

Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands

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Summary

1. Semi-natural habitats have been shaped by human disturbance regimes for centuries. Spatially and temporally heterogeneous land-use practices, such as cutting, burning, grazing and turf-cutting, have resulted in complex mosaic landscapes that are of high priority for conservation in Europe. Contemporary conservation subjects these systems to management regimes that are generally less diverse, in terms of disturbances and fine-scale temporal and spatial variability, than traditional land use, but the ecological consequences of these simplifications are unclear.

2. We investigated the interactive effects of fire and grazing on plant species composition and diversity along local environmental (moisture) gradients in coastal heathlands. A replicated series of post-fire successions ($n = 12$) was initiated in three heathland habitats and the areas subjected to two grazing regimes. Floristic and environmental data were recorded in permanent plots over a 5-year period. Community data were analysed using multivariate ordination techniques (principal components analysis, partial redundancy analyses, and principal response curves) and generalized linear models.

3. Fire induced strong successional trends in the species composition of the heathlands. These trends differed among heathland habitats, and with grazing. Strong interactions between fire, habitat and grazing implied that the effect of grazing on the successional dynamics differed among habitats. Species diversity decreased in the first year after fire but increased beyond the pre-fire levels during succession. This trend was not affected by local environment or grazing, although there were main effect differences in diversity between environments and grazing regimes.

4. *Synthesis and applications.* Our results demonstrate that the two management practices do not have simple additive effects within the semi-natural system studied, as grazing created ecological opportunities for additional sets of species, increased variability among habitats, and added complexity to the post-fire successional dynamics. In order to preserve diversity, conservation management should thus aim to preserve the level of complexity of the traditional management regimes, both in terms of the actual disturbances (e.g. fire and grazing) as well as the spatial scales at which they are applied. Further, the considerable change in these effects along the local environmental gradient brings into question the efficiency of general management prescriptions, and indicates that local environmental variability should be taken into account in the conservation of semi-natural habitats.

Key-words: *Calluna vulgaris*, conservation management, disturbance regimes, diversity, generalized linear models, interactive effects, principal response curves, spatial variation

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Introduction

One of the central ideas in modern ecology is that disturbance plays an important role in natural communities, influencing population persistence, community composition and maintenance of diversity (Pickett & White 1985). Individual disturbances may be seen as ecological 'reset' mechanisms, creating a link to the concept of succession; the idea is that the recovery from disturbance over time is, at least to some extent, predictable (Underwood & Anderson 1994). Successional pathways after disturbance may be considerably modified by, for example, local factors, chance effects and the non-equilibrium status of most communities (McCune & Allen 1985; Glenn-Levin, Peet & Veblen 1992; Samuels & Drake 1997). The key question is therefore not 'if' but rather 'to what extent' different patches, when subjected to a disturbance, will respond in similar ways. The recovery after disturbances may indeed be considerably moderated by interactions with local environmental variation (Swanson *et al.* 1988; Menges & Hawkes 1998; Stohlgren, Schnell & van den Heuvel 1999; Harrison, Inouye & Safford 2003; Freckleton 2004; Parr *et al.* 2004) or by interactions or synergisms with other disturbances (Paine, Tegner & Johnson 1998; Wolfe-Bellin & Moloney 2000; Kulakowski, Veblen & Bebi 2003; Fuhlendorf & Engle 2004).

The understanding of relationships between disturbance, heterogeneity and succession is crucial to our ability to conserve semi-natural habitats, as these systems have emerged over millennia of often complex human-directed disturbance regimes (Fægri 1988; Lawton 1999). Traditional land-use practices are no longer economically viable and there is a general trend in developed countries of discontinuation or intensification of management practices (Edelmann 1997; Mannion 2002; WallisDeVries, Poschod & Willems 2002). The successional changes that follow abandonment have been identified as major factors adversely affecting the flora and fauna of Europe (Bernes 1993; Stanners & Bordeau 1995; Fremstad & Moen 2001). Today, different management practices are being introduced as conservation and restoration tools. These modern management systems are generally less diverse in terms of disturbance regimes and fine-scale temporal and spatial variability (Webb 1998), but it is unclear whether these simplifications have consequences for the flora and fauna of semi-natural systems.

The coastal heathlands of north-western Europe developed *c.* 4000 years ago as a result of forest clearance, and have since been maintained by spatially and temporally heterogeneous disturbance regimes, including grazing by domestic and wild animals, burning, turf-cutting and harvesting heather and bracken (Gimingham 1972; Webb 1998). For the past 50 years, these traditional management regimes have gradually been discontinued, resulting in reforestation (Skogen 1987; Granström 1988; Fremstad, Aarrestad & Skogen 1991; Webb 1998; Mitchell *et al.* 1999). The heathland ecosystem has recently

been classified as greatly endangered (EC Habitats Directive 92/43/EEC; Fremstad & Moen 2001). Different modern management regimes, including grazing at different stocking rates (Bokdam & Gleichman 2000; Pakeman *et al.* 2003), burning (Hobbs & Gimingham 1984a, 1984b; Mallik & Gimingham 1985; Øvstedal & Heegaard 2000; Britton *et al.* 2001), mechanical cutting (Calvo, Tárrega, & de Luis 2002) and turf stripping (Bokdam & Gleichman 2000), have been applied to halt the loss of this habitat. Successional trajectories may vary among areas with different environmental conditions and history (Hobbs & Gimingham 1984b; Britton *et al.* 2000), but little research effort has been directed at investigating to what extent the response to, and relationship between, different management practices are affected by the environmental heterogeneity of the landscapes.

