown graphically in Fig. 5A and detailed in Table 3, the difference between the sub-alpine zone and the low-alpine belt is particularly strong. Statistically significant differences are consistently shown between subadjacent zones (i.e. sub-alpine/mid-alpine and low-alpine/high-alpine) and between the sub-zones defining the top and bottom of the high-altitude belt.

Values of the ordinal-scale similarity coefficient (S_o) shown in Figure 5B are similar and of the order of 10% lower than those of S_n. However, as the altitudinal gradient of S_o is less steep and the correlation coefficients are somewhat weaker, mean values of the altitudinal zones are correspondingly lower and the differences between them are less clear.

The altitudinal gradients for the nominal-scale pioneer persistence index (PP_n; Fig. 5C) are very similar to those for the nominal-scale similarity index. Most of the species present in the high-altitude pioneer communities of sorted-circle sites (>70%) persist in the mature vegetation but the confidence intervals for the sub-zones are wider than for S_n, reflecting greater relative variability between sites. At roadside-verge sites in the high-alpine belt, about half of the pioneer species persist in the mature vegetation, but the proportion falls to 5-25% in the sub-alpine zone. Higher relative variability in the ordinal-scale pioneer persistence index (PP_o; Fig. 5D) is responsible for the absence of a statistically significant altitudinal gradient at the high-alpine sorted circle sites. At the roadside-verge sites, however, the altitudinal gradient is significant and similar to that of S_o.

Figs 5E and 5F show altitudinal variations in the nominal-scale and ordinal-scale pioneer importance indices, PI_n and PI_o, respectively. Both altitudinal gradients are statistically significant but PI_n gradients are consistently stronger than the PI_o gradients and PI_n values also tend to be greater. Thus, at roadside-verge sites, the ordinal-scale pioneer importance index varies from only ~30% in the high-alpine belt to ~15% in the sub-alpine zone. Consequently, differences between the zones/belts are less clearly separated by this index than by any other. This reflects large variations in cover values (and hence rank-order) in the mature communities of species that do not occur as pioneers.

5. Discussion

5.1 Autosuccession in the high-alpine zone

Autosuccession was conceived by Muller (1940, 1952) as a nominal-scale concept, which describes the situation where there is no difference in species composition between the pioneer community and the mature stage of succession. As such, autosuccession is directly quantified by the S_n coefficient and is characterised by values of 100%. As our data do not distinguish between early- and later-colonising pioneer species, we cannot separate non-selective autosuccession from selective autosuccession in which, by definition, some pioneers colonise before others.

Nevertheless, during selective autosuccession, S_n would tend towards 100% as the pioneer community itself develops. Values of S_n approximating to 100% therefore clearly demonstrate autosuccession, whether it is non-selective or selective.

Our results in Fig. 5A indicate that autosuccession occurs only at a limited number of sorted-circle sites in the upper part of the high-alpine belt (>2000 m a.s.l.) where S_n is consistently >90%. There, the species in our pioneer communities are the same as those characteristic of the mature communities, including *Cetraria nivalis, Stereocaulon alpinum, Alectoria ochroleuca, Thamnolia vermicularis, Racomitrium canescens, Luzula arcuata, Poa alpina, and Ranunculus glacialis*. At the sorted circle sites lower in the high-alpine belt values of S_n are closer to ~70%, which suggests appreciable differences between the species composition of the pioneer and mature communities and hence that the autosuccession concept is not applicable there. Similar values exhibited by the nominal-scale pioneer persistence (PP_n) and pioneer importance (PI_n) indices (Fig. 5C and 5E) support these conclusions. However, there are few if any pioneer colonisers that do not persist into the mature community and few if any species in the mature community that are not pioneers. Species do not fall consistently into either category due to the occurrence of scattered individuals in particular places often being a matter of chance.

Extending the analysis to the ordinal-scale coefficients and indices (Fig. 5B, 5D and 5F) demonstrates that not only species composition but also the rank-order of species importance tends to be preserved during succession at the sorted-circle sites in the high-alpine belt. Values of S_o, PP_o and PI_o at the sites in the upper part of high-alpine belt tend to be between 70% and 90% and, on average, are only 15-20% lower than those of the corresponding nominal-scale measures.

