



Fire and grazing controlling a tropical tree line: Effects of long-term grazing exclusion in Bale Mountains, Ethiopia

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Abstract

Aims: Tropical tree lines are often associated with abrupt shifts in vegetation, soils and disturbance regimes, but the underlying mechanisms are poorly understood. We analysed the role of grazing, fuels and fire in maintaining a sharp tree line with flammable heathland above non-flammable forest.

Location: Bale Mountains, Ethiopia.

Methods: The study used grazing exclosures, repeated vegetation sampling, soil analyses and burning and sowing experiments along an altitudinal gradient with *Hagenia abyssinica* forest, *Erica trimera* forest and *Erica* heathland; all were heavily grazed, the *Erica* heathland also burnt on short rotation.

Results: Contrary to expectation, livestock exclusion did not increase flammability in the forest, but instead resulted in a dense carpet of non-flammable herbs. In the heathland, livestock exclusion led to somewhat faster post-fire fuel recovery, but no major change in vegetation. Seeding of tree species resulted in some seedling establishment, but notably *Hagenia* grew poorly in the heathland, even when protected from livestock. A bioassay, as well as observations of outpost trees on atypical soil above the tree line, suggests that this poor growth is caused by the acidic soils, rather than harsh climate. Despite frequent fires, heathland soils had lower pH and higher organic matter content than forest soils. Below the tree line, tree seedling establishment was successful only in forest gaps, and if livestock was excluded. In both forest and heathland rapid vegetative regeneration in the ground flora after disturbance restricted major species shifts.

Conclusions: These results suggest that the contrasting fire potential between heathland and forest, and thus the sharp tree line would be maintained, or possibly even accentuated, in the absence of livestock grazing, and that *Hagenia* colonization upwards into the heathland is restricted not only by fire and grazing, but also the acidic soils, which is a legacy of centuries of dominance by *Erica*.

KEY WORDS

Erica arborea, *Erica trimera*, Ericaceous soils, forest regeneration, *Hagenia abyssinica*, heathlands, livestock grazing, pastoral fire, post-fire succession

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1 | INTRODUCTION

The structuring of vegetation involves complex interactions of many factors, notably climate, soils, species pools and disturbance regimes (White, 1979). Along elevation gradients on high tropical mountains there are typically distinct vegetation zones, but some potentially important structuring factors should be possible to discount here: species pools are essentially the same owing to short dispersal distances between zones; similarly, the soil parent material is often the same, although biogenic processes may have substantially altered top soils (Read and Perez-Moreno, 2003). Climatic gradients are, however, steep: With each 100 m increase in elevation there is an average decrease in temperature of around 0.6°C (Körner, 2012). This has several direct and indirect effects for the vegetation. The risk of frost at high altitudes increases, particularly when there are clear nights. Soil temperatures also decrease. In addition there is an increase in precipitation but a decrease in potential evaporation (Hedberg, 1951; Körner, 2012).

Although climatic gradients are continuous, vegetation belts often have distinct boundaries, which suggest that other factors are more critical. Candidates would be competitive interactions among dominant plant species (Friis, 1986), vulnerable life history steps such as seedling establishment (Wesche et al., 2008) or the effect of disturbances such as fire or grazing (Bader et al., 2007; Oliveras et al., 2018). From climate alone, the potential for fire disturbance would be expected to decrease with elevation owing to increased precipitation and decreased evaporation. Instead, tropical mountains often have a higher frequency of fire above the tree line than below owing to a higher flammability of the alpine heathlands or grasslands (Wesche et al., 2000; Spehn, 2006; Crausbay and Martin, 2016). Numerous examples exist in South America (Ellenberg, 1979; Rehm and Feeley, 2015), Asia (Smith, 1980) and Africa (Hedberg, 1951; Wesche et al., 2000). Often, the fires are set by people to improve grazing and their spatial extent is controlled by post-fire fuel limitation, which prevents landscape-covering fires (Johansson and Granström, 2014).

