

# NORDIC JOURNAL OF BOTANY

## Research article

## Restoring heathlands after afforestation on two islands in western Norway

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Nordic Journal of Botany

2023: e03971

doi: [10.1111/njb.03971](https://doi.org/10.1111/njb.03971)

Subject Editor: Marianne Evju

Editor-in-Chief: Sara Cousins

Accepted 14 April 2023

Published 13 June 2023



The ongoing loss of red-listed coastal heathlands is a threat to biodiversity and cultural heritage legacies throughout the Atlantic coastal regions of Europe. It is possible to restore degraded and afforested heathlands, but restoration interventions are often labour-intensive and costly, and the outcome of specific restoration actions are not well documented. We assess the efficiency of restoring coastal heathlands through natural succession (i.e. 'passive restoration') after removal of Sitka spruce *Picea sitchensis* (Bong.) Carr. plantations. The study was replicated on two neighbouring islands in a nature reserve in Western Norway. Low-intensity free-range sheep grazing was implemented as part of the reserve management plan. Furthermore, we tested the effect of leaving the clear-felled woody material as chips on site, this being a cost-efficient strategy on islands. Succession was monitored 1, 2, 4/5 and 8 years after clear-felling, and revegetation of vascular plants and bryophytes was compared to target heathland vegetation. Surprisingly, we found different successional trajectories on the two islands. Species composition on one island approached target heathland vegetation during succession, but not on the other. Wood chips reduced species richness and slowed the restoration process, but these negative effects were only short-term (<8 years). Differences in seed bank composition and soil conditions due to land use may explain the deviating successional trajectories on the two islands. We also found that management actions beyond clear-felling and introducing sheep grazing are necessary due to the rapid seed regeneration of the Sitka spruce.

Keywords: *Calluna vulgaris*, clear-felling, natural succession, *Picea sitchensis*, species composition, wood chips

### Introduction

Coastal heathlands are semi-natural landscapes found along the Atlantic coast of Europe from Portugal in the south to Nordland county in Norway in the north (Webb 1998a, Kaland and Kvamme 2013). These are open, treeless lowland areas dominated by heather



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*Calluna vulgaris* Hull (hereafter referred to as *Calluna*) and other dwarf-shrubs that thrive on acid and nutrient-poor soils (Gimingham 1992, Halvorsen et al. 2015). Although species composition and structure change along the latitudinal gradient from south to north, the European coastal heathlands share many features (Janssen et al. 2016). The open landscape is a result of management by fire and free-range grazing, and the oldest heathlands have been maintained actively by grazing and regular burning, alongside heather harvest and turf cutting for fuel and animal bedding, for more than 4000 years (Gimingham 1992, Webb 1998b). The coastal heathlands are now threatened throughout Europe by pollution and a host of concomitant land use changes, especially urbanisation and infrastructure development, along with land abandonment, transformation to agricultural use, and afforestation (Webb 1998b, Fagúndez 2013, Southon et al. 2013, Janssen et al. 2016, Artsdatabanken 2018, IPBES 2018).

Coastal heathlands are recognized for their historic value reflecting the way of life of former times, and the landscape itself is valuable for recreation and for its characteristic species composition (Webb 1998b, Kaland and Kvamme 2013, IPBES 2018). Conservation of heathlands is therefore given special status, e.g. in the UK the lowland heathlands are designated as sites of special concern (SSSIs, SPAs and SACs) (Symes and Day 2003, JNCC. n.d.) and in Norway coastal heathlands are red-listed and designated as prioritised landscapes and are under protection (LOVDATA 2011, Artsdatabanken 2018, Miljødirektoratet n.d.).

Several million hectares were formerly covered by heathlands, but loss of heathland areas has been formidable over the last 70–100 years and the remaining heathlands are often degraded (Webb 1998a). Without management, heathlands are prone to shrub and tree encroachment through natural succession (Mitchell et al. 1997, Kaland and Kvamme 2013). In Norway, only 10% of the heathland area is currently intact (Hjeltnes 1997, Hovstad et al. 2018). Heathland restoration has been suggested as an approach to improve the ecological condition of degraded heathlands and to increase the heathland area. The potential for heathland re-creation or restoration has been assessed across Europe (Willems 1988, Owen and Marris 2000, Degn 2001, Pywell et al. 2011, Gallet and Sawtschuk 2014), but restoration projects have had varying success (Owen and Marris 2000, Pywell et al. 2011, Gallet and Sawtschuk 2014). Major challenges to heathland restoration include airborne N-deposition, elevated pH and soil fertility, especially in soils of heathlands that have been transformed to agricultural use, and depletion of *Calluna* propagules from the soil seed bank (Pywell et al. 1994, Owen and Marris 2000, Eycott et al. 2006, Wamelink et al. 2009).

Arable land and improved grasslands are often selected as heathland restoration sites, which necessitates the implementation of amendment practices such as soil acidification (e.g. by sulphurous addition), nutrient depletion (by top soil scarification) and propagule addition from heather clippings (Owen and Marris 2000, Allison and Ausden 2004, Walker et al. 2007, Pywell et al. 2011, Tibbett et al. 2019). These practices are expensive and time-demanding, and

success is not guaranteed (Walker et al. 2004). On other sites, such as abandoned farmland on acidic and nutrient-poor soils, clear-felled forests, or degraded heathlands, natural succession can be an approach to heathland restoration and conservation (Willems 1988, Degn 2001, Jamoneau et al. 2011).

Conifer plantations have similar soil conditions to heathlands with respect to acidity and nutrient status (Pywell et al. 2002, Walker et al. 2004), and the soil seed bank of heathland species (mainly *Calluna* and *Erica tetralix*) may be viable and undisturbed (Pywell et al. 2002, Walker et al. 2004), but see Eycott et al. (2006). It may therefore be possible to re-create heathlands with high *Calluna* cover through natural succession after removal of conifer plantations (Walker et al. 2004, Allison and Ausden 2006). This would be a cost-effective method, but empirical assessments are few and we are not aware of any studies from northern Europe on the restoration potential of heathlands on clear-felled sites after coniferous plantations.

Forest mastication (chipping) after thinning has become increasingly common to reduce fire hazard and to promote ecosystem restoration, and it is cost-effective to distribute the wood chips on site (Coop et al. 2017, Fornwalt et al. 2017, Miller and Seastedt 2009, Rubin and Roybal 2018, Wolk and Rocca 2009). Wood chips is one of several mulches that are used within horticulture to ameliorate soil conditions and as weed control (Chalker-Scott 2007), but it may also be used as a tool for conservation. For instance, wood chips and agricultural straw have been used to reduce soil erosion on degraded lands (Breton et al. 2016) or after wild fires (Kim et al. 2008, Santana et al. 2014). Mulching can alter soil conditions such as temperature, moisture, pH and nitrogen availability, and mulches such as wood chips can act as a physical barrier which suppresses plant establishment and/or growth (Greenly and Rakow 1995, Chalker-Scott 2007, Miller and Seastedt 2009). Mulches such as wood chips and agricultural straw are found to slow down revegetation, reduce species richness and/or alter species composition, especially during the first years after application and with increasing mulch depth (Greenly and Rakow 1995, Miller and Seastedt 2009, Wolk and Rocca 2009, Dodson and Peterson 2010, Santana et al. 2014). However, mulching is also reported to have no effects or even positive effects on vegetation cover and diversity (Kruse et al. 2004, Kim et al. 2008, Wolk and Rocca 2009, Bontrager et al. 2019). Ecological consequences of mulching are still poorly understood, and there is a need for more long-term studies on mulching as a tool for conservation (Miller and Seastedt 2009, Coop et al. 2017, Fornwalt et al. 2017, Bontrager et al. 2019).

This study investigates the potential of restoring coastal heathlands after removal of plantation forests in western Norway. About 300 000 ha of Norway spruce *Picea abies* H. Karst. and Sitka spruce *P. sitchensis* are planted along coastal Norway, including former heathland areas (Øyen and Nygård 2007). Upon harvest, the spruce plantations are often replanted, but exceptions are made for areas designated for conservation purposes.

Our study area consists of two islands where heathlands had been afforested with Sitka spruce in the 1930s–1970s as part of a broadscale scheme by the Norwegian forestry authorities to improve the forestry industry in western Norway. The islands constitute a bird sanctuary and were clear-felled in 2010 to improve breeding conditions for the seabirds. All tree biomass was chipped as transport and sale of the timber was not economically viable. On one of the islands, the chips were left behind, covering 50% of the area in the first year. We examine the regeneration of vascular plants and bryophytes through natural succession, and changes in soil conditions, during the first eight years after removal of the spruce plantations on both islands. The only management action on the islands was the placement of old Norse sheep that grazed the islands all year. We also study the effect of wood chip cover, and depth, on the heathland restoration process. Species composition was compared with data from mature coastal heathlands on four large islands in western Norway. The criterion for successful restoration is that the successional vegetation (species composition, vegetation cover and species richness) approaches similarity to target heathland vegetation in the

region. A necessary requirement for successful restoration is that the key heathland species *C. vulgaris* should increase in abundance in the plots and should attain dominance over time, whilst the planted and clear-felled tree species Sitka spruce should not re-establish in the plots. Our main research questions (RQ) are: RQ1- Can coastal heathland be restored by spontaneous succession? Specifically, we assess unassisted restoration with clear-felling, followed by year-round grazing by old Norse sheep. RQ2- To what extent does chips cover delay the succession towards heathland vegetation, and does chips cover alter the species composition in a direction that is less desirable for heathland restoration?