5.2 Substrate effects in the high-alpine zone

Significantly lower values for S_n (40-50%), S_o (30-40%) and the other indices at the roadside-verge sites compared with the sorted-circle sites at similar altitudes within the lower part of the high-alpine belt (Fig. 5) is incompatible with autosuccession. The main difference in species composition between the two pioneer site-types appears to be a richer flora on the verges, with forbs such as *Cerastium alpinum, Cardamine bellidifolia, Minuartia biflora, Silene acaulis, Draba* spp., *and Saxifraga* spp. occurring more commonly on the verges. Different pioneer communities from those characteristic of the circle sites must be accounted for by differences in the substrate under otherwise similar environmental conditions. The sorted circles have developed in till, which contains abundant silt-sized sedimentary particles as well as some clay, sand and larger clasts (Winkler et al., 2016). The fine particles are much in evidence in the disturbed centres of the sorted circles. In contrast, the roadside verges are constructed of well-sorted sand and gravel material, which tends to be better drained and less frost-susceptible than till (Ballantyne, 2018), and is deliberately used in road construction to preserve the road from destruction by ice-lense growth (Harris et al., 2018). Both sets of pioneer sites are subject to disturbance: the circle centres as a result of winter freezing and summer thawing of near-surface groundwater in the active layer; and the verges by gravel movement and dust additions from passing traffic in the summer months. Circle centres are disturbed by frost heave (Rempel, 2011) and cryoturbation (Bockheim, 2007): the minority of sites involving sorted stripes rather than sorted circles are additionally disturbed by downslope solifluction (cf. Matsuoka, 1998, 2001; Harris et al., 2008).

5.3 Relay succession in the sub-alpine zone

In the sub-alpine zone, the coefficients and indices indicate very little similarity between the pioneer species and those species characterising the adjacent mature vegetation. The mean values of S_n, PP_n, PI_n, S_o, PP_o and PI_o from this zone all lie within the range of 14–19% (Fig. 5 and Table 3), to which the substrate difference between the gravel of the verge and the till of the mature vegetation will have contributed. Offset in values discussed above between site types in the high-alpine zone indicates that the substrate effect could reduce the degree of similarity by as much as 20-30%. However, the tendency towards convergence of the regression lines shown in Fig. 5 suggests that this reduction in similarity is likely to be less at lower altitudes and to be least in the sub-alpine zone.

The low similarity values recorded in the sub-alpine zone are therefore inconsistent with autosuccession. Instead, this result indicates that a new set of species replaces the pioneer species during succession, in keeping with the traditional concept of relay floristics, replacement change or relay succession (cf. Egler, 1954, McCormick, 1968, Svoboda and Henry, 1987; Matthews, 1992), which is characterised by high species turnover over time and is a widespread feature of primary succession in less severe environments elsewhere (see below). The long list of species that characterise mature vegetation in the sub-alpine zone include not only trees (*Pinus sylvestris, Betula pubescens* and *Alnus incana*) and shrubs (*Juniperus communis, Betula nana, Vaccinium myrtillus, V. vitis-idaea, Empetrum hermaphroditum* and *Salix* spp.) but also graminoids, forbs and ferns (e.g. *Deschampsia flexuosa, Luzula sylvatica, Aconitum septentrionale, Geranium sylvaticum, Melampyrum sylvaticum, Linnaea borealis, Oxalis acetosella* and *Gymnocarpium dryopteris*). Pioneer communities in the sub-alpine zone consist of a diverse mixture of grasses and forbs, including some species typical of the alpine zone (e.g. *Deschampsia alpina, Cerastium alpinum, Epilobium anagallidiflium* and *Polygonum viviparum*) and agricultural weeds (e.g. *Rumex acetosella, Plantago lanceolata* and *Trifolium repens*) (cf. Robbins, 2007). *Salix glauca* is the only shrub that occurs frequently but in low numbers amongst the pioneers in the sub-alpine zone. Colonisation of these verges by tree seedlings of *Betula pubescens* and *Pinus sylvestris* also occurs and accounts for the coefficient and indices failing to achieve a value of zero at one of the eight sites in the sub-alpine zone.

