Afforestation of moorland leads to changes in crenarchaeal community structure

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Abstract
Group 1 Crenarchaeota are an abundant component of soil microbial communities. A number of distinct lineages have been discovered, and the Group 1.1b lineage is present in most soil types. Others, such as the Group 1.1c lineage, may be restricted to specific soil types, such as acidic forest soils. To determine the effects of afforestation on the Archaea of moorland soils, archaeal community structure was examined across three parallel 180 m transects, running from open heather moorland into a Scots pine forest. Communities were characterized using a combination of cloning and denaturing gradient gel electrophoresis (DGGE) analysis of 16S rRNA reverse transcriptase-polymerase chain reaction products. Although forest soils selected for a reproducibly distinct crenarchaeal community structure from moorland soils, both habitats contained similar populations, indicated by comigrating DGGE bands. Archaeal communities in soils of both ecosystems were dominated by Group 1.1c crenarchaea, and reproducible differences in community structure within this lineage were observed between forest and moorland soils. The findings indicate that the afforestation of moorland soils can lead to changes in crenarchaeal community structure with a potential impact on ecosystem function.

Introduction
Archaea are recognized as a ubiquitous and abundant component of microbial communities in terrestrial and aquatic environments. In particular, a lineage of mainly mesophilic organisms, placed within the kingdom Crenarchaeota (termed ‘Group 1’), may be the most abundant Archaea in soil, and represents c. 6% of all prokaryotes in terrestrial and aquatic habitats (Nicol & Schleper, 2006). The Group 1 lineage is composed of a number of clades that exhibit some level of ecological differentiation. For example, Group 1.1a crenarchae are estimated to constitute c. 20% of all marine planktonic prokaryotes (Karner et al., 2001), organisms belonging to the Group 1.1b lineage appear to be the most abundant and ubiquitous in soil (Ochsenreiter et al., 2003), and sequences placed within the Group 1.1c lineage are also found in soil, but have a more restricted distribution than the Group 1.1b lineage (Nicol et al., 2005). The majority of Group 1.1c sequences have been recovered from coniferous forest soils (e.g. Jurgens et al., 1997; Bomberg et al., 2003; Yrjälä et al., 2004) and grassland soils (together with dominating Group 1.1b sequences) (e.g. Nicol et al., 2003a, 2005). Indeed, in some soils, such as those of Scandinavian boreal forests, Group 1.1c crenarchae appear to dominate, with a distinct lack of Group 1.1b organisms that are prevalent in other soils (Jurgens et al., 1997; Jurgens & Saano, 1999; Bomberg et al., 2003; Yrjälä et al., 2004). As boreal forest habitats represent the largest of all terrestrial biomes, comprising 17% of terrestrial ecosystems (Lindahl et al., 2002), Group 1.1c may actually represent a significant proportion of all soil crenarchaeas. Groups 1.1b and 1.1c represent two distinct evolutionary lineages, with Group 1.1b crenarchaea more closely related to Group 1.1a crenarchaea (Nicol & Schleper, 2006). A number of recent metagenomic studies have indicated that members of the Group 1.1a/b lineage are involved in nitrogen cycling (Schleper et al., 2005), and an ammonia-oxidizing mesophilic crenarchaeote (Group 1.1a lineage) has also been isolated recently (Könneke et al., 2005).

Native Scottish pinewoods represent the westernmost point of the Fennoscandian boreal forest. Today, native pinewoods are composed of a number of isolated areas which represent less than 1% of the Caledonian forest that covered more than 15 000 km2 of northern Scotland after the last ice age (Kinloch et al., 1986; Forrest, 1992). As these habitats are considered to be of high biodiversity value and
support a large number of unique plant and animal species, the expansion of native pinewoods is currently encouraged. Most of this expansion is onto highly organic heather moorland soils, and afforestation may have important long-term consequences on the soil carbon balance, sequestration and turnover (Chapman et al., 2003).

The major aim of this study was to determine whether native woodland expansion significantly affects archaeal community structure, which may have subsequent consequences on the contribution to particular ecological functions. An additional aim was to determine whether crenarchaeal communities in native Scots pineland are similar to those in mainland European boreal forests, i.e. whether they are dominated by Group 1.1c organisms and lack detectable Group 1.1b crenarchae.