## Material and methods

### Study area

The study area consists of two small islands within Ilholmane Nature Reserve, the 7.38 ha Nordre Ilholmen (NIL) and the 5.25 ha Søre Ilholmen (SIL) (Fig. 1). The islands are situated in Vindafjord municipality, in the county Rogaland, western

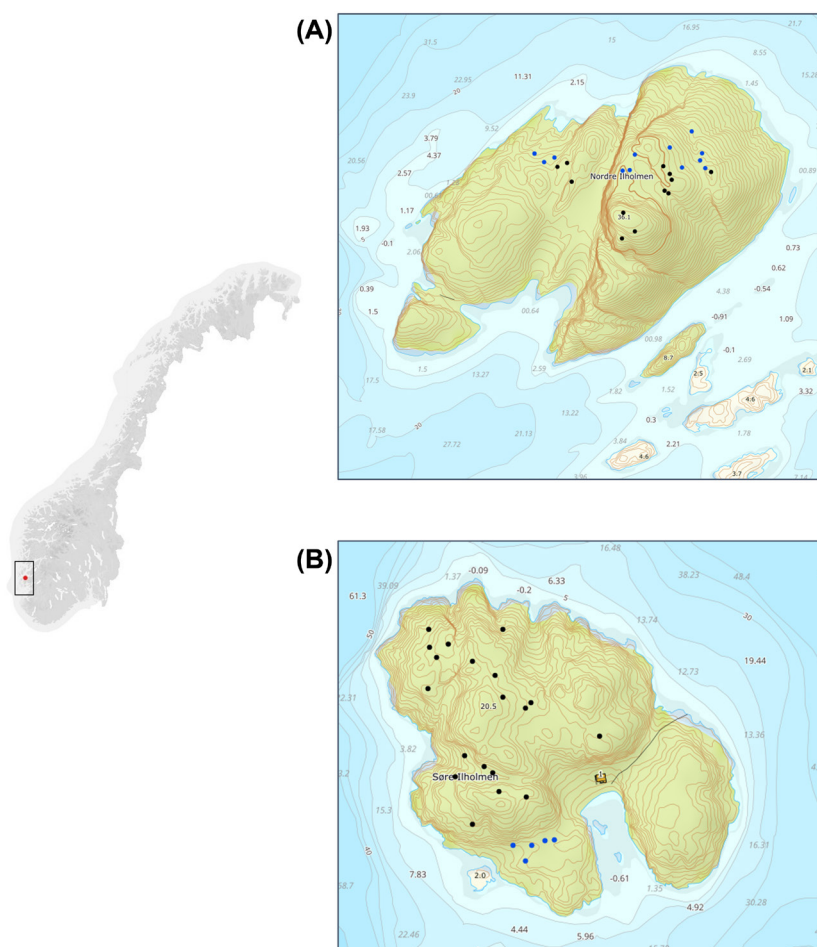


Figure 1. Maps showing the position of Ilholmane nature reserve, Vindafjord municipality in Rogaland, Norway. (A) Nordre Ilholmen (NIL) and (B) Søre Ilholmen (SIL). Sample plots are indicated by black (non-chips area) and blue (chips area) dots. Maps are generated from ©norgeskart.no.



Norway. The nature reserve covers 30 ha, of which ca 12 ha are terrestrial (LOVDATA 1987). The distance between the two islands is ca 1.3 km, and distance to the mainland and large, inhabited islands, is between 3 and 10 km. The climate is oceanic, with mild winters and high annual precipitation. Bedrock on the two islands is fairly similar, consisting of tonalite, partly trondhemite on NIL, and dioritic to granitic gneiss, with touches of migmatite on SIL (Norges Geologiske Undersøkelse n.d.). These are hard bedrocks that release relatively low amounts of mineral nutrients available for plants.

Both islands were originally treeless, sheep-grazed coastal heathlands. NIL was dominated by *Calluna* whereas SIL had more grassland (Ankarstrand, V. 2010. Chief engineer at the County Governor of Rogaland). The mild winters enable establishment of *Ilex aquifolium* and the hyperoceanic *Erica cinerea*.

The islands were gradually afforested from the 1930s onwards (Ankarstrand, V. 2010. Chief engineer at the County Governor of Rogaland). At NIL 5.4 ha were densely planted with Sitka spruce and mountain pine *Pinus mugo* ssp. *uncinata* (Ramond) Domin in 1975–1978. Thicket covered 0.1 ha, the rest was exposed bedrock along the shores. By 2010 the plantation forest was mostly of development class 3 (i.e. large trees, thinning may be required). SIL was afforested twice: Sitka spruce and some Scots pine *Pinus sylvestris* was planted in 1930. The major planting event was in the 1950s, when most of the island was afforested with Sitka spruce. Additionally some Norway spruce, mountain pine and mountain dwarf pine *P. mugo* ssp. *mugo* was planted. A small leisure cabin was built on SIL in 1959. Grazing on SIL ended in the 1950s as the planted forests began to attain height. 6–8 sheep were grazing on SIL at that time. By 2010 approx. 3.1 ha was dense conifer plantations, 0.7 ha shrubs and the rest was smooth rocks. Up to 0.4 ha of the plantations were development class 5 (ready for harvest), the rest was development class 3–4.

Ilholmane Nature Reserve was designated as a bird sanctuary in 1987 (LOVDATA 1987). Prior to afforestation Ilholmane had a colony of breeding lesser black-backed gull *Larus fuscus* and also common gull *L. canus*, and a mixed colony of terns *Sterna hirundo* and *S. paradisaea* (Byrkjeland 2015). As the planted forests grew dense and tall, seabirds continued breeding on the open rocky edges of the islands. Before clear-felling in 2010 the seabirds constituted vital colonies on the islands, and they have increased since (Byrkjeland 2015). The dominating species today are lesser black-backed gull and the red-listed European herring gull *L. argentatus*, while the red-listed common gull and the terns respectively have been drastically reduced and disappeared. Other breeding sea birds are e.g. the red-listed common eider *Somateria mollissima*, great black-backed gull *L. marinus* and European shag *Phalacrocorax aristotelis*. High numbers of greylag goose *Anser anser* breed and/or rest on the islands during summer (Byrkjeland 2015, Statsforvalteren 2022). American mink *Negoale vison* has formerly been observed on the islands, but it is not known if it is still present and negative effects are not reported for the seabird populations (Byrkjeland 2015).

All forest on NIL was cleared in February 2010, when the trees were felled by chain saw and chipped. The wood chips (hereafter called chips) were left on the island, and approximately half the area of NIL was covered by chips of different depths (Fig. 2A). SIL was clear-felled in November and December 2010. Trees were chipped and the chips were removed from the island, except from a remnant layer of chips on the pre-removal storage site. Re-established Sitka spruce was manually removed on NIL in 2015, except for a small area that was left as reference.

Grazing by old nose sheep was introduced to NIL after clear-felling in 2010. The first two summers (2010, 2011) there were respectively four and nine sheep on NIL. In 2017

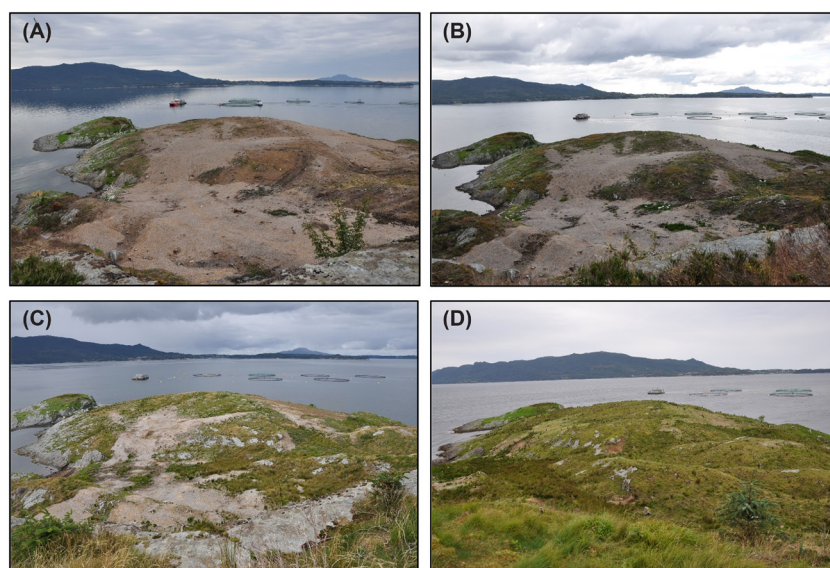


Figure 2. Natural succession from 2010–2017 on areas with and without chips on NIL. (A) Year one. (B) Year two. (C) Year five. (D) Year eight.

we counted more than 30 individuals on NIL, including lambs. Sheep were introduced to SIL in 2012. By the end of our study 10–15 adult sheep were grazing on both islands throughout the year with their lambs born on the islands (Dunkley, A. 2017. Operations manager at Friluftsrådet Vest) (Supporting information).