5.4 Mixed-mode succession in the low-alpine and mid-alpine belts

Mean values for the nominal-scale measures are 30-35% for the low-alpine and ~40% for the mid alpine, whereas they are 20-30% and 25-35%, respectively, using the ordinal-scale measures (Fig. 5 and Table 3). These relatively low similarity values indicate that the differences between these belts are consistently less than between the low-alpine belt and the sub-alpine zone. Furthermore, the intermediate values of all coefficients and indices in the mid- and low-alpine belts suggest that succession there is transitional in character between autosuccession, which occurs in the upper high-alpine sites, and the relay succession/replacement change of the sub-alpine zone.

Throughout the low- and mid-alpine belts most of the pioneer species do not persist into the mature vegetation. Many of the pioneer species are the same as in the sub-alpine zone with additional alpine species, including *Gnaphalium supinum*, *Silene acaulis, Luzula spicata, L. arcuata, Festuca ovina, Trisetum spicatum, Poa alpina, Saxifraga* spp. and the moss, *Polytrichum sexangulare*. The shrubs (*Betula nana, Juniperus communis, Empetrum hermaphroditum, Phyllodoce caerulea, Calluna vulgaris, Vaccinium myrtillus, V. uliginosum, V. vitis-idaea, Loiseleuria procumbens, Arctous alpine, A. uva-ursi, Salix glauca* and *S. lanata*), lichens (e.g. *Cetraria nivalis, C. islandica, Stereocaulon alpinum, Cladonia arbuscula, C. alpestre, Alectoria nigricans, A. nigricans*), forbs (e.g. *Trientalis europea, Potentilla crantzii, Solidago virgaurea, Hieracium spp., Saussurea alpina, Pedicularis lapponica, Bartsia alpina, Sibbaldia procumbens, Viola biflora, Pyrola* spp. *and Polygonum viviparum*), and graminoids (e.g. *Carex bigelowii,Juncus trifidus, Anthoxanthum odorata* and *Nardus stricta*), that characterise the mature low- and mid-alpine heaths rarely occur as pioneers.

The transition from the low to mid-alpine zones is gradual and is accompanied by a decline in the number and abundance of the woody species, apart from *Salix herbacea*, which increases in abundance as the area affected by late snowbeds increases. A strong element of relay floristics/replacement change therefore occurs in both belts, although it is strongest in the shrub-dominated low-alpine belt. This altitudinal variation in the mode of succession between pioneer and mature stages still applies if account is again taken of the offset of up to 20-30% in the differences between the pioneer and mature communities of verge sites relative to sorted-circle sites (an offset that may be greater for the mid-alpine belt than for the low-alpine belt, as argued above).

Our interpretation vis-à-vis the relationship between autosuccession and altitudinal zonation differs from that those of Muller (1952), Matthews (1992) and Robbins and Matthews (2010) in that autosuccession appears to be more restricted than previously envisaged. In particular, autosuccession (or selective autosuccession) seems to be less important than relay succession/replacement change in the mid-alpine belt. In general, therefore, our results support the conclusion that autosuccession without significant turnover of species is limited to the uppermost part of the high-alpine belt, essentially in agreement with the conclusion of Brown et al. (2006) that autosuccession is an untenable model in the context of secondary succession in New Zealand high-alpine cushionfield.

5.5 An altitudinal continuum in the nature of successional change

Despite the existence of significant differences between conventional altitudinal zones, the strong altitudinal gradients exhibited for each of the coefficients and indices indicate that altitudinal variation in the nature of successional change can be regarded as a continuum. Although the concept of altitudinal zonation of mature vegetation has a very long history in Scandinavia, including alpine vegetation in Norway (Nordhagen, 1943, Gjærevoll, 1956; Dahl, 1956, 1986; Moen, 1999; Löffler and Finch, 2005), the continuum concept provides an alternative interpretation (cf. Gleason, 1939; McIntosh, 1967; Whittaker, 1967; Oksanen and Minchin, 2002), which may be particularly appropriate in the context of succession. No consistent steps are apparent in Fig. 5 and there is little evidence to suggest that between-zone variability exceeds within-zone variability, which would be necessary to recognise non-arbitrary altitudinal zones in the pattern of succession.