Our aim was to investigate the interactive effects of fire, grazing and habitat on topographically diverse coastal *Calluna vulgaris* (L.) heathlands in western Norway by testing: hypothesis 1, fire induces successional change via a directional compositional response in *Calluna* heathlands; hypothesis 2, revegetation dynamics change along local environmental gradients; hypothesis 3, grazing (fine-scale disturbance) affects the revegetation dynamics; and hypothesis 4, the effects of grazing on revegetation dynamics vary with the local environment. We recorded species composition and diversity in burnt and control permanent plots ($n = 84$) from a replicated series of post-fire successions ($n = 12$) initiated in three different heathland habitats, which were subjected to two different grazing regimes (grazed or not grazed), for 5 years.

Materials and methods

STUDY AREA

The island Lurekalven (60°42'N; 5°5'E) is situated in a fjord approximately 20 km inland from the Norwegian west coast. The highest point is 54 m above sea level, and the topography is relatively rugged following the strike direction (north-west–south-east) of the Bergen Arc System (Kolderup & Kolderup 1940). Climate is oceanic, with July and January mean temperatures of 12 °C and 2 °C, respectively (Aune 1993), a long growing season (*c.* 220 days above 5 °C), abundant precipitation (1600 mm) (Førland 1993) and strong winds.

A mixed deciduous forest covered most of the island until it was cleared in *c.* AD 700 by a local farmhold (Kaland 1979). The larger part of the island then developed into *C. vulgaris* heaths, while smaller areas were used for pastures, meadows and cultivated infields. The farm was abandoned in *c.* AD 1350, and the island has since been managed for grazing (Kvamme 1982). From AD 1950 onwards the island gradually fell out of use, causing rapid reforestation, mainly by *Betula pubescens* Ehrh., in the 1980s (Kaland & Vandvik 1998). Trees and shrubs were cleared and burning and grazing

re-introduced in 1995. The overall grazing pressure has been *c.* 1 sheep ha⁻¹ year⁻¹ (S. Øpstad, unpublished data). Today, the island is largely covered by *Calluna* heath, with mires and *Salix* shrubs in wetter areas and mixed grass–heaths on more nutrient-rich soils along beaches and in former infields. Moisture is a major source of local environmental variability; dry heath on shallow soils often occurs on ridges or in south-facing areas, whereas moist heath on deeper soils often occurs on north-facing slopes or in convex, poorly drained areas.

EXPERIMENTAL DESIGN AND SAMPLING

Three heathland habitat types were chosen for this study: M, moist, north-facing; I, intermediate, on relatively flat ground; D, dry, south-facing on shallow soils. These were chosen to (i) span as wide a range of heathland environments as possible, (ii) be relatively representative of the heathlands on the island, and (iii) occur throughout the island, so that replicate sites could be established in both grazing treatments (see below). It was not possible to create and maintain ungrazed areas at several different localities on the uninhabited island. Therefore, a fence was erected across the island, dividing it into two parts, excluding grazers from one part of the island (i.e. two treatments, grazed vs. ungrazed). We established 12 experimental blocks (*c.* 100 m²), two replicates for each combination of habitat type × grazing treatment. Within each block, we laid out five 1-m² permanent plots in random positions, marked them with metal poles, and recorded frequencies of all vascular plants, bryophytes and lichens using a 1 × 1-m metal frame divided into 16 subplots. After the baseline survey in July–August 1993, all 12 sites were burnt in April 1994 and re-analysed in July–August of the following 4 years. Control plots could not be established prior to treatment because of difficulties with controlling the fires, so two control plots were placed in unburnt heath, as close as possible to each site and at similar inclinations, aspects and soil depths, in 1995. Species diversity data were compiled at three different spatial scales: site richness (number of species recorded in at least one plot site⁻¹ year⁻¹, separate data for burnt and control areas), plot richness (number of species plot⁻¹ year⁻¹) and average species density (average richness per 25 × 25-cm subplot plot⁻¹ year⁻¹). Nomenclature follows Lid & Lid (1994) for vascular plants, Smith (1978, 1990) for bryophytes, and Krog, Østhagen & Tønsberg (1980) for lichens.

Although environmental variability within and between habitat types was not the focus of the current investigation, we measured topography, slope, aspect and soil depth. Soil samples were analysed for loss-on-ignition, pH, Kjeldahl total nitrogen and exchangeable cations (Aarrestad & Vandvik 2000) for illustrative purposes.

NUMERICAL ANALYSES

A detrended correspondence analysis (DCA; Hill & Gauch 1980) suggested that linear-based ordination

methods were most appropriate. Principal components analysis and (partial) redundancy analyses (PCA and RDA; ter Braak 1994; Jongman, ter Braak & van Tongeren 1995) on a covariance matrix were used for all ordinations. Some preliminary ordinations enabled an evaluation of the experimental set-up. First, there were no significant overall differences between grazed and ungrazed areas before the experiment was initiated in 1993 ($P = 0.318$), indicating that the sampling regime was successful in selecting the same range of heathland habitats for the two grazing treatments. Secondly, there were no significant differences between the 1993 baseline and the 1995 control data ($P = 0.08$), and no temporal trend in the controls from 1995 to 1997 ($P = 0.08$). Thus, we tested treatment effects in 1994, when we lacked controls, against the 1995 control data.