## Sampling

We performed the vegetation analyses on NIL and SIL in 2010–2018 (Table 1). Permanent plots (1 m<sup>2</sup>) were established as described below and analysed in the summer of 2010 on both NIL and SIL. At this time only SIL had intact Sitka spruce plantations. NIL vegetation was surveyed the first (2010), second (2011), fifth (2014) and eighth (2017) growing season after clear-felling. On SIL we surveyed vegetation the first (2011), second (2012), fourth (2014) and eighth (2018) growing season after clear-felling.

Permanent plots (1 m<sup>2</sup>) for vegetation analysis were placed within areas dominated by Sitka spruce. Aerial photos and observations in field enabled positioning of the NIL plots, as NIL was clear-felled a few months before commencement of the research project. Chips-covered areas on NIL were divided into three categories of different chips depths and replicated so that four sample plots (1 m<sup>2</sup>) were analysed within each chips depth category. Altogether 12 sample plots were analysed on chips areas and 12 sample plots were analysed on non-chips areas on NIL (Table 1). Similarly, 24 plots (1 m<sup>2</sup>) were analysed on clear-felled areas on SIL, and five of these plots were positioned on the chips-covered area. On SIL, 18 plots were analysed within the Sitka spruce plantations in 2010 before clear-felling (Table 1). 12 plots were positioned within the older and more open Sitka forests and six plots were placed within the younger and very dense Sitka spruce plantations. Forestry machines were used to clear the plantation forests, causing almost all metal tubes from fixed plots to disappear. Plots were therefore re-established on the clear-felled sites in 2011. In the older parts of the forests, plots were re-established based on GPS coordinates, descriptions and pictures from 2010, but that was not always possible in the denser Sitka spruce plantations. However, the vegetation within the young plantations was very homogenous and we consider new plots to be comparable to re-established plots. We added six more plots on clear-fellings of the young plantation forests, so that we had 12 plots from open and older plantations and 12 plots from dense and younger plantations. Altogether, both NIL and SIL have 24 permanent plots for

vegetation analyses on clear-felled Sitka spruce sites. The sample plots were placed on relatively flat areas to facilitate comparable between-plot conditions of exposure and slope.

Each sample plot (1 m<sup>2</sup>) was tagged with GPS coordinates and fixed by metal tubes that were placed in all four corners. Metal tube length varied with the different depth of the soil/chips substrate. In 2014 a labelled wooden peg was placed adjacent to one corner of each plot to help re-finding the plots in subsequent years, and in 2017/2018 another peg was positioned at the diagonal corner. All sample plots and surroundings were photographed during the subsequent surveys. GPS-coordinates and close-up photographs were used to reposition some plots where metal tubes were not easily found.

We used a metal frame (1 × 1 m) for vegetation analyses. Metal rods were slid into permanently positioned metal tubes in the ground through a hole in each corner to fix the frame in position during analysis. The frame was divided into 16 subplots (0.25 × 0.25 m). Within each subplot we noted presence of bryophytes, vascular plants and counted the number of Sitka spruce seedlings (first and second growth season only). We also estimated the percentage cover to the nearest 5%, of tree, shrub, field and ground layer, chips, bare rock and bare soil/litter. In the final survey (2017 and 2018) we also used a modified Hult–Sernander scale to estimate percentage cover of individual plant species: 1 = 0–1.56%, 2 = 1.56–3.125%, 3 = 3.125–6.25%, 4 = 6.25–12.5%, 5 = 12.5–25%, 6 = 25–50%, 7 = 50–100%. Plants that were not determined to species in field were collected and identified in the laboratory. Soil was sampled next to each plot, with the exception of chips plots where it often was difficult to extract soil. Soil samples were stored frozen and analysed at a professional laboratory.

Chips layers on NIL were categorised as follows: I = up to 10 cm and some bare soil could be visible. II = 10–20 cm deep, and III = deeper than 20 cm.

It was often difficult to separate the abundant *Juncus* species in field, and *Juncus effusus* and *J. conglomeratus* are therefore treated as one species in the statistical analyses. This also applies to *Hypnum cupressiforme* Hedw. and *H. jutlandicum* Holmen and Warncke.

Coastal heathland data from islands in the same region (Saure et al. 2013) were used as a proxy for target vegetation after restoration (Table 1). The target heathland vegetation can be classified as acid coastal heath (T34-C2) (Halvorsen et al. 2015). Lack of maintenance has allowed encroachment of *Juniperus communis* and individual trees on these sites (e.g. Sitka spruce, Scots pine and birch *Betula pubescens* Ehrh.),

Table 1. Sites with information on number (n) and type of sample plots (1 m<sup>2</sup>), and year of sampling. For more information about target vegetation sites see Saure et al. 2013.

Sites	Vegetation	n		Sampled (years)	Years after clearing
		All plots	Chips plots		
Nordre Ilholmen (NIL)	Clear-felled Sitka spruce plantations	24	12	2010, 2011, 2014 and 2017	1, 2, 5 and 8
Søre Ilholmen (SIL)	Clear-felled Sitka spruce plantations	24	5	2011, 2012, 2014 and 2018	1, 2, 4 and 8
SIL	Sitka spruce plantations	18	–	2010	
Karmøy, Austevoll, Øygarden and Radøy	Coastal heathland (target vegetation)	24	–	2009	

but no trees are growing in the target vegetation sample plots. A dense field layer is dominated by *Calluna* and other ericaceous species (e.g. *Vaccinium* species, *Empetrum nigrum* and *E. tetralix*), and graminoids such as *Avenella flexuosa* Drejer, *Carex* species, *Trichophorum cespitosum* Hartm. and *Molinia caerulea* Moench. The most common herbs are *Potentilla erecta* Rausch. and *Trientalis europaea*. The high bryophyte cover consists mainly of *H. cupressiforme/jutlandicum*, *Pleurozium schreberi* (Willd. ex. Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., *Rhytidiadelphus loreus* (Hedw.) Warnst., *R. squarrosus* (Hedw.) Warnst. and *Sphagnum* species.

Data from 16 sample plots (0.25 × 0.25 m) were combined to one «target plot» (1 m<sup>2</sup>) with frequencies 0–16, and a total of 24 such 1 m<sup>2</sup> target plots were created to match the number of sample plots (1 m<sup>2</sup>) on the NIL and SIL islands. The target plots were surveyed by using the same methods as for the experimental plots described above.

## Data analysis

Species richness is measured as mean species number per sample plot, and was calculated for plant functional groups (herbs, ericaceous species, woody species, graminoids and bryophytes). Mean frequency (0–16) per plot (1 m<sup>2</sup>) of a species or functional plant group is used as a measure of abundance. Functional group frequency is mean sum of frequency (0–16) of all species within each functional group per sample plot. Differences in species richness, functional group frequencies and soil conditions between treatments (islands (NIL and SIL), and chips application (with and without chips)) were tested by Welch two-sample t-tests in R ([www.r-project.org](http://www.r-project.org)).

Successional trend for species composition on the two islands was modelled using detrended correspondence analysis (DCA) with downweighting of rare species. Ordination analyses were done in Canoco 5 (ter Braak and Šmilauer 2012). Target heathland vegetation sample plots and pre-clearing Sitka spruce forest sample plots from SIL 2010 were included in the analyses for each island. Centroids, the weighted average location of samples for each treatment, are shown in the DCA diagrams to indicate the direction of the successional trajectory. Species data are within-plot frequencies (0–16).

As the target plots were from a limited area, differences between successional plots and the full range of relevant target vegetation may be larger than indicated in the ordinations, although the low variance in species composition for target plots along axis 1 in the DCA ordinations indicate that the target plots represent a stable proxy for this project's target coastal heathland vegetation.

## Results

### Revegetation and abundances of functional groups

Before clear-felling, vegetation cover was low (20%) within the plantation forests on SIL (Fig. 3). At the onset of succession on non-chips plots, vegetation cover was higher on

NIL than on SIL because of a high bryophyte cover (54%) which was maintained throughout the succession (Fig. 3). Revegetation commenced earlier on SIL than on NIL, but vegetation cover was complete on both islands by the fourth/fifth year of the succession on non-chips plots (Fig. 4A, E). After chipping, a high chips cover (>90%) was stable in the first two years of the succession (Fig. 3). Revegetation on chips treatment was faster on SIL than on NIL throughout the succession, but vegetation cover was almost complete on both islands by year eight (Fig. 4D). It was a clear trend that vegetation cover was lower for chips plots than for non-chips plots during succession, especially for the ground layer, NIL field layer and shrub layer (Fig. 3). At the end of this study (year eight) non-chips shrub cover was low (8%), field layer cover was high (65% and over 85% on NIL and SIL respectively) and ground layer cover varied from high on NIL treatments (ca 60%), to very low on SIL chips plots (8%).