Our study therefore suggests a more-or-less linear continuum from pure autosuccession at the highest sites investigated (altitudes above ~2000 m a.s.l.) to pure relay succession at the lowest (below the tree line at ~1000 m a.s.l.). The element of autosuccession decreases as the element of relay succession increases throughout the descent from conventional high-alpine to sub-alpine. Nevertheless, it appears that the differences in the mode of succession between the sub-alpine zone and the low-alpine zone are greater than between the other contiguous altitudinal zones at higher altitudes, possibly associated with major differences in ecosystem structure and function above and below the tree line.

The main controls on the successional continuum seem to be related directly or indirectly to the thermal climate, which is known to be a major control on the decline in the number of plant species (species richness) with altitude in alpine zones throughout the world (Rahbek, 1995; Körner and Spehn, 2002; Nagy et al., 2003). In the Norwegian alpine zone, including the Galdhøpiggen massif, the decrease in vascular plant species richness with altitude is approximately linear and is strongly correlated with mean July air temperature (Jørgensen, 1932; Dahl, 1951; Odland and Birks, 1999; Holten, 2003). However, a number of climatic factors may affect the upper altitudinal limits of particular species, including soil temperature, moisture as well as heat availability in the growing season, and interactions between winter temperature, snow and wind conditions (Gauslaa, 1984, 1985, Dahl, 1986; Holten, 2003; Körner, 2007; Odland et al., 2017).

Substrate disturbance following freezing and thawing of the ground in the active layer is an indirect effect of the thermal climate that has a major influence on plant communities, ecosystems and succession in polar and alpine environments (Sigafoos, 1951; Raup, 1957, 1971; Johnson and Neiland, 1983; Chernov and Matveyeva, 1997; Matthews et al., 1998; Walker et al., 2004; Haugland and Beatty, 2005; Kade et al., 2005; Haugland, 2006; Shur and Jorgenson, 2007; Vonlanthen et al., 2008; D’Amico et al., 2015). Frost disturbance, which may include frost heave, solifluction and/or cryoturbation, occurs at all altitudes investigated in this study but tends to be more extensive and operate at higher intensity under the permafrost regime at sites in excess of ~1450 m a.s.l. Furthermore, it is only in the high-alpine belt with underlying permafrost that frost heave, solifluction and particularly cryoturbation appear sufficiently active to produce bare, unvegetated surfaces in the fine centres of patterned ground. Through mid- and low-alpine belts with seasonally-frozen ground, visible cryoturbation ceases, solifluction is constrained by the complete vegetation cover, and frost heave diminishes. We hypothesise, therefore, that succession tends to become simpler with increasing altitude as fewer plants tolerate increasing climatic stress and substrate disturbance, culminating in pure autosuccession at sites above ~2000 m a.s.l.

5.6 Implications for geo-ecological processes and models of primary succession

Succession can be regarded as a geo-ecological process because it involves spatio-temporal dimensions in the landscape and interactions between autogenic (organic/biological) and allogenic (inorganic/physical) driving and/or conditioning factors (Clements, 1928; Matthews, 1992, 1999; Cutler et al., 2008). An explicitly geo-ecological model is particularly appropriate in the alpine zone because of spatial variations in the dynamics of succession, which reflect the increasingly severe or stressful and disturbed environment with increasing altitude.

Our schematic geo-ecological model for the high-alpine/sub-alpine continuum is summarised in Fig. 6. The first part of this model (Fig. 6A) depicts the linear relationship between altitude and species composition change as quantified by the coefficients and indices used in this study. This relationship is interpreted as a continuum in the mode of succession from high-altitude autosuccession to relay succession below the tree line (Fig. 6C), which is driven by the relative importance of allogenic and autogenic processes along the altitudinal bioclimatic gradient (Fig. 6B).