Multivariate analyses: principal response curves

We tested the four hypotheses of heathland succession after fire and quantified their effects on community composition using principal response curves (PRC; van den Brink & ter Braak 1997, 1998; van den Brink, van den Brink & ter Braak 2003). PRC is a recent derivative of RDA (ter Braak 1994) that analyses the effect through time of one or more treatments relative to a control. It is coded as a partial RDA that allows for time-specific treatment effects (e.g. time × fire) while controlling for the overall temporal trend (time) and variation among experimental blocks (sites). Thus, hypothesis 1 was tested by a simple PRC contrasting burnt plots with controls, and hypothesis 2 by partialling out the main post-fire successional trend and coding the fire effects in the different habitats as different ‘treatments’. Hypothesis 3 was similarly tested by partialling out the main post-fire successional trend and then coding the fire effects in grazed vs. ungrazed sites as different ‘treatments’. Finally, hypothesis 4 was tested by partialling out the post-fire succession in different habitats and under different grazing regimes and analysing the interactions between fire, grazing, habitats and time. As the three latter hypotheses deal with among-site variation, we estimated the potential variance explained if all sites were allowed to have differential responses (i.e. the site × fire × time interaction) for comparative purposes.

Treatment effects (C_{dr}) quantify the compositional difference between treated plots and controls at each sampling date, and temporal trends can be visualized by plotting C_{dr} against time. The species weights (b_k) can be interpreted as the affinity of the species with this diagram; species with high positive values follow the overall community response and species with high negative values respond in the opposite way. To visualize and interpret differences between grazed and ungrazed post-fire successions, separate PRC were performed on data subsets and successional trends and species responses were compared.

Monte Carlo permutation tests were carried out to evaluate statistical significances. The PRC axes were tested by permuting the whole time series from individual

plots freely within sites. Changes in treatment (or contrast) effects through time were evaluated in sequential tests, where five data subsets (one per year) were constructed and the first RDA axis in each of these tested by permuting plots freely within sites. The overall compositional variation between the 12 sites (i.e. the main effects of sites) was partialled out in all PRC analyses, and permutation tests were run with 999 permutations. These analyses were performed using the software package CANOCO 4.5 (ter Braak & Šmilauer 2002), and ordination diagrams were drawn in CanoDraw 4 (ter Braak & Šmilauer 2002).

Univariate analyses: a generalized linear model equivalent to PRC

Analyses to test for the interactive effects of fire, grazing habitats and time on species diversity at different scales (measured as site richness, plot richness and subplot species density) were designed to parallel the multivariate PRC. As the data were counts and as the variance of the response variables increased with the mean, we assumed a Poisson distribution and used a generalized linear model (GLM; McCullagh & Nelder 1989) as a basis for the analyses.

As for the multivariate analyses, we started out by removing any overall temporal trend in the data (i.e. standardized for the main effect of time factorized). Successional trends were then analysed with backward elimination from full models, including the four-way interaction between time, fire, grazing and habitat. The study design implies considerable temporal and spatial dependency within the system, and classical statistical tests were therefore not reliable (Legendre & Legendre 1998). The statistical significance of each term to be eliminated from the model during the backwards selection procedure was evaluated in a permutation test where whole time series (i.e. the five censuses from each plot) were permuted freely within sites, and the sites were permuted freely among each other (Fortin & Jaquez 2000).

Results

Fire had strong effects on the heathland vegetation structure (Fig. 1) and species composition. Out of the 137 taxa encountered over the 5-year study (69 taxa of vascular plants, 58 bryophytes, and 10 lichens; see the Appendix), 16 taxa, including *Cladonia gracilis* Flörke (18 occurrences), *Cladonia furcata* Hudson (11) and *Cladonia uncialis* L. (eight), were only encountered in the 1993 baseline census or in the controls, whereas 24 species, including *Veronica officinalis* L. (26), *Leptodontium flexifolium* (Dicks.) Hampe. (23), *Hypochoeris radicata* L. (nine) and *Digitalis purpurea* L. (seven), were encountered only after fire.

The primary floristic gradients in the data reflected this strong overall effect of burning (Fig. 2). The controls and baseline samples are located at the lower right side of the diagram, and the burnt-plot trajectories

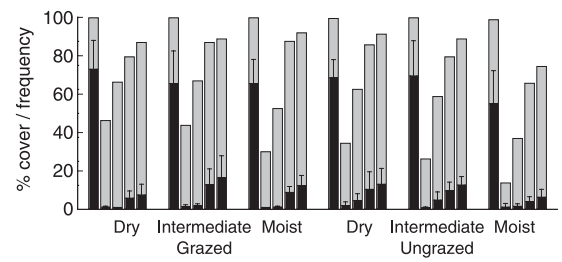


Fig. 1. Revegetation dynamics of *Calluna vulgaris* from the pretreatment year (left bar within each group) and 4 years following burning in three habitat types and under two grazing regimes. Black bars, percentage cover ± 1 SD; grey bars, subplot frequency.