Abundances (mean sum of frequencies) of functional groups such as herbs, graminoids and woody species were mostly higher on SIL non-chips plots throughout the succession, than on the other treatments (Fig. 5). Similarly, functional group abundances tended to be higher on non-chips plots than on the chips plots within each island, although these differences were mostly non-significant by year eight. In contrast, non-chips bryophyte cover was higher (non-significant) on NIL than on SIL, and abundances of ericaceous species were higher on NIL treatments than on SIL treatments after year two (Fig. 5). From this stage in the succession, ericaceous species, including the key heathland species *Calluna* and *E. tetralix*, increased on NIL treatments whilst they steadily decreased on SIL non-chips plots, and were nearly absent by the eighth year (Fig. 5). In year eight *Calluna* was present in almost all sample plots on NIL, and frequencies were high (11–16) within 40% of the non-chips plots (not shown). However, its mean cover was low (ca 5%). On NIL, abundances were higher (non-significant) on non-chips plots than on chips plots, whilst ericaceous species never established on SIL chips plots.

### Successional trajectories and species composition

DCA gradient lengths on NIL and SIL are 4.9 and 3.84 SD, respectively. The first DCA axis provides the highest explanation of variation in species composition (14.13 and 15.09%, respectively), the second axis adding 6.6% (gradient length 3.12 SD) and 5.86% (gradient length 3.60 SD). NIL island successional plots (first, second, fifth and eighth year after clear-felling) are positioned between target heathland vegetation plots (target vegetation) and SIL Sitka spruce plantation plots (spruce forest) along DCA axis 1 (Fig. 6A). As indicated by the centroids, there is a successional trend that NIL vegetation plots move towards the target vegetation plots along DCA axis 1. In contrast, SIL island plots are more clearly separated from target vegetation plots (Fig. 6C), and they have moved away from the target vegetation during succession. Centroids indicate that chips plots on SIL are moving further away from target vegetation plots than non-chips plots. Successional plots



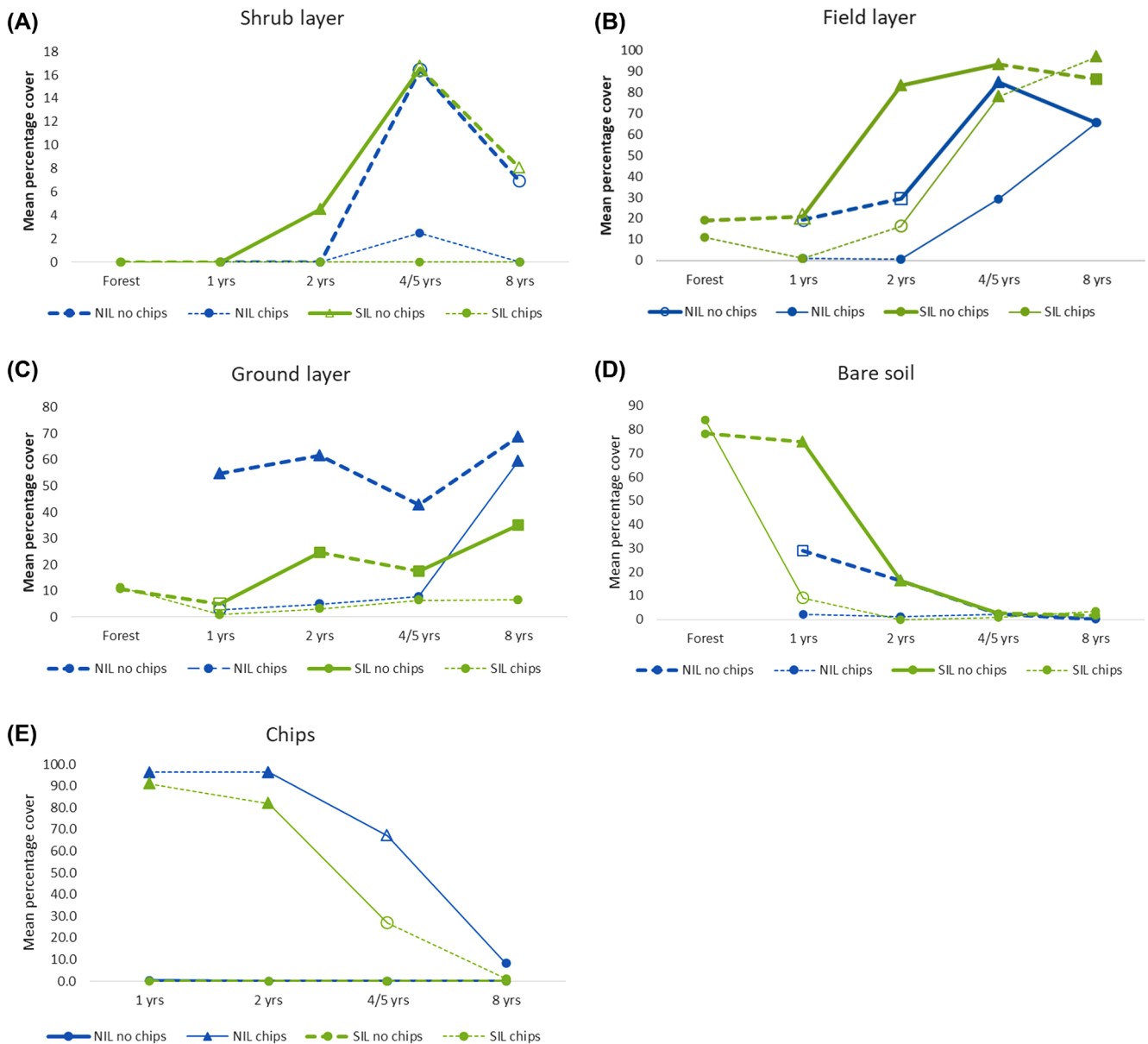


Figure 3. Mean percentage cover of vegetation layers (A–C), bare soil (D) and wood chips (E). Significant changes ( $p < 0.05$ ) between surveys are shown with full lines. Significant differences between treatments ( $p < 0.05$ , within same survey) are shown with different symbols (open symbols are regarded as similar). Forest = Sitka spruce plantations before clear-felling. Yrs = years/growth seasons after clear-felling. Colour indicates island (NIL/SIL), thick lines indicate plots without chips (no chips) and thin lines indicate chips plots.

on NIL and SIL move downwards along DCA axis 2 (Fig. 6A, C). Centroids also indicate that SIL plots are moving away from spruce forest plots along DCA axis 2 (Fig. 6C).

The target heathland vegetation consists mostly of the functional groups of ericaceous species and graminoids. The most frequent target species is *C. vulgaris*, along with *A. flexuosa*, *Vaccinium vitis-idaea*, *E. nigrum*, *P. erecta*, *V. uliginosum*, *E. tetralix*, *J. communis*, *Carex* species, *T. cespitosum*, *T. europaea*, *M. caerulea* and *V. myrtillus*. Next in abundance are e.g. *Salix repens*, *Narthecium ossifragum* Huds., *Eriophorum* species, *Agrostis* species and *Nardus*

*stricta*. Few bryophytes have high frequencies in the target heathland vegetation. The most frequent bryophytes are *H. cupressiforme*/jütlandicum, *P. schreberi*, *H. splendens* and *R. loreus*. Next in abundance are *R. squarrosus*, *Sphagnum* species, *Racomitrium lanuginosum* (Hedw.) Brid., *Calypogeia muelleriana* (Schiffn.) Müll.Frib., *Pseudoscleropodium purum* (Hedw.) M. Fleisch., *Polytrichum commune* Hedw., *Thuidium tamariscinum* (Hedw.) Schimp. and *Plagiothecium undulatum* (Hedw.) Schimp. Target heathland species are positioned on the upper half of positive DCA axis 1 of the ordinations of NIL and of SIL (Fig. 6B, D).