## Materials and methods

### Site description and sampling

Samples were obtained from an area of Scots pine (*Pinus sylvestris*) woodland at the southern edge of the Abernethy Forest, Cairngorm, Scotland (57°15′N, 34°0′E) on 25 August 1998. The underlayer was dominated by *Vaccinium* spp. and the woodland is currently extending into open moorland soils, and afforestation may have important long-term consequences on the soil carbon balance, sequestration and turnover (Chapman et al., 2003).

The underlayer of moorland dominated by heather (*Calluna vulgaris*) with an underlayer of *Sphagnum* spp. Chapman et al. (2003) provide a detailed description of plant cover across the transect. Moorland and forest soils were peaty and humus iron podzols, respectively. Three parallel 180 m transects (A–C) were established across the boundary of forest and moorland, 50 m apart from each other. Each transect was divided into ten 18 m sections providing 11 sampling points, with the first sampling point (A1/B1/C1) situated in moorland and the last sampling point (A11/B11/C11) in the forest. The moorland – forest boundary was slightly different across each transect, with sampling points A7, B7 and C8 situated in the boundary area, and colonizing pine seedlings were present over points 2–6 across the transects. A sample of the organic layer was obtained at each sampling point using a 5 cm × 5 cm square-sectioned corer to a depth of 30 cm, or to the mineral layer if the organic layer was less than 30 cm. Four additional samples were taken at intervals of 1 and 2 m, either side of and perpendicular to the direction of the transect. The top 15 cm of F (fermentation) and H (humic) layers below the litter layer was then separated and combined before sieving (mesh size, 5 mm). Subsamples were frozen at −80 °C immediately after sieving for nucleic acid analysis.

A wide range of physiochemical properties have been described across the site using the same soil samples as analysed in this study (Chapman et al., 2001, 2003; Anderson et al., 2003). A number of trends were observed across the site from moorland into forest soil, including decreases in soil pH (from c. 2.9 to around 2.5), moisture content (from c. 80–85% to 70–75%) and microbial biomass carbon [(from c. 8 to 3–4 mg C g⁻¹ (dry weight)]. However, no significant difference was observed in the percentage content of carbon or nitrogen.

### Nucleic acid extraction

Nucleic acids were extracted using a method based on that of Griffiths et al. (2000). Briefly, 0.5 g of soil was placed in a 2-mL screw-cap Blue Matrix tube (Hybaid, Ashford, Middlesex, UK) with 0.5 mL of extraction buffer [120 mM potassium phosphate buffer (pH 7.8), 5% (w/v) hexadecyltrimethylammonium bromide (CTAB), 0.35M NaCl] and 0.5 mL of phenol–chloroform–isoamyl alcohol (25:24:1). The tubes were then placed in a Hybaid Ribolyser (Hybaid) and shaken for 30 s at speed 4.0 to lyse the cells. The tubes were then centrifuged at 16 000 g for 5 min at 5 °C and the aqueous phase was removed and extracted with 0.25 mL of chloroform–isoamyl alcohol (24:1), followed by further centrifugation at 16 000 g for 5 min at 5 °C. The aqueous phase was then removed and the nucleic acids were precipitated by adding two volumes of 30% (w/v) polyethylene glycol (PEG) 6000 in 1.6M NaCl and incubating at 5 °C overnight. The precipitated nucleic acids were pelleted by centrifugation at 16 000 g for 10 min at 5 °C, and washed in 1 mL of ice-cold 70% (v/v) ethanol before further centrifugation at 16 000 g for 5 min. The ethanol wash was poured off, residual liquid was removed by a pipette and the pellets were dried by warming for c. 1 min at 55 °C in a hot-block. The pellets were resuspended in 50 μL of sterile H₂O.