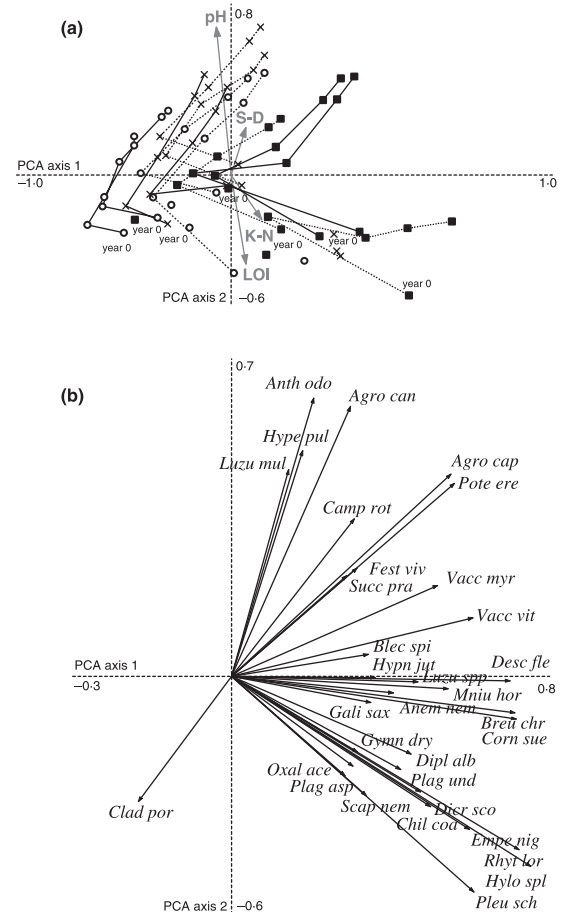


Fig. 2. PCA ordination diagram of sites (a) and species (b) from the *Calluna* heath revegetation experiment at Lygra, Norway ($n = 420$). The compositional change within the 12 sites from the 1993 pretreatment census (lower left, marked year 0) to 1997 (upper right) is drawn as trajectories on (a) with solid lines representing grazed sites and broken lines representing ungrazed sites. Controls are represented by unconnected symbols. Squares, moist, north-facing environments; crosses, intermediate; circles, dry, south-facing environments. Trends in soil pH, loss-on-ignition (LOI), total Kjeldahl nitrogen (K-N) and soil depth (S-D) are indicated. Abbreviations for species names are the four + three first letters of the genus and species names, respectively.

from each of the 12 sites run roughly parallel to PCA axis 1 (19.3% variance), with the first-year censuses located at the lower right, and the second, third and fourth post-burning years having progressively higher

Table 1. Summary of the (partial) RDA and PRC analyses. The model for each analysis is the effects specified in 'Variables' after accounting for effects specified in 'Covariables'. The percentage of the total floristic variance in the data accounted for by each model, and the significance based on a Monte Carlo permutation test (see text), is reported. S, a set of dummy variables representing the 12 sites; T, time; F, fire; E, environment (dry, intermediate or moist heath); G, grazing; $n = 420$

Testing for effect of	Hypothesis	Variables	Covariables	Variance	$P(999)$
Site		S		28.8	< 0.001
Time		T	S	10.0	< 0.001
Post-fire successional trend	1	F × T	S + T	7.8	< 0.001
Different trends among environments	2	E × F × T	F × T + S + T	3.0	< 0.001
Different trends because of grazing	3	G × F × T	F × T + S + T	1.5	0.017
Environment-specific grazing effects	4	E × G × F × T	E × F × T + G × F × T + S + T	3.9	< 0.001
Different trends among sites		S × F × T	F × T + S + T	15.4	< 0.001
Total explained by site, fire and time		S × F × T	–	62.0	< 0.001

Table 2. Summary of the Monte Carlo permutations to test the total effects of fire through time in the full data (model S × F × T; Table 1) and the grazed and ungrazed subsets (Fig. 3a,b, respectively). Year 0 is the pre-treatment baseline

	Full data			Grazed subset			Ungrazed subset		
	Trace	F -ratio	$P(999)$	Trace	F -ratio	$P(999)$	Trace	F -ratio	$P(999)$
PRC axis 1	0.06	38.7	0.001	0.07	22.5	0.001	0.07	21.3	0.001
Year 0	0.03	3.3	0.077	0.05	2.6	0.129	0.05	3.0	0.012
Year 1	0.20	24.2	0.001	0.21	12.6	0.001	0.22	13.3	0.001
Year 2	0.11	11.9	0.001	0.11	6.3	0.001	0.12	6.7	0.001
Year 3	0.08	8.5	0.001	0.11	5.9	0.001	0.08	4.2	0.001
Year 4	0.09	9.7	0.001	0.12	6.5	0.001	0.09	4.5	0.001

PCA axis 2 scores (12.2% variance). The different habitats follow partly distinct trajectories in PCA axis 1 and 2 space but, while this suggests differential revegetation trends, it is difficult to quantify and test the specific effects within a classical ordination framework.