Although we are unable to separate the precise roles of specific processes and mechanisms on the basis of our data, it may be speculated that the interaction of a stressful thermal climate, frost disturbance, variable vegetation cover and plant biomass, competition and the reaction of plants on their environment are of fundamental importance in accounting for the successional continuum. At the highest altitudes investigated, climatic stress and frost disturbance limit the species pool, the vegetation cover and plant biomass. Relatively few plants comprise the pioneer community and form an incomplete vegetation cover of very low biomass. This leads to the dominance of autosuccession. Even in the mature community, plants tend to be isolated from each other, rarely form extensive mats and are unlikely to be affected by competition, reduce disturbance or react on their environment in any way that may significantly facilitate change towards a different community. At lower altitudes, with a larger species pool, complete cover, greater biomass, less stressful environment and lower disturbance levels, competition and reaction are likely to increase in intensity. Consequently, species turnover/replacement change driven by biological interactions is possible within the conventional mid-alpine belt, increases in significance in the low-alpine zone and appears to be the overwhelmingly dominant mode of succession in the sub-alpine zone. A similar geo-ecological model would seem to be applicable to Arctic-subarctic bioclimatic gradients (cf. Svoboda and Henry, 1987; Walker et al., 2004; and Kade et al., 2005).

Finally, the question may be raised as to whether, from a theoretical point of view, ‘autosuccession’ is really a true succession at all. The answer depends, at least in part, on the interpretation of the limiting or controlling factor. If the pioneer stage persists unchanged due to widespread and frequent disturbance, this could be interpreted as permanent blockage of the transition to a mature stage (i.e. ‘no succession’). If, on the other hand, the pioneer stage persists directly due to climatic stress, increasing cover, biomass and competition within a limited species pool would be more consistent with the idea of a very simple succession to maturity (i.e. ‘succession’). The same dichotomy underlay ‘the problem of Arctic vegetation’ recognised by Griggs (1934). He posed the question in terms of whether or not the Arctic tundra represents a ‘climatic climax’, the alternative being that continuous disturbance prevents succession and the attainment of a stable community.

6. Conclusion

1. The altitudinal bioclimatic gradient in Jotunheimen provides a wide range of alpine environments within which autosuccession and related concepts can be tested. Autosuccession, also known as direct succession or non-replacement change, is the simplest form of succession in which there is no difference in species composition between pioneer and mature stages. In this study, specific tests of autosuccession involve comparing pioneer communities on roadside verges and areas of patterned ground disturbed by cryoturbation with mature communities at regular 25-m intervals over an altitudinal range of 1350 m from sub-alpine woodland to high-alpine fjellfield.

2. Use of community similarity coefficients and indices of pioneer persistence and importance to measure differences in species composition between paired samples of pioneer and mature plant communities enables numerical testing of the concept of autosuccession for the first time. Autosuccession is indicated by values of 100 % for these measures. Using data on the presence and absence of species in nominal-scale coefficients and indices provides the closest approximation to a test of autosuccession as conceived by Muller (1940, 1952). Parallel tests taking the rank-order of species abundance into account by using related ordinal-scale coefficients and indices substantiate the results based on nominal-scale data.

3. Although values based on ordinal-scale data are generally ~10% lower than those based on nominal-scale data, all coefficients and indices exhibit statistically significant linear relationships with altitude. At disturbed sorted circle sites, mean values of nominal-scale coefficients and indices vary from 92-94% to 70-72% in the upper (2075-2200 m a.s.l.) and lower (1750-1850 m) parts of the high-alpine belt, respectively. At roadside verge sites, comparable mean values for the high- (1625-1850 m), mid- (1375-1600 m) and low-alpine (1000-1350 m) belts and the sub-alpine zone (850-1025 m) are 43-51%, 40-42%, 31-35% and 17-19%, respectively. The ~20% offset in regression lines based on pioneer sites from roadside verges and disturbed sorted circles indicates that substrate differences are an effective influence.