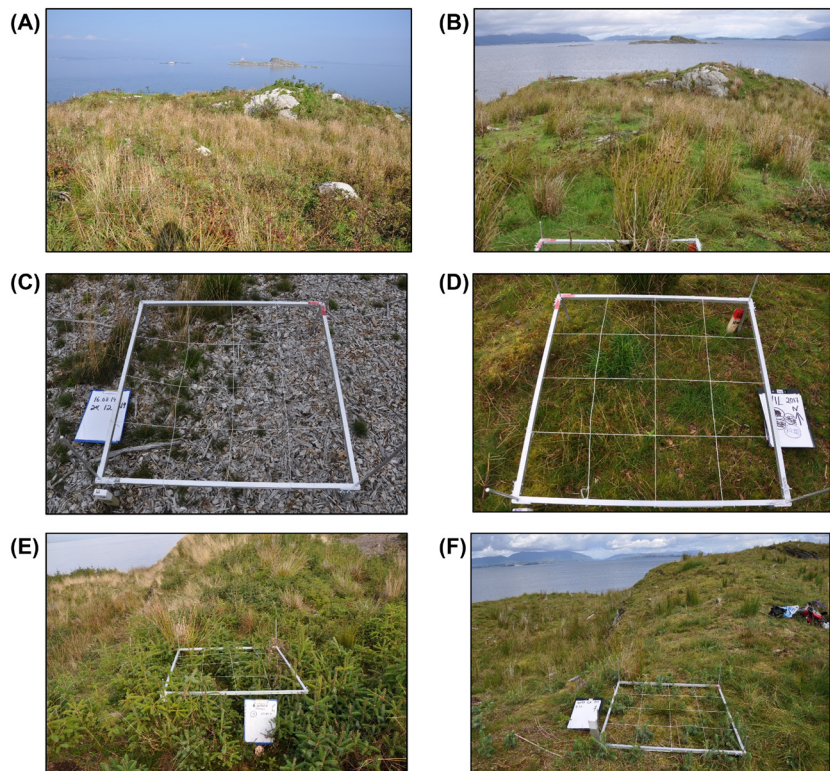


Figure 4. Vegetation on SIL (A and B) and NIL (C–F). (a) SIL non-chips area in year four. (B) The same non-chips area in year eight. View towards NIL. (C) NIL sample plot on deep chips layers in year five. (D) The same plot on deep chips layers in year eight. *Calluna* frequency (i.e. presence in subplots) was six. (E) NIL non-chips area in year five with re-established Sitka spruce. (F) The same plot on non-chips area in year eight. Re-established Sitka spruce had been manually cleared in 2015. *Calluna* frequency was 13 in year eight.

NIL shared many species with the target heathland vegetation, especially on non-chips plots, and most of these species were ericaceous species (Supporting information). These species are positioned on the mid-section of positive DCA axis 1 (Fig. 6D), and along the positive DCA axis 2. Species with the most similar abundances (frequency) to target vegetation were *Calluna*, *V. myrtillus*, *Carex* species and *P. erecta*. Other ericaceous species had markedly lower frequencies than in target vegetation, especially *E. nigrum*. Furthermore, NIL was lacking *V. uliginosum*. Chips plots had similar abundances of *Carex* species and *P. erecta* compared to non-chips plots, otherwise their abundances were lower than on non-chips. *A. flexuosa* was shared with target vegetation, but its abundances were much higher on NIL than in the target vegetation and there were small differences between non-chips and chips plots. NIL and target vegetation shared the most common target bryophytes, such as *H. cupressiforme/jutlandicum*, *H. splendens*, *P. schreberi* and *R. loreus*. It varied how similar the frequencies were between target vegetation and treatments with and without chips, but the heathland bryophyte *P. schreberi* was markedly more frequent in target vegetation. Other heathland species that had low abundances in target vegetation, had much higher abundances on NIL (e.g. *P. undulatum* and *P. purum*). Non-target vegetation species are positioned along the mid-section of DCA axis 1, and mostly at the negative part of DCA axis 2 (Fig. 6B). Non-target vascular plants

on non-chips plots included the woody species *Picea sitchensis* juv., graminoids such as *Holcus lanatus*, *Agrostis capillaris*, *J. effusus/conglomeratus* and *Luzula pilosa* Willd., and a few herbs like *Galium saxatile* and *Sedum anglicum* Huds. Sitka spruce seedling establishment was markedly higher on non-chips treatment than on chips (500 versus 83 seedlings in year one, respectively), and seedling numbers were reduced on deeper chips layers (not shown). In year five young *P. sitchensis* (juv.) had attained a height of up to 1.3 m and formed dense mats on parts of NIL (Fig. 4E). Before the final survey this species was partially removed by intervention, but in year eight *P. sitchensis* (juv.) was still present on 50% of the non-chips plots. The graminoids were less frequent on chips plots, but there were more herbs (e.g. *S. anglicum*, *Rumex acetosella*, *R. acetosa*, *Senecio vulgaris* and *Digitalis purpurea*). Only *S. anglicum* was of fairly high frequency. Bryophytes that separated the target vegetation from NIL were mainly frequent species (other heathland species above), as well as higher frequencies of e.g. *Dicranum scoparium* (Hedw.) and *Polytrichastrum formosum* (Hedw.) G. L. Smith. On chips *Campylopus flexuosus* (Hedw.) Brid. was also a frequent bryophyte.

SIL shared few species with the target vegetation, and there were almost no ericaceous species in year eight. Shared vascular species were *A. flexuosa*, *Carex* species and *P. erecta*. *P. erecta* was less frequent on SIL than in target vegetation, but the graminoids had quite similar frequencies compared



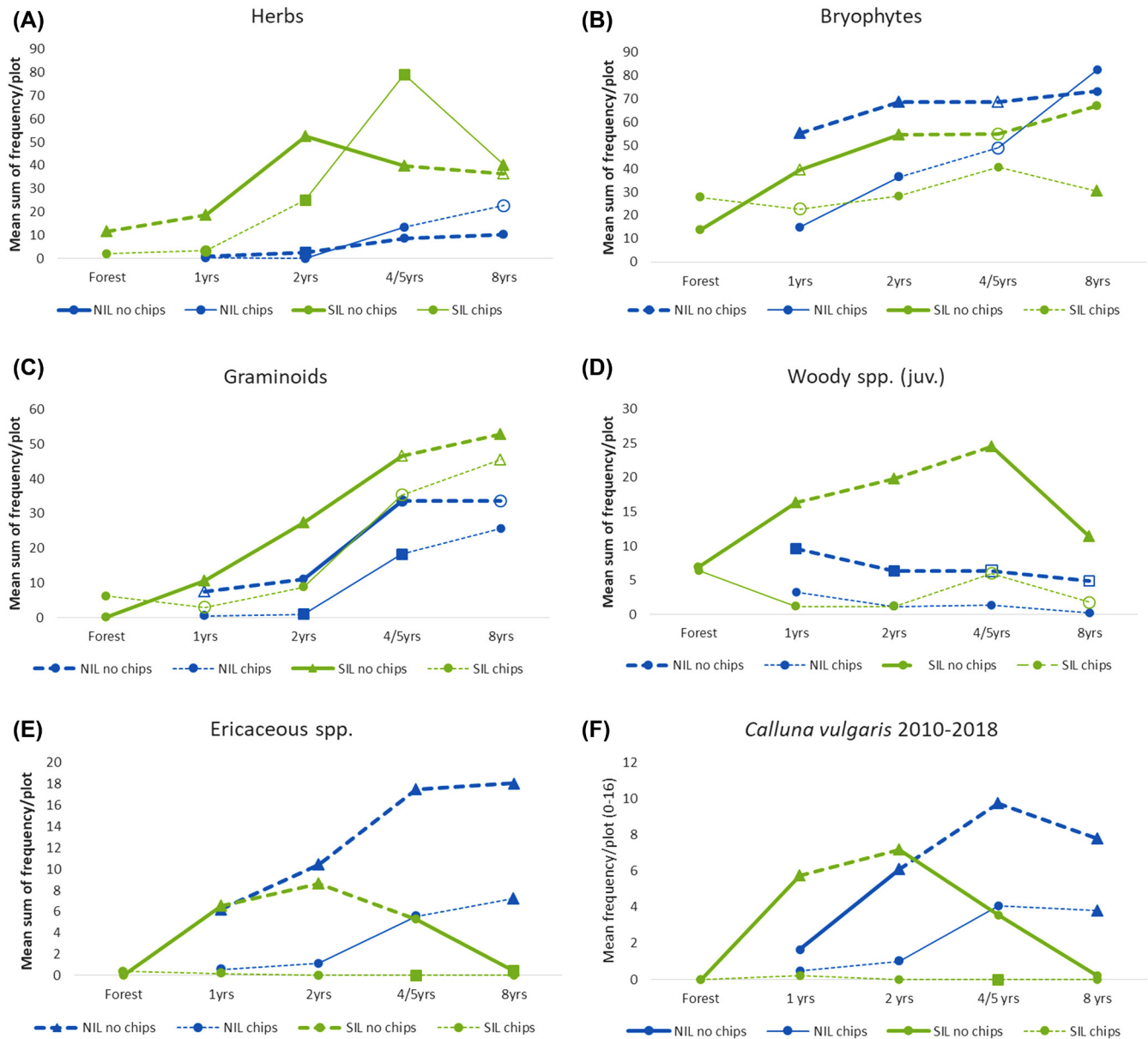


Figure 5. Mean sum of frequencies for different functional groups (A–E), and *Calluna vulgaris* (F), per 1 m<sup>2</sup> plots. Significant changes ( $p < 0.05$ ) between surveys are shown with full lines. Significant differences between treatments ( $p < 0.05$ , within same survey) are shown with different symbols (open symbols are regarded as similar). Forest = Sitka spruce plantations before clear-felling. Yrs = years/growth seasons after clear-felling. Colour indicates island (NIL/SIL), thick lines indicate plots without chips (no chips) and thin lines indicate chips plots.