EFFECTS ON SPECIES COMPOSITION

All hypotheses were supported in the multivariate analyses (Table 1), which implied that the strong compositional trends during post-fire succession were habitat-specific, modified by grazing, and had complex interactions. The effect of fire on compositional trends through time (hypothesis 1) accounted for 7.8% of the variance (Table 1), and was highly statistically significant, both overall and at all sampling dates except from the 1993 baseline census (Table 2). Revegetation trajectories differed significantly among habitats (hypothesis 2) and with grazing regime (hypothesis 3), but these effects were relatively weak, adding only 3.0% and 1.5% to the explained variability in the data, respectively. If different grazing effects among habitats were allowed for (hypothesis 4), a further 3.9% was added to the explained variance. Hypotheses 2, 3 and 4 were all dealing with different causes of among-site variation in post-fire successional trends, and combined they accounted for 8.4% of the total variance, just above half of the total among-site variation in successional trends (the model S × F × T; Table 1). Overall, post-fire succession in the 12 sites through the 5-year experiment explained 23.2% of the total inertia, and if the overall differences among sites and sampling times (which were partialled out in

the PRC analyses) were also taken into account, then 62% of the total variance in the data could be accounted for by the model S × F × T with no covariables (Table 1). The 38% not accounted for was variation that occurred among the replicate plots within sites at each census.

In order to visualize and interpret the interactive effects of grazing and habitat on species composition, the data were split into a grazed and an ungrazed subset, and separate PRC allowing for differential responses among sites was run for each subset. The overall results were broadly comparable, both in terms of the fraction of variance accounted for, the F -ratios, and the statistical significances of the first PRC axes. However, the sequential tests and the PRC diagrams revealed some interesting differences (Fig. 3). The immediate response was strong in the ungrazed subset, the habitats had distinct responses (dry south-facing > intermediate flat > moist north-facing), and succession towards the unburnt control appeared quickly. The grazed subset, in contrast, had less clear patterns, both among habitats and through time. While the overall species composition in the grazed and ungrazed data was very similar (Pearson's correlation between abundances in the two data sets: $r = 0.92$), there was an indication that individual species responded differently to post-fire successions in grazed and ungrazed heaths (Pearson's correlation between PRC axis 1 species scores in the two data sets was lower: $r = 0.76$) (see the Appendix). There was considerable variation in these species-specific responses; in some species strong negative effects of fire under grazing would change to positive when grazing was removed (e.g. *Blechnum spicant* L. and *Galium saxatile* L.), whereas

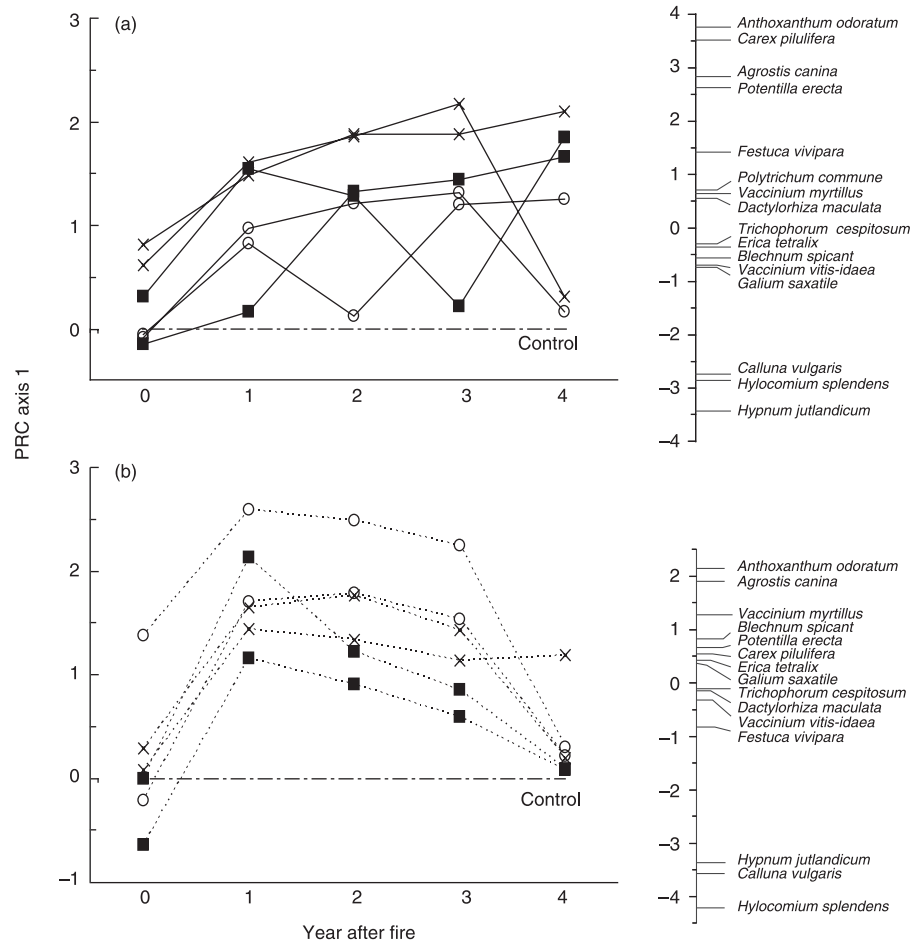


Fig. 3. PRC showing the effects of fire on the heathland species composition (treatment effects; C_{dt}) relative to the unburnt controls in grazed (a) and ungrazed (b) heathlands. The responses (species scores; b_k) of some selected species are shown to the right, a full list is given in the Appendix. The statistical significance of the overall fire effect, and of the differential responses to fire among grazing regimes and environments, is reported in Table 1, and changes over time are reported in Table 2. Solid line, grazed sites; broken line, ungrazed sites; squares, moist, north-facing environments; crosses, intermediate; circles, dry, south-facing environments.