### Reverse transcriptase-polymerase chain reaction (RT-PCR) amplification of crenarchaeal 16S rRNA genes for denaturing gradient gel electrophoresis (DGGE) analysis

Reverse transcription of the extracted 16S rRNA was performed as described previously (Nicol et al., 2005). Nucleic acids were treated with RQ1 DNase (Promega, Southampton, Hampshire, UK) before the production of archival cDNA using Superscript II RNase H⁻ reverse transcriptase (Invitrogen, Paisley, Renfrewshire, UK), according to the manufacturer’s instructions, with primer Ar9R (Jurgens et al., 1997) to select for the archaeal 16S rRNA. First-round PCR products were obtained by amplifying cDNA with the archaeal-specific primers A109F (Großkopf et al., 1998) and Ar9R, producing a PCR product of c. 800 bp in length (corresponding to positions 80–881 of the 16S rRNA gene of *Sulfolobus acidocaldarius*). The PCR cycling conditions were 95 °C for 5 min, followed by five cycles of 94°C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by 30 cycles of
92 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, and a final cycle of 72 °C for 10 min. The PCR products were then used as a template for a nested PCR with primers rSAf (with GC-clamp) (Nicol et al., 2005) and PARCH519r (Ovrevás et al., 1997), generating a PCR product of 150 bp in length plus the GC-clamp (corresponding to positions 337–483 of the 16S rRNA gene of Sulfolobus acidocaldarius). The cycling conditions were the same as those for the first-round PCR, except that an annealing temperature of 63 °C was used. All PCR amplifications were performed in 50-μL reactions on a Hybiad Express thermal cycler using BioTaq DNA polymerase (Bioline, London, UK) at 1 U per reaction, MgCl₂ at 2 mM, dNTPs at 1 mM and each primer at 0.2 mM.

**Cloning, sequencing and phylogenetic analysis of crenarchaeal 16S rRNA gene PCR products**

First-round PCR products selected for cloning were purified before ligating into pGEM-T Easy vector (Promega) and were transformed into XL1-Blue supercompetent Escherichia coli cells (Stratagene, Cambridge, Cambridgeshire, UK). Transformants were screened for inserts by colony PCR using vector primers M13f/M13r. To obtain sequences representative of major DGGE migration positions, individual M13f/M13r PCR products were used as template for PCR with the DGGE primer set rSAf/PARCH519r. Amplions of individual clones were then compared with the corresponding community DGGE profile for screening purposes. PCR products generated using this primer set have been demonstrated to produce highly reproducible DGGE profiles (e.g. Nicol et al., 2003b, 2005). Fragments that differ by only 1 bp can be distinguished easily in DGGE analyses, and clones with identical migration patterns form monophyletic groups in phylogenetic analyses (Nicol et al., 2005, 2006).

Selected M13f/M13r PCR products were sequenced along both strands in four sequencing reactions using the primers A109f, PARCH519r, PARCH533f (reverse complement of A90f) and Ar9R, and assembled using Sequencher 4.1 (Gene Codes Corp., Ann Arbor, MI). Assembled sequences were imported into BIOEDIT (Hall, 1999) with references and aligned using ClustalW (Thompson et al., 1997), implemented in BIOEDIT, before making manual adjustments. Using unambiguously aligned positions only, LogDet/Paralinear distances (Lake, 1994) were calculated using variable positions (Lockhart et al., 1996) estimated from a maximum-likelihood model implemented in PAUP version 4.01 (Swofford, 1998). Bootstrap support was calculated 1000 times and phylogenetic trees were constructed by the neighbour-joining method (Saitou & Nei, 1987), with multifurcation indicating where the relative branching order could not be determined in the majority of resamplings.

All sequences have been deposited in the GenBank database with accession numbers DQ449486–DQ449506.