to target vegetation (although *A. flexuosa* was little established on chips plots). These species are positioned at the mid-section of positive DCA axis 1 (Fig. 6D). Except for *P. schreberi*, the target bryophytes were mostly present on SIL. The most abundant target vegetation bryophytes had markedly lower frequencies on SIL (e.g. *H. cupressiformeljutlandicum* and *H. splendens*), *R. loreus* had similar frequencies to target vegetation, and some target vegetation bryophytes had markedly higher frequencies on SIL (e.g. *R. squarrosus* and *P. purum*). Vascular plants on SIL were mostly graminoids (e.g. *H. lanatus*, *J. effusus/conglomeratus*, *Poa annua*, *A. flexuosa*, *A. capillaris* and *Carex* species) and herbs (e.g. *Oxalis acetosella*,

*D. purpurea*, *P. erecta*, *Epilobium* species, *Cerastium fontanum* Baumg., *Stellaria media* Vill. and *S. vulgaris*). These species are mostly positioned on the lower half of positive, and the negative side of, DCA axis 1, and on both sides of DCA axis 2 (Fig. 6D). On chips plots other herbs were also present, such as *R. acetosella*, *Plantago lanceolata*, *Scutellaria galericulata* and *Galeopsis bifida* Boenn., and these species are positioned along the negative part of DCA axis 2 (Fig. 6D). The woody species *Rubus fruticosus* was highly frequent on non-chips plots (Supporting information) together with some *Sambucus racemosa*, and they are positioned on the positive part of DCA axis 2. The most abundant (frequent) bryophytes

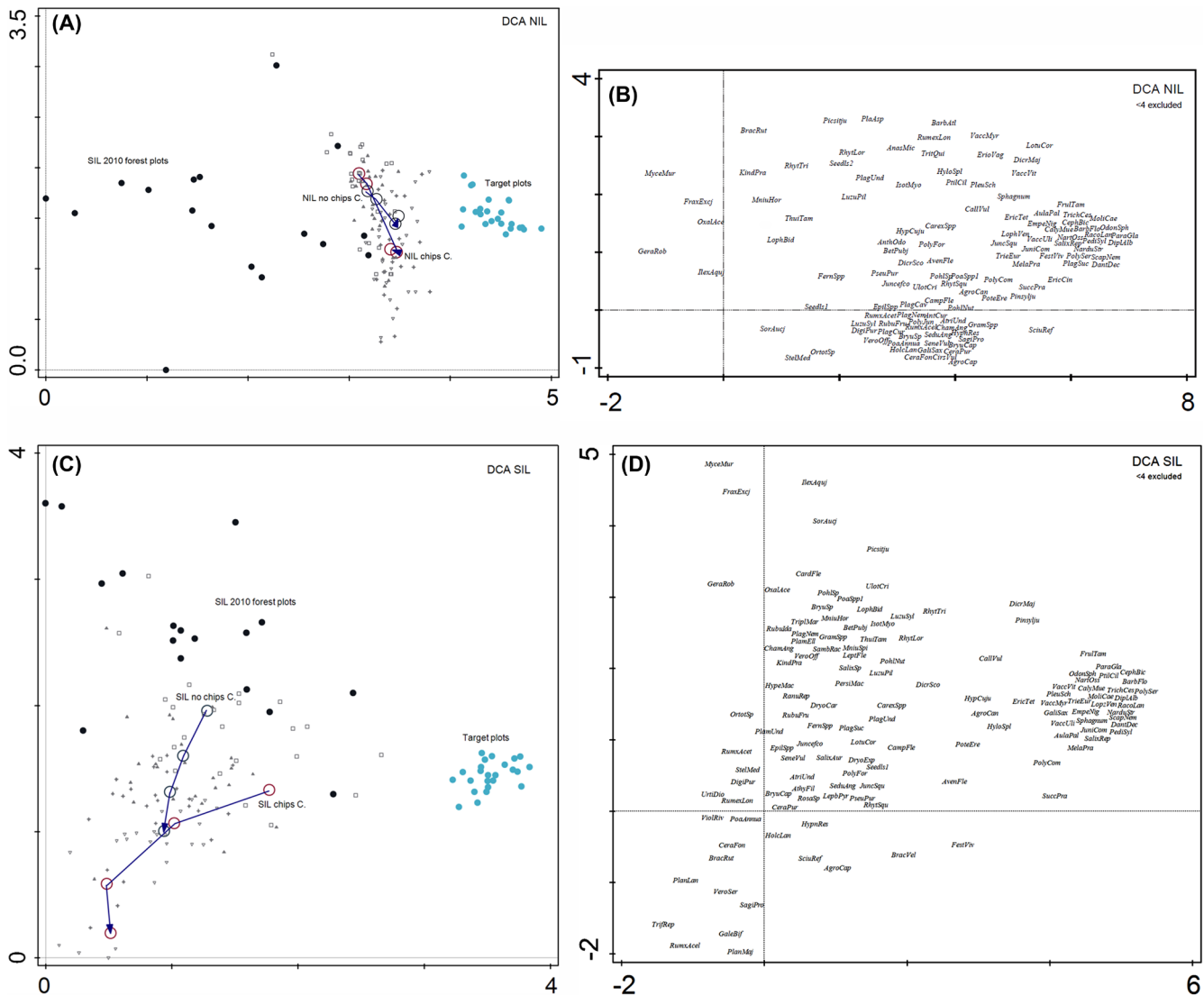


Figure 6. DCA ordination diagrams of vascular plants and bryophytes on NIL (A and B) and SIL (C and D), both including target coastal heathland vegetation and SIL spruce plantations before clear-felling. Tree layer species from spruce plantations are excluded from the analyses. Species present in less than four plots are not shown (B and D). The successional trajectory for treatments with and without chips is displayed by one centroid (C) for each survey (years 1, 2, 4/5 and 8) and sample plots are shown with different symbols for each survey (square, upward triangle, star and downward triangle from year 1–8) (A and C).

on SIL were *Kindbergia praelonga* (Hedw.) Ochyra, *R. squarrosus* and *R. loreus*. Other bryophytes included *P. purum*, *P. formosum*, *H. cupressiformeljutlandicum*, *H. splendens* and *Brachythecium rutabulum* (Hedw.) Schimp. Chips plots had few abundant bryophytes, *B. rutabulum* was one of the most frequent together with *R. squarrosus* and *K. praelonga*.

### Species richness

Before clear-felling, mean species richness was low within the SIL plantation forests (<10 species per plot, Fig. 7). Mean species richness increased immediately after clear-felling on *non-chips* treatments on SIL and reached a maximum of ~ 33 species per plot at the second year (Fig. 7). On NIL, species

richness increased gradually throughout succession, reaching its maximum in year eight (~19 and 22 species per plot on *non-chips* and *chips*, respectively). Treatments with chips had lower mean species richness than their respective *non-chips* treatments during the first and second year (Fig. 7). At the eighth year, species richness was highest on *non-chips* treatment on SIL, whilst there was no longer any difference in species richness between the other three treatments (Fig. 7).

### Soil chemistry

Soil chemistry (loss on ignition, cations, phosphorous and pH) was largely similar on NIL and SIL throughout the succession (Supporting information). Mean pH was 4.9 within

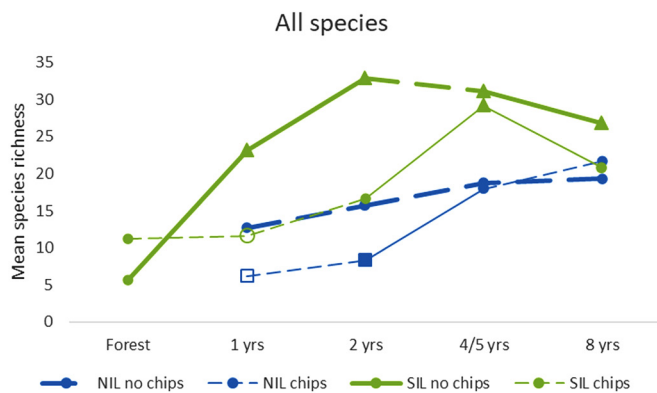


Figure 7. Mean species richness of vascular plants and bryophytes for treatments (1 m<sup>2</sup>) with and without chips on NIL and SIL. Significant changes ( $p < 0.05$ ) between surveys are shown with full lines. Significant differences between treatments ( $p < 0.05$ , within same survey) are shown with different symbols (open symbols are regarded as similar). Forest = Sitka spruce plantations before clear-felling. Yrs = years/growth seasons after clear-felling.

the planted Sitka spruce forests, and the highest mean pH values on both NIL and SIL were measured two years after clear-felling (non-chips pH 5.1 and SIL chips pH 5.8, Supporting information). By year eight, pH was higher on SIL than on NIL (non-chips 4.9 versus 4.6,  $p = 0.01$ , chips 5.1 versus 4.7  $p = 0.02$ ). Plant available phosphorous (P) and cations (magnesium, calcium, potassium and sodium) displayed a drop in measured values during the last 3–4 years of succession, but calcium (Ca) levels were markedly higher on SIL than on NIL during the first four years of succession (Supporting information).