Table 3. Summary of the GLM model selection. Starting from models judged significant by an F -test, a backwards selection based on a permutation test that takes better account of the data structure was performed (see text). Res. d.f., residual degrees of freedom; Res. dev., residual deviance; $P(F)$, P -values based on F -tests; $P(\text{perm})$, P -values based on permutation tests; T, time; F, fire; G, grazing; E, environment (dry, intermediate or moist heath)

Response	Model	Res. d.f.	Res. dev.	F -value	$P(F)$	$P(\text{perm})$
Site richness	F + G + E + T × F + G × E + F × G + F × E + F × G × E	100	62.4			
	F + G + E + T × F + G × E + F × G + F × E	102	67.7	4.2	1.73×10^{-2}	0.487
	F + G + E + T × F + G × E + F × G	104	69.1	1	0.357	0.818
	F + G + E + T × F + G × E	105	69.8	1	0.321	0.670
	F + G + E + T × F	107	98.2	21.4	1.61×10^{-8}	0.017
Plot richness	F + G + E + T × F + G × E	405	10578.4			
	F + G + E + T × F	407	13362.5	53.3	2.20×10^{-16}	0.195
	F + E + T × F	408	13385.4	0.7	0.405	0.888
	F + E	416	15444.2	7.8	8.03×10^{-10}	< 0.000
Subplot density	F + G + E + T × F + F × E + G × E	403	174.5			
	F + G + E + T × F + G × E	405	180.6	7.1	9.60×10^{-4}	0.013

others responded more positively to fire under grazing (e.g. *Agrostis* spp., *Festuca vivipara* (L.) Smith, *Dactylorhiza maculata* (L.) Soó and *Polytrichum juniperinum* Hedw.). Much of this variability could be found within major life-form groups (see the Appendix).

EFFECTS ON DIVERSITY

The univariate analyses showed that the strong compositional response to fire was paralleled by changes in species diversity (Table 3 and Fig. 4), supporting

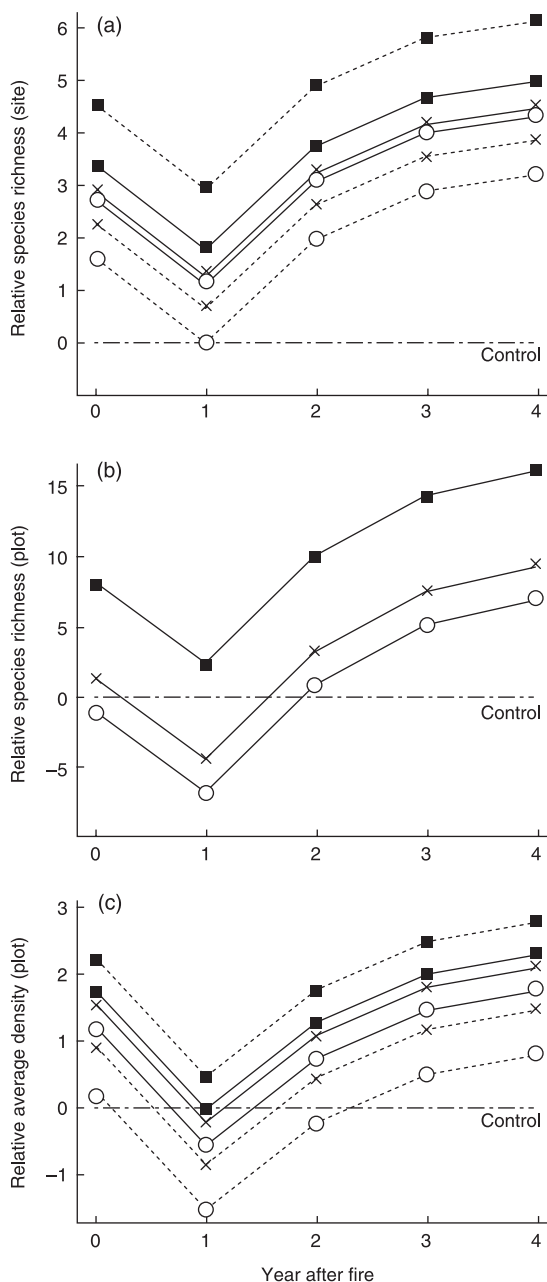


Fig. 4. GLM (repeated measurement) curves showing effects of fire on (a) site richness, (b) plot richness and (c) subplot species density relative to the controls. Offset among the curves reflects the differences (i.e. G, E and G \times E; Table 3) in diversity among environments and grazing regimes. Squares, moist, north-facing environments; crosses, intermediate; circles, dry, south-facing environments. In (a) and (c), solid line, grazed sites; broken line, ungrazed sites.

hypothesis 1 for diversity. At all scales, species diversity decreased the first autumn after fire, reached pre-fire levels in the second year, and continued to increase for the following 2 years. Grazing or environment did not influence this strong trend in species diversity during the post-fire succession (no significant three-way interactions involving F \times T and E or G; Table 3), and hypotheses 2, 3 and 4 were not supported. There were overall differences among habitats, however, as richness

was highest in the moist heath and lowest in the dry heath across scales (main effect of E; Table 3). Grazing also influenced diversity, but in more complex ways, as effects differed among habitats and scales of study (G and G \times E; Table 3). Mean species density and site richness decreased in the grazed dry and intermediate sites, but increased in the grazed moist sites (Fig. 4). These effects, however, were not discernible at the plot scale.