**Results**

**RT-PCR DGGE analysis of archaeal 16S rRNA genes**

All first-round PCRs contained a high yield of product (c. 50 ng·mL⁻¹), and 1 μL of a 1:100 dilution was used as template for nested PCR. All nested PCR products were of an equivalent yield, and 2 μL of PCR product was loaded for each sample for DGGE analysis. DGGE gels were scanned and analysed using densitometry software to determine the relative band intensities. DGGE profiles were relatively consistent between replicate transects and contained a level...
of diversity typical of the primer set used with soil samples, with c. 8–12 band ‘doublets’ (an artefact of unavoidable degeneracies in the DGGE primer set) (Fig. 1). The profiles contained several band positions (e.g. 4, 7 and 8) with uniform relative (within-lane) intensity across all three transects, indicating that afforestation did not select for or against these populations. However, the relative intensity of several bands increased or decreased in a reproducible manner in forest and moorland soil samples, indicating the selection of some populations in the different ecosystems. The greatest changes were seen in four band positions (3, 5, 9 and 10) (Fig. 2). The relative intensities of bands 3 and 9 increased in forest soil, whereas those of bands 5 and 10 decreased. For these four band positions, all woodland samples had significantly different relative band intensities \((P < 0.05)\) from all moorland samples, except for those at \(0 \text{m} = 54 \text{m}\) in the moorland samples for bands 3 and 10. Boundary samples (0 m) for these band positions also showed the greatest similarity to forest samples, exhibiting the same significant differences in relative intensities to moorland samples.

The relative band intensities for bands 3, 5, 9 and 10 were correlated with the soil and vegetation data for the same soil samples as taken by Chapman et al. (2003) (Table 1; Fig. 3). Band 3 was only weakly correlated with tree number, but was significantly and positively correlated with the presence of Vaccinium spp. and with the absence of Sphagnum spp. and Calluna vulgaris vegetation. Conversely, band 5 was significantly and positively correlated with the presence of C. vulgaris and Sphagnum spp., with the absence of trees and of Vaccinium spp. and with increasing pH. Band 9 showed similar trends and significant correlations to band 3, whereas band 10 was most significantly correlated with pH, but also with moisture.

**16S rRNA gene sequence analysis**

DGGE analysis of archaeal communities involved the amplification of a short, 150-bp fragment, and subsequent excision and sequencing of DGGE bands provided limited phylogenetic resolution. Therefore, to obtain greater phylogenetic information that correlated with the DGGE analysis of archaeal communities, selected first-round PCR products (from samples A1, A2, A3, A5, A8, C2 and C11) were cloned, and individual clones were screened using DGGE against an environmental profile of the same sample. To confirm that bands migrating to the same position were representative of a particular sequence or monophyletic sequence group, at least two clones with identical DGGE migration patterns were obtained from different libraries, representing 10 major migration positions on DGGE profiles (Fig. 1). Cloned sequences were prefixed with MFT (moorland–forest transect) and 1–10 (describing DGGE migration positions) 1–10 (describing DGGE migration positions) and 1–10 (describing DGGE migration positions) and 1–10 (describing DGGE migration positions). Each
sequence contained a minimum of 95% identity to sequences deposited previously in GenBank.

A band migrating to position 1 appeared sporadically in samples of moorland soil only, and sequences of representative clones (MFT1-A2 and MFT1-C2) were identical.

Phylogenetic analysis (Fig. 4) showed that these clones exhibited high similarity to sequences retrieved previously from a wide range of environments (including plant roots, freshwater and subsurface habitats), and fell within a lineage distinct from, but specifically associated with, the Group 1.1a lineage.

Despite the relatively high water content of the soils, they displayed relatively low methane production potentials (Chapman et al., 2003), and sequences from methanogenic euryarchaea were not a significant component of DGGE profiles. Thus, only one band position (2) was of euryarchaeal origin. This was detected in only one soil sample (A5) and displayed 97% identity (over 747 bp) to sequences within the *Methanobacteria* (e.g. Huang et al., 2003; Ma et al., 2005). As only one clone was obtained for this band position, confirmation was performed by excision and sequencing of the DGGE band, as described by Nicol et al. (2005). Comparison with the cloned sequence and BLAST searches confirmed that this band position represented the same euryarchaeal sequence.

Phylogenetic analysis revealed that all other sequences, representing migration positions 3–10, were placed in well-supported clades within the Group 1.1c lineage.