## Discussion

### Restoration potential after clear-felling

Eight years after clear-felling there are clear differences between the successional vegetation on the two investigated islands and target heathland vegetation, as indicated by the ordination analyses. Graminoids dominate the vegetation on both islands (NIL and SIL), rather than a characteristic vegetation layer of ericaceous species. However, the successional trajectory on one of the islands (NIL) is showing increased similarities to target heathland vegetation. These similarities are reflected in the presence and abundances of the key heathland species *Calluna*, other ericaceous species (*Vaccinium myrtillus*, *V. vitis-idaea* and *E. tetralix*), heathland graminoids (e.g. *A. flexuosa* and *Carex* species), *P. erecta*, *H. cupressiformel jutlandicum*, *H. splendens*, *R. loreus* and *P. schreberi*. In contrast, species composition on SIL has developed in a direction away from target heathland vegetation, during the eight years of natural succession. The two investigated islands have opposing successional trends with respect to the key heathland species *Calluna*, and different functional groups dominate on NIL and SIL, there are more herbs, graminoids and

shrubs (woody species) on SIL, but markedly lower abundances of ericaceous species than on NIL. Furthermore the two islands differ in which woody species that establish to constitute potential threats to heathland restoration.

Restoration of coastal heathlands depends on the successful re-establishment of ericaceous species, and especially the key heathland species *Calluna* (Gimingham 1992). *Calluna* has become one of the most common vascular plants on NIL eight years after clear-felling of the Sitka spruce plantations, and *E. tetralix* (and even *E. cinerea*) establishes during the latter half of the succession. This indicates that there is a potential for further increase through natural succession after clear-felling, and that ericaceous species with time can attain a dominant position typical for coastal heathlands. Cover of *Calluna* on NIL is still very low (ca 5%). Restoration projects that rely on natural succession have achieved high *Calluna* cover within the time frames of our study (mean *Calluna* cover of 40% on former pine plantations in the UK, Walker et al. 2004), but it can also be a longer process, as showed by Degn (2001) and Allison and Ausden (2006) where *Calluna* became a dominant species after 12–15 years of natural succession on former pine plantations and agricultural fields, respectively. A limiting factor on the NIL and SIL islands could be the lack of access to wind-borne propagules to assist *Calluna* establishment (Barclay-Estrup and Gimingham 1994, Degn 2001, Pywell et al. 2002, Allison and Ausden 2006).

Interestingly, *Calluna* established immediately after clear-felling on both islands. This is most likely due to germination from a persistent *Calluna* soil seed bank, facilitated by clear-felling and soil disturbance by forestry machines (Walker et al. 2004, Allison and Ausden 2006, Henning et al. 2017) and favourably acidic and nutrient-poor soil conditions (Pywell et al. 2002, Walker et al. 2004). It is known that seed longevity of *Calluna* may exceed 60 years in the soil (Bakker et al. 1996). The initial decrease of *Calluna* on SIL, following the first two years of succession, coincided with the successful development of *R. fruticosus*, a shade-tolerant perennial woody plant that is scarcely present on NIL. *R. fruticosus* is known to negatively influence establishment of other species (Decocq et al. 2004), and *Calluna* is sensitive to shade when germinating (Gimingham 1972). It is therefore possible that *R. fruticosus* has overshadowed *Calluna* on SIL at this stage of succession. Similarly, the significantly higher abundance of graminoids and non-heathland herbs on SIL than on NIL, is likely to have contributed to outcompete ericaceous species on SIL only (Aerts 1999, Owen and Marrs 2000, Walker et al. 2007). However, a well developed graminoid cover on NIL may have contributed to the stagnation of ericaceous abundances during the last three years of our survey. Availability of soil nutrients could facilitate the high abundances of graminoids such as *H. lanatus*, *A. capillaris* and *J. effusus/conglomeratus* on SIL (Wolff et al. 2017), but measured soil conditions are not likely to explain why *Calluna* failed to establish a viable population on this site. Although pH is higher on SIL than on both NIL and target heathlands during the latter half of the succession (4.9 vs 4.6



at the eighth year, and 4.6 respectively), pH is still within the range that ought to be suitable for *Calluna* establishment (up to pH 5 (Pywell et al. 2002)). Calcium levels are 3–4 times higher on SIL than on NIL during early-mid succession, but calcium concentrations three times higher than on SIL are found on a restored heathland in Denmark, where otherwise pH and cations were fairly comparable to NIL and SIL (Degn 2001), indicating that the SIL calcium levels are not directly detrimental for *Calluna's* establishment.

The establishment of woody species that constituted a fairly extensive shrub layer on NIL and SIL, such as Sitka spruce, *S. racemosa*, and *R. fruticosus*, is a potential threat to heathland restoration when they produce dense and widespread thickets (Mitchell et al. 1997, Borchard et al. 2017). We do not know why the shrub layer on SIL declines after mid-succession of our study, and future studies are necessary to see if the *Sambucus* and *Rubus* species will continue to decline or whether they will regain a high cover in parts of the island. The dense and tall mats of re-established Sitka spruce that covered parts of the NIL island required manual removal of this non-target species in 2015. Had no action been taken, dense patches of Sitka spruce could eventually have outshaded heathland species (Saure et al. 2013, Saure et al. 2014). Our findings are in line with other studies where re-emergence of Sitka spruce poses a threat for the restoration of coastal heathland on clear-felled sites (Vesterbukt 2018, 2019). Grazing by old Norse sheep can reduce the survival of Sitka seedlings, but manual removal of Sitka spruce is sometimes necessary (Vesterbukt 2018, 2019).

Our results indicate that one cannot expect to rely solely on natural succession to restore coastal heathland after removal of coniferous plantations, as the key heathland species *Calluna* failed to establish on the SIL island, *Calluna* cover is still very low on the NIL island, and manual removal of re-emerging Sitka spruce was deemed necessary on the NIL island. Streitberger et al. (2021) similarly found that natural succession is not sufficient to restore montane heathland on wind-felled clearings in Germany. Read and Bealey (2021) reported partially successful restoration of dry and wet heath in the UK after clear-felling of secondary woodland, but *Calluna* cover remained fairly low and colonisation of woody species had to be kept in check. Seed transfer (e.g. via hydroseeding) and addition of chopper material from heathlands could enhance the establishment of target species such as *Calluna* on both NIL and SIL (Walker et al. 2004, Tibbett et al. 2019, Streitberger et al. 2021), but such management strategies are expensive. The different successional trends on NIL and SIL demonstrate that it is difficult to foresee the results of restoration projects, underlining that there cannot be one prescribed method of restoration (Marrs and Britton 2000, Owen and Marrs 2000, Kreyling et al. 2011, Gallet and Sawtschuk 2014). Indeed, passive restoration may be successful—some studies find that natural succession may restore heathlands after clear-felling of conifer plantations in the UK (Walker et al. 2004, Allison and Ausden 2006) or after fencing of heavily trampled heathlands in France (Sawtschuk et al. 2010).

## Impact of wood chips cover on heathland restoration

Our study of eight years of succession on Ilholmane Nature Reserve shows that although there are initial negative impacts of chips cover on revegetation and species richness, the effects are rather short-term. These findings are in line with other studies that report reduced vegetation cover and species richness after mulching during the first 1–5 years after treatment (Greenly and Rakow 1995, Miller and Seastedt 2009, Wolk and Rocca 2009, Dodson and Peterson 2010, Santana et al. 2014), and that mulching effects are enhanced with increasing depth (Greenly and Rakow 1995, Wolk and Rocca 2009, Dodson and Peterson 2010). However, early mulching effects could also be neutral or positive (Kruse et al. 2004, Kim et al. 2008). For ecological restoration, revegetation is key, and our study shows that it could take more than five years to revegetate when mulching with wood chips on clear-felled sites, but that after eight years the study sites are almost completely revegetated, irrespective of chips depth, and there is little difference in species richness between the treatments with and without chips. Santana et al. (2014) only found wood chip effects on revegetation and species richness the first two years when using mulch as a post-fire rehabilitation treatment. Bontrager et al. (2019) did not monitor the early stages of post-fire succession, but found no effects of straw-mulching on revegetation, species richness or species composition on 9–13 year old sites. This indicates that mulching effects can be short-term, and that mulches such as wood chips may be left on restoration sites without having prolonged negative impact on vegetation cover or species richness.