Discussion

HYPOTHESES 1 AND 2: RESPONSES TO FIRE

The strong compositional responses to fire in these heathlands were paralleled by changes in species richness. At all scales (625-cm² subplots, 1-m² plots, 100-m² sites), richness decreased in the first year after fire, then increased to well above pre-fire levels in the following 3 years. In combination, these compositional and richness responses create complex patterns, and the overall landscape-scale effect of fire on the heathland vegetation structure and diversity depend on the spatial scales of the fire regime. Under the patchy fire regimes characteristic of traditional heathland management in western Norway (Webb 1998), fire would increase heathland diversity, first by allowing a new assemblage of species in the newly burnt patches, and secondly by increasing fine-scale species density within sites. The rapid spread and increase after fire of a number of grasses and herbs, including *Carex pilulifera* L., *Festuca vivipara*, *Hypericum pulchrum* L., *Lotus corniculatus* L. and *Potentilla erecta* (L.) Raeusch, along with the fire-dependent bryophytes *Ceratodon purpureus* (Hedw.) Brid. and *Leptodontium flexifolium* and acrocarpous mosses such as *Polytricum* spp. in the majority of burnt sites, indicate that these populations were generally not seed or spore limited in the habitat (Eriksson 1993; Aarrestad & Vandvik 1997). This may be attributed to high dispersal rates into the newly burnt areas, or germination from buried propagule banks, or both. For many characteristic heathland plants, including *C. vulgaris*, the immediate responses to fire were strongly negative, and the long-term persistence and abundance of these species within the heathlands would depend strongly on their capacity to re-establish from seed or vegetative organs during the post-fire succession. Studies of *C. vulgaris* in Britain and Spain show that vegetative resprouting may fail if the fire is too hot, if grazing is too severe, if the *Calluna* plants are too old, or at high-elevation sites (Webb 1986; Hobbs & Gimingham 1987; Hulme *et al.* 2002; Pakeman *et al.* 2003), whereas seed regeneration can be strongly susceptible to drought (Calvo, Tárrega & de Luis 2002) and also to the cool summer conditions found in oceanic mountains (Miller & Cummins 2001). In this study *C. vulgaris* regenerated profusely; while it was only found in 37% of the subplots the first year after fire, 87% were colonized after 3 years (Fig. 1, average

across treatments), recruits originating both from seed and by vegetative resprouting (V. Vandvik, personal observation).

The three habitats investigated in this study were not very floristically distinct. Their distributions appear continuous and overlapping in two-dimensional PCA space. The pre-fire starting points of the successional trajectories spanned *c.* 2.0 SD along DCA axis 1, which implies *c.* 50% shared species. Still, post-fire successional trajectories differed, both quantitatively, as the PRC axis 1 scores increased from moist to dry, and qualitatively, as the compositional responses were statistically independent. The fraction of the total biomass removed in a fire depends strongly on factors such as soil and ground-layer moisture content, ground-layer thickness and topography (Forgeard 1990; Legg, Maltby & Proctor 1992). Fire effects will therefore tend to differ predictably among habitats, being most severe and removing all vegetation including bryophytes and the upper part of the soil in dry (south-facing) sites. The quantitative difference in fire response was paralleled by this gradient in fire intensity, a relationship also found by Øvstedal & Heegaard (2000). The qualitative differences, in contrast, implied that species with narrow niches along the floristic moist-to-dry heathland gradient responded differentially to fire. This was clearly seen among the bryophytes (see the Appendix), where many often pleurocarpous species, characteristic of moist heathlands, were strongly negatively affected by fire, whereas the fewer, often acrocarpous, bryophytes of dry heathlands tolerated fire better (Esposito, Mazzoleni & Strumia 1999). This corresponds to a major dichotomy in bryophyte life strategies, as the acrocarpous growth form is characteristic of fugitive species, whereas the pleurocarpous growth form is more common among species that are locally persistent (During 1992; Hedderson & Longton 1995).

HYPOTHESES 3 AND 4: RESPONSES TO GRAZING

Some recent studies into the ecological effects of ungulate grazers have argued that while grazing increases fine-scale diversity, it causes only localized changes in plant abundances, and should therefore be seen as a homogenizing factor in plant communities (Olf & Ritchie 1998; Stohlgren, Schnell & van den Heuvel 1999; Harrison, Inouye & Safford 2003). In contrast, we found that the effects of grazing on diversity were habitat-specific; the fine-scale species density and site-scale species richness increased under grazing in moist heath but decreased in dry heath (Fig. 4). More importantly, while grazing induced only weak main effects on the species composition, the differential responses among habitats were considerable (Table 1), and there were conspicuous effects on the temporal dynamics, with slower succession and higher levels of random variation among replicate sites through time in grazed sites (Fig. 3). In other words, grazing created colonization oppor-

tunities for additional species, induced different compositional trends in the three habitats, and resulted in more complex successional dynamics. Based on these findings, we conclude that grazing acts as a heterogenizing factor in these heathlands.