### Table 1. Correlations between the relative intensities of the denaturing gradient gel electrophoresis (DGGE) band positions 3, 5, 9 and 10 and the presence of dominating vegetation and soil parameters

<table>
<thead>
<tr>
<th></th>
<th>Calluna vulgaris</th>
<th>Sphagnum spp.</th>
<th>Vaccinium spp.</th>
<th>Tree number</th>
<th>Seedlings</th>
<th>Moisture (%)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Band 3</td>
<td>–0.48**</td>
<td>–0.55**</td>
<td>–0.60**</td>
<td>0.17</td>
<td>–0.25</td>
<td>–0.25</td>
<td>–0.44**</td>
</tr>
<tr>
<td>Band 5</td>
<td>0.51*</td>
<td>0.70**</td>
<td>–0.81**</td>
<td>–0.53*</td>
<td>0.07</td>
<td>0.61**</td>
<td>0.74**</td>
</tr>
<tr>
<td>Band 9</td>
<td>–0.51*</td>
<td>–0.78**</td>
<td>–0.71**</td>
<td>0.65**</td>
<td>–0.27</td>
<td>0.55*</td>
<td>–0.63**</td>
</tr>
<tr>
<td>Band 10</td>
<td>0.51</td>
<td>0.58</td>
<td>–0.63**</td>
<td>–0.43*</td>
<td>0.21</td>
<td>0.50*</td>
<td>0.66**</td>
</tr>
</tbody>
</table>

*Significant at *P* ≤ 0.01.

**Significant at *P* ≤ 0.001.
Fig. 4. Phylogenetic tree showing LogDet/Paralinear distances of moorland–forest transect (MFT) crenarchaeal sequences calculated from the estimated variable sites (65%) of 716 unambiguously aligned positions. Cloned sequences are described by the denaturing gradient gel electrophoresis (DGGE) migration positions of the rSAf/PARCH519r PCR products (MFT1–10) and the soil samples from which they were obtained (A1–C11). Reference sequences are described as 'name (environmental source, accession number)'. Sequences highlighted with a superscript 1 or 7 denote those which possess an identical sequence over the 150-bp DGGE fragment to those of MFT1 or 7, respectively. Bootstrap support was calculated from 1000 resamplings, with multifurcating nodes indicating where the relative branching was not supported in the majority of bootstrap replicates. The tree was rooted with Group 1.3 reference sequences.
sequences displayed 95% or greater identity to previously described sequences, all of which were recovered from soil. In particular, sequences showed high similarity to forest soil sequences recovered from Finland, Germany and the USA. These included those sequences identified as being specifically associated with either moorland (band positions 5 and 10) or forest (band positions 3 and 9) soil.

Although the primers used in this study exhibited good coverage of the archaeal domain (including all major Group 1 lineages), no sequence belonging to the Group 1.1b lineage was identified in any clone library.

Discussion

Afforestation led to a reproducible change in archaeal community structure, although community profiles for both moorland and pine woodland forest soil were dominated by Group 1.1c sequences. Changes in the patterns of archaeal community structure along the transects correlated with changes in other microbiological and physicochemical characteristics determined previously for these soil samples (Anderson et al., 2003; Chapman et al., 2003). In particular, the relative intensities of the four band positions associated with Group 1.1c populations correlated with changes in both plant community composition and soil properties. Although these correlations cannot necessarily be interpreted as evidence of direct specific associations with the presence of specific plant species or environmental variables, they suggest that the distribution of the different crenarchaeal species detected is distinct and is a result of different plant-soil interactions. The transect moved from open moorland (A1/B1/C1) to a transitional zone of pine seedling colonization, where intermediate characteristics in soil and microbiological properties may have been expected. However, changes in community structure were mainly associated with a large boundary effect. Anderson et al. (2003) profiled the fungal communities across the same transect soil samples using internal transcribed spacer (ITS)-PCR DGGE analysis, and observed that the major shifts in fungal community structure were also at the boundary. In addition, these shift changes were reflected in pH, water content and microbial biomass (Chapman et al., 2003). Therefore, the observed trends in this study are not 'archaeal-specific', but reflect overall trends in the biological and physicochemical properties of soil samples across the site.