4. Statistically significant differences between conventional altitudinal belts within the alpine zone can be interpreted as reflecting a successional continuum related to altitude and its associated bioclimatic gradient. Pure autosuccession (or non-directional, non-replacement change) affects only the uppermost part of the high-alpine belt whereas, in the sub-alpine zone, pioneer and mature communities have few species in common, major species turnover occurs and relay succession (or relay floristics) is characteristic. Between these two extremes, mixed-mode succession is recognised with progressively greater replacement change through the mid- to low-alpine transition.

5. Spatial variation in the nature of primary succession is consistent with a geo-ecological model of succession in which predominantly allogenic controls (climatic stress, associated especially with the thermal climate, and high levels of cryoturbation and other forms of substrate disturbance) at high altitudes give way to increasing autogenic controls (biological interactions, including competition between species and the reaction of plants on their environment, and substrate stability) at lower altitudes. However, separation of the roles of successional processes and mechanisms is not possible on the basis of our data. Areas requiring further investigation include the following: the possibility of selective autosuccession (directional non-replacement

change); differences in the roles of climatic stress and frost disturbance along the successional continuum, between conventional altitudinal vegetation belts and between areas affected by permafrost and seasonal frost; feedbacks between vegetation and frost disturbances; and mechanisms of vegetation change at the species level.

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FIGURE CAPTIONS

Fig. 1. The study area in northeastern Jotunheimen. Study sites at altitudinal intervals of 25 m are located on two overlapping transects: the long Juvflye transect extends from 850 m a.s.l. alongside the road from Galdesanden, across the plateau area of Juvflye, to 2050 m a.s.l. on the southeastern slope of Galdhøe; the shorter Galdhøe transect extends from 1900 to 2200 m a.s.l. on the north and east-facing slope of Galdhøe. At each study site comparable areas of pioneer and mature vegetation were analysed.

Fig. 2. Vegetation of the alpine belts in their landscape setting: (A) high-alpine belt; sparsely vegetated sorted circles with frost-disturbed centres at ~1850 m a.s.l.; (B) mid-alpine belt; lichen heath on relict sorted circles without disturbed centres at ~1550 m a.s.l.; (C) low-alpine belt; dwarf-shrub heath at ~1250 m a.s.l.

Fig. 3. Paired pioneer and mature sites: (A) mid-alpine roadside verge and (B) adjacent mature grass heath at ~1600 m a.s.l.; (C) sub-alpine roadside verge and (D) adjacent mature community with pine and birch trees and fern understorey at ~900 m a.s.l.

Fig. 4. Schematic sampling strategy for quadrat sampling at paired pioneer and mature sites associated with the vegetation of (A) sorted patterned ground and (B) roadside verges. Note use of sixteen 0.5 x 0.5 m quadrats at pioneer sites and four 1.0 x 1.0 m quadrats at mature sites.

Fig. 5. Altitudinal variation in community similarity coefficients and pioneer indices based on nominal- and ordinal-scale data: (A) nominal-scale S_n coefficient; (B) ordinal-scale S_o coefficient; (C) nominal-scale PP_n index; (D) ordinal-scale PP_o index; (E) nominal-scale PI_n index; (F) ordinal-scale PI_o index. Separate regression lines are shown for sites based on roadside verges (left) and sorted circles (right). Shaded areas show conventional altitudinal zones (sub-, low-, mid- and high-alpine) and three subdivisions of the high-alpine belt for sites using sorted circles; 95% confidence intervals around zone mean values are also shown for each altitudinal zone, belt or subdivision. Further explanation in the text.

Fig. 6. Schematic geo-ecological model of successional change along the sub-alpine/high-alpine altitudinal gradient in Jotunheimen: (A) altitudinal variation in species compositional change during succession as measured by community similarity coefficients (S_n, S_o) and indices of pioneer species persistence (PP_n, PP_o) and importance (PI_n, PI_o); (B) altitudinal variation in the relative importance of allogenic and autogenic processes during succession; (C) the continuum in the nature of successional change from autosuccession in the upper high-alpine belt to relay succession in the sub-alpine zone.