Why is grazing a heterogenizing factor in this semi-natural system? First, animals do not graze landscapes evenly (Senft *et al.* 1987; Hester *et al.* 1999; Rao *et al.* 2003; Fuhlendorf & Engle 2004), and this is especially true in systems where free-ranging grazers have access to large and topographically diverse areas at relatively low stocking rates (Coughenour 1991). At Lurekalven, the sheep prefer burnt to unburnt heath, ridges with a good view over the landscape to steeper or lower-lying areas, and dry to moist grounds (S. Øpstad, personal communication). Thus the local grazing pressure can be summarized as a response to the interactive effects of topography, moisture and fire. This was reflected in the compositional patterns, as the response to fire, in ungrazed heath, was strongest in the dry sites (Fig. 3b) but became stronger in the intermediate sites (i.e. the preferred flat hilltops and ridges) under grazing (Fig. 3a). This suggests that, although grazing may decrease local species richness in the preferred sites, the fine-scale variation of grazing intensity may result in increased floristic heterogeneity at the landscape scale. Secondly, the grazing responses of species depended on their distributions along the moisture gradient and post-fire successional gradients. While the floristic moisture gradient was relatively short (*c.* 2 SD), moist heaths were generally richer in woody plants, while grasses made up a larger proportion of the dry and intermediate heath flora. As woody plants are generally less disturbance-tolerant than grasses (McIntyre, Lavorel & Tremont 1995; Díaz, Noy-Meir & Carbido 2001), such shifts along the gradient will result in systematic differences in responses to grazing, which may contribute to an increased heterogeneity. A similar change in functional groups was also found within the bryophytes, as moist heaths were rich in pleurocarpous perennials, which do not withstand disturbance very well, whereas fugitive acrocarpous species were more common in dry and intermediate heaths (During 1992; Hedderson & Longton 1995). Similar differences in functional types occurred between the unburnt and the burnt heaths. Thirdly, the fire responses of several widespread species changed under grazing (see the Appendix), as positive effects of fire in ungrazed heath changed to negative effects under grazing for *Galium saxatile*, *Gymnocarpium dryopteris* L., *Vaccinium* spp. and *Cladonia* spp. The opposite trends were observed for *Carex pilulifera*, *Festuca vivipara*, *Pohlia* spp. *Polytrichum juniperinum* and *Potentilla erecta* (see the Appendix). These differences can be related to the species' disturbance tolerances, which is relatively low in the former group and higher in the latter. This indicates that the responses to fire and grazing can, at least partially, be understood as additive components of the species' general disturbance responses.

CONCLUSIONS AND IMPLICATIONS FOR
MANAGEMENT

Fire and free-range grazing are essential components of the traditional management systems of the coastal heathlands of Europe (Webb 1998), and our results demonstrate that these two disturbances can have strong, and interactive, effects on the vegetation and, further, that the specific responses may change along local environmental gradients. Thus, within the strong successional trend in species composition and diversity after fire, grazing created ecological opportunities for additional sets of species, induced greater variability among habitats, and added complexity to the successional dynamics within habitats. The higher levels of floristic and compositional heterogeneity under the combined management regime may in turn allow for higher diversity of other organisms, such as hemipterans (Hartley, Gardener & Mitchell 2003) and other invertebrates. Management should thus aim at preserving the level of complexity of the traditional land-use regimes, both in terms of the actual disturbances (i.e. fire and grazing) as well as the spatial scales at which they are applied. In the case of heathlands, this could be achieved relatively straightforwardly by controlling fires to create a fine-scale spatial mosaic of patches in different successional stages after fire, while allowing free-range grazing.

Our results further highlight the importance of including not only the local environmental conditions (Britton *et al.* 2000; Hartley, Gardener & Mitchell 2003) but also the environmental heterogeneity within the landscape (this study; Palmer & Hester 2000) in studies on the effects of natural disturbances, and eventually into management prescriptions for these systems. For example, longer intervals between fires could be beneficial in habitats recovering more slowly or in habitats where burning has a less positive effect on diversity, such as dry heathlands. In calling for such local considerations, we echo other recent studies questioning the efficiency of general management prescriptions, and arguing for inclusion of site-specific considerations into conservation management (Britton *et al.* 2000; Palmer & Hester 2000; Hartley, Gardener & Mitchell 2003).

Conservation management has traditionally been based on mean-field and equilibrium paradigms (Briske, Fuhlendorf & Smeins 2003; Freckleton 2004). Recently, studies from a wide range of habitats managed for conservation have found that fine-scale temporal and spatial heterogeneity may be of considerable importance for the diversity and community structure of these systems (Fuhlendorf & Engle 2004; Parr *et al.* 2004; this study). These findings highlight the importance of basing management prescriptions on ecological theory that incorporates the role of spatial and temporal heterogeneity (Leibold *et al.* 2004). Such considerations are particularly important because management regimes involving disturbances may present a dilemma for the conservation of semi-natural systems. Disturbances are integral parts of the very systems that we want to

conserve, but at the same time disturbance may facilitate change, for example by opening up regeneration niches for exotic species or for natives that become invasive under new environmental pressures (Hobbs & Hunneke 1992; Thompson *et al.* 1995; Harrison, Inouye & Safford 2003).

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE982/JPE982sm.htm>.

Appendix. The species scores on PRC axis 1 in the grazed and ungrazed subsets and the number of occurrences in each of these subsets

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