Group 1.1b organisms are considered to be the most widely distributed and abundant crenarchaea in soil (Ochsnerreiter et al., 2003), and have been recovered from a diverse range of soil types and ecosystems, including agricultural soils, alpine grassland and rice paddies. As a result of their almost ubiquitous distribution, it is not possible to identify specific factors that select for this particular lineage. However, the lack of detection of these sequences in the forest (and moorland) soils investigated here correlates specifically with other studies of boreal and acidic forest soils containing archaeal communities dominated by Group 1.1c (Jurgens et al., 1997; Jurgens & Saano, 1999; Bomberg et al., 2003; Yrjälä et al., 2004). Pesaro & Widmer (2002) reported the recovery of a number of novel lineages of soil crenarchaeae in forest soil. The region of the 16S rRNA gene does not overlap with either that studied here, or the Group 1.1c communities found in Finnish forest soils (e.g. Jurgens et al., 1997). However, comparison with near full-length crenarchaeal sequences from Nicol et al. (2006) reveals that one group of sequences that was part of the most abundant clone group, identified by restriction fragment length polymorphism (RFLP) analysis (‘B’), also falls within Group 1.1c (data not shown).

Although the ecological drivers and function of Group 1.1c organisms are not yet known, these crenarchaea may be adapted to soils of relatively low pH, e.g. coniferous forest soils. All soil samples analysed in this study (including moorland soils) had pH < 3 (measured in 0.01 M CaCl₂). Nicol et al. (2005) examined crenarchaeal community structure over a chronosequence of developing acidic alpine grassland across a glacier forefield, and detected Group 1.1c crenarchaeae only in the most developed soil substrates where pH was less than 5 (from initial near-neutral pH values). In addition, Nicol et al. (2003a, b) reported that managed grassland plots with pH ≥ 7 did not contain detectable Group 1.1c communities, whereas they were abundant in more acidic grassland plots.

As a result of a lack of cultivated representatives or genomic data, the physiology and ecological function(s) of Group 1.1c organisms remain unknown. Recent evidence from metagenomic, stable isotope and cultivation studies indicate that organisms placed within both Group 1.1a and 1.1b lineages are chemolithoautotrophic organisms, using ammonia as a source of energy, analogous to characterized ammonia-oxidizing bacteria (Nicol & Schleper, 2006). Although these two groups could be considered as neighbouring lineages to Group 1.1c, they represent a well-supported monophyletic lineage, to the exclusion of Group 1.1c organisms, and it is therefore difficult to infer that they are also ammonia oxidizers. Although both Group 1.1b and 1.1c organisms are recovered in the same environmental samples, it is possible that Group 1.1b crenarchaeae are unable to thrive in particularly acidic soils, such as coniferous forest soils, and Group 1.1c organisms may fulfil a similar ecological function to Group 1.1b crenarchaeae (e.g. oxidation of ammonia), which dominate in soils with higher pH values. The oxidation of ammonia is a particular challenge to characterized autotrophic ammonia-oxidizing bacterial populations in acidic environments, as ionized ammonia (i.e. ammonium) cannot be transformed by ammonia monooxygenase. However, autotrophic ammonia...
oxidation has been reported in acid soils (Kowalchuk & Stephen, 2001), and it is possible that other autotrophic ammonia-oxidizing organisms could be responsible for this activity. Alternatively, the lack of detectable Group 1.1b crenarchaea in certain acidic forest soils could indicate that autotrophic archaeal ammonia oxidation is not an important component of nitrogen cycling in these habitats, and that Group 1.1c organisms are involved in other functional processes.

Plant community composition could potentially be an important driver of crenarchaeal community composition. Crenarchaea have been found in association with a variety of different plant roots (Großkopf et al., 1998; Simon et al., 2000; Chelius & Trippelt, 2001), and plant rhizospheres can select for specific crenarchaeal assemblages (Sliwinski & Goodman, 2004). Bomberg et al. (2003) detected Group 1.1c crenarchaea in the ‘(ecto)mycorrhizosphere’ of Scots pine seedlings, suggesting that specific mycorrhizal associations may influence crenarchaeal populations. The presence of ecto- and ericoid mycorrhizas associated with Scots pine and ericaceous plant species, respectively at the site, could therefore potentially select for Group 1.1c organisms, rather than those that dominate in most other soil ecosystems.

These results demonstrate that native Scots pine woodland soil contains crenarchaeal communities analogous to those of other coniferous forest soil systems, indicating a particular archaean community structure associated with a specific habitat. In addition, although phylogenetically similar populations dominated forest and neighbouring moorland soils, it is likely that afforestation onto moorland will select for a distinct archaean community structure, although the functional consequences of these shifts cannot yet be predicted.

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References