In our study we find some differences in species composition between areas with or without chips, such as more non-target herbs and fewer woody species on chips plots. In general, the islands' contrasting successional trajectories towards target heathland vegetation (i.e. restoration potential), are also displayed on chips-covered areas. The ordination analyses indicate that the impact of chips on species composition is larger on one of our study sites (SIL), than on the other (NIL). This is reflected in a poorly developed bryophyte cover, no establishment of ericaceous species, and a high establishment of herbaceous species that peaked during mid-succession on SIL. A likely immediate impact of wood chips cover is to act as a physical barrier for the *Calluna* seed bank (Pywell et al. 2002, Chalker-Scott 2007), which may explain the delayed establishment of ericaceous species found on chips plots. Our study shows that this delay could be short-term as all key heathland species, including *Calluna*, are shared between the two treatments on NIL by year eight. In contrast, no ericaceous species established on the SIL chips plots during the eight years that we monitored the succession.

Many non-target species that established during the clearing-induced succession were pioneers and ruderal herbs, graminoids and bryophytes that easily disperse by wind-borne propagules. The covering of large areas with wood chips create available sites for establishment, with reduced competition from species that germinate from a soil seed

bank. This may explain why herbaceous plants seem to establish to a greater extent on chips plots than on non-chips areas, and low bryophyte cover on SIL chips plots may have further facilitated their establishment.

Interestingly, fewer Sitka spruce seedlings established on chips plots in year one than on areas not covered by chips, and even though several seedlings survived, their cover was significantly lower on chips during early to mid-succession. Also, we find that the functional group of woody species that also includes *S. racemosa* and *R. fruticosus* establish to a markedly lower extent on chips plots. This indicates that woody species establish to a lower extent on mulch, such as wood chips, than on unmulched clear-felled sites. However, other studies show mixed effects of mulch (Kruse et al. 2004, Miller and Seastedt 2009, Dodson and Peterson 2010, Bontrager et al. 2019). We are not aware of other studies on wood chips mulch after clear-felling, but Santana et al. (2014) found that high wood chips cover on post-fire sites reduced initial establishment of one woody species but did not affect the other (*Cistus albidus* and *Ulex parviflorus* Pourr., respectively). Although manual removal did not eliminate all Sitka individuals on NIL, no Sitka spruce was found on chips plots at the end of our survey. Woody species encroachment is a direct threat to coastal heathlands (Mitchell et al. 1997, Borchard et al. 2017). We do not know whether Sitka spruce establishment eventually failed on the chips substrate, or whether it was easier to target and manually remove the Sitka spruce seedling during the action in 2015, or if both factors have contributed to this result. The lack of Sitka spruce eight years after clear-felling nevertheless indicates that it may be beneficial to leave wood chips on clear-felled sites in order to reduce re-establishment of Sitka spruce, and that deep chips layers are more efficient than shallow layers. Leaving wood chips on site may therefore be a useful strategy to both reduce cost-demanding management action and facilitate restoration towards coastal heathland.

Another important factor for Sitka spruce recruitment is timing of clear-felling. This may explain the differences in the degree of re-establishment of Sitka spruce between our two study sites. If cones are open when the tree is felled, there will be an extensive seeding as the trees fall to the ground, but it is possible that cones were not yet open when the plantations were clear-felled in November on SIL (Vikane, J. H. 2022. Associate Professor at Volda University College). Avoiding clear-felling at mast years or when cones are open is therefore wise in order to reduce unnecessary and costly removal of unfavourable coniferous species that reemerge on a restoration site.

### Possible effects of grazing and land-use history

Several factors that we have not investigated could also contribute to the successional trajectories that we find on the Ilholmane islands.

First, to facilitate the establishment of coastal heathland on SIL, management authorities should consider carefully the degree of winter grazing. Old Norse sheep are grazing

all year on the islands and there are more sheep than in the earlier years after clear-felling. In general, grazing is positive for development of coastal heathland, and somewhat intensive grazing at spring can be especially beneficial to avoid graminoids outcompeting ericaceous species (Kvamme, M. 2017. Consultant at Ballast Miljøhistoriske Fagtenester). Heavy grazing may shift vegetation development towards a higher cover of graminoids, at the cost of ericaceous species (Gimingham 1992, Bullock and Pakeman 1997, Newton et al. 2009). Increased levels of fertilisation by nitrogen addition from the sheep and seabirds, which inhabit the islands to a much higher degree than earlier (Dunkley, A. 2017. Operations manager at Friluftsrådet Vest), could enhance the establishment of the graminoid-dominated field layers on NIL and SIL (Bakker et al. 1983, Southon et al. 2013). Fodder is more scarce at winter and too high a grazing pressure in winter may be part of the explanation of why *Calluna* abundances have stagnated on NIL and why *Calluna* disappears on SIL (Kvamme, M. 2017. Consultant at Ballast Miljøhistoriske Fagtenester). Grazing by sheep reduces the size of *Calluna* individuals (Critchley et al. 2013), and we observed that *Calluna* individuals were of smaller stature in the sample plots during our last survey than during mid-succession. We therefore suggest that grazing could be a contributing factor to the low cover of *Calluna* on NIL, despite the fairly high frequency of this key heathland species in sample plots.

The different successional trajectories on the two islands in our study may reflect former differences in vegetation. Regular burning of heathlands has been a traditional way of maintaining this landscape (Webb 1998b, Kaland and Kvamme 2013), but we do not know if this was practiced here. It is reported that SIL had a higher degree of grass-dominated vegetation than NIL before the islands were afforested, and this would have resulted in a more poorly developed *Calluna* soil seed bank on SIL. *Calluna*'s steady decline, after the initially successful establishment on SIL, could arguably be explained by a depleted soil seed bank under the older Sitka spruce plantations (60–80 years old). Numbers of viable *Calluna* seeds have been found to decrease with time, suggesting that regeneration of *Calluna* may be restricted on older plantations (Walker et al. 2004), yet relatively large seed banks can survive for more than 70 years on conifer plantations (Pywell et al. 2002). The marked difference in species composition of woody species on SIL and NIL, could also be related to soil seed bank composition. The abundant *Rubus* species (*R. fruticosus* and *R. idaeus*) and *S. racemosa* on SIL are known to produce a viable soil seed bank (Bossuyt et al. 2002, Decocq et al. 2004, Abe et al. 2008), and different land use (e.g. reflected by presence of a leisure cabin on SIL) might have caused a different soil seed bank to develop on the two neighbour islands. Seeds of *S. racemosa* can be transported by birds (Traveset and Willson 1997, Abe et al. 2008), and we can only speculate that one or more fruiting trees have been present on SIL and that bird droppings have spread seeds very locally. That could explain why *S. racemosa* is found on SIL, but not in the surveyed vegetation on NIL.

## Conclusion

The successional changes observed over eight years demonstrate that a potential is present for restoration of coastal heathlands by spontaneous succession, although it may not be possible to rely entirely on an unassisted restoration regime. There is a restoration potential on NIL as *Calluna* establishment and survival is good, and it seems that the *Calluna* soil seed bank is still viable after more than forty years under Sitka spruce plantations. However, competition with functional plant groups, such as woody plants and graminoids, may cause stagnation or even failure of *Calluna* establishment, as seen on SIL. Leaving wood chips on site slows down revegetation, but this seems to be a short-term effect, and the chips may help to reduce the establishment of woody species that are a threat to the restoration success. The difference in successional trajectories for *Calluna* on NIL and SIL underlines how difficult it is to predict successional trends after clear-felling. Factors to take into consideration to improve the restoration potential through natural succession after clear-felling and chipping include cutting mature trees in non-mast years or when cones are unopened, grazing pressure and the amount and depths of wood chips on site.

**Acknowledgements** – We thank U. Kjær, V. Ankarstrand (CGR), R. Nordås (SNO), J. H. Vikane, K. Follesøy (SNO) and N. M. Lancaster for their field work assistance from 2010–2018. We also thank two anonymous reviewers for useful comments to our manuscript.

**Funding** – The field work was funded by the County Governor of Rogaland Norway (CGR) and NLA University College. The Norwegian Nature Inspectorate (SNO) contributed with field assistants in 2014 and 2017. All other work has been funded by the authors' respective employers. HIS: CGR, SNO, NLA; ORV: CGR, UiB; VV: UiB; KH: NTNU.

## Author contributions

**Heidi Iren Saure:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ole Reidar Vetaas:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (supporting). **Kristian Hassel:** Data curation (equal); Writing – review and editing (supporting). **Vigdís Vandvik:** Conceptualization (equal); Formal analysis (supporting); Methodology (supporting); Visualization (supporting); Writing – review and editing (supporting).

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dr7sqvb3m> (Saure et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

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