Herbivory is a disturbance factor with some similarities to fire, but which more selectively removes plant biomass (Bond and Keeley, 2005). The most nutrient-rich and palatable parts of the plants will be selected, usually the youngest foliage (Davis, 1967). Similarly, palatable species will be preferred over less palatable ones, altering their competitive balance (Johansson et al., 2009). Fire regimes affect herbivory, by for example keeping vegetation short enough for grazing or browsing animals (Jáuregui et al., 2009) and by increasing the proportion of early-successional and palatable species. Indirectly, herbivory can also affect the fire regime by altering the composition of the fuel bed and the vertical connectivity of fine fuels, reinforcing or reducing a contrasting flammability between shrubland and forest (Johansson and Granström, 2014; Blackhall et al., 2017; Tiribelli et al., 2018). Thus, fire regimes and regimes of herbivory are interlinked, not least through culture, as people in many parts of the world supply both the bulk of the herbivores and the ignition of most fires.

On the high mountains of the East-African highlands, there is typically a sharp tree line at around 3,500 m with shrubby Ericaceous heathlands above a forest belt dominated by tree-shaped *Erica* species (Hedberg, 1978; Miehe and Miehe, 1994). Many *Erica* species, such as *Erica arborea*, are highly flammable because of oil-rich ericoid leaves, multi-stemmed shrub canopies and dead twig retention (Dehane et al., 2017). The species present here form lignotubers when exposed to frequent fires (cf. Paula and Ojeda, 2011). In the Bale Mountains, livestock grazing is the main land-use throughout the altitudinal gradient, but fire is more or less restricted to the zone above the tree line, where local pastoralists have burnt the heathland on short rotation for centuries (Gil-Romera et al., 2019) to keep it within browsing height (Johansson et al., 2012).

In order to analyse fire and grazing as controlling factors for the tree line, we did experimental and observational studies on the northern slopes of the Bale Mountains, Ethiopia. To elucidate the effects of grazing on vegetation dynamics and fire potential above and below the tree line, we constructed a set of grazing exclosures at six sites within a relatively restricted elevation range of ~150–250 m around the tree line. Fuel succession after fire in *Erica* heathland vegetation has been reported elsewhere (Johansson and Granström, 2014). Here, we analyse fire potential and vegetation colonization using experimental data collected mainly during the first five years after livestock exclusion. Potential for seedling colonization was assessed through seeding of the dominant woody species (*Erica* spp., *Hypericum revolutum* and *Hagenia abyssinica*) in the different vegetation zones. Further, we characterized soil properties and performed a soil bioassay using *Hagenia*.

An overall aim of the study was to identify whether the current fire regime and high grazing pressure would be sufficient to (a) control the surface fuel situation in the forest below the tree line and (b) to prevent tree colonization above the tree line. This would clarify the role of grazing in maintaining the contrasting flammability between the two vegetation zones, which in turn stabilizes the tree line at its current altitude.

2 | METHODS

2.1 | Study area

The study area is located on the northern slopes of Bale Mountains, Ethiopia, in a ~45 × 10 km area centred at N 6°50', E 39°18' ranging in elevation from ~2,950 m to 3,700 m (Figure 1). The Bale Mountains has the largest area of subalpine and alpine vegetation in Africa and harbours many endemic and threatened species (Fetene et al., 2006). For a description of the geology and climate see the Supporting Information and Figure 1.

The vegetation shows a distinct altitudinal zonation (Friis, 1986; Miehe and Miehe, 1994). At an elevation of ~3,000–3,350 m a.s.l., there is typically a mixed broadleaved forest, with a height of 18–20 m, dominated by *H. abyssinica*, *H. revolutum* and *Myrsine melanophloeos*, hereafter referred to as the *Hagenia*

FIGURE 1 (a) Location of the study area in Bale Mountains, in the Southern highlands of Ethiopia. (b) Climate diagram for the northern aspect tree line at 3,400 m.a.s.l., average monthly rainfall, average daily T_{\max} (red line) and RH_{min} (blue line) for 4 years (2006–2009). (c) Schematic overview of the northern aspect vegetation zones [Colour figure can be viewed at wileyonlinelibrary.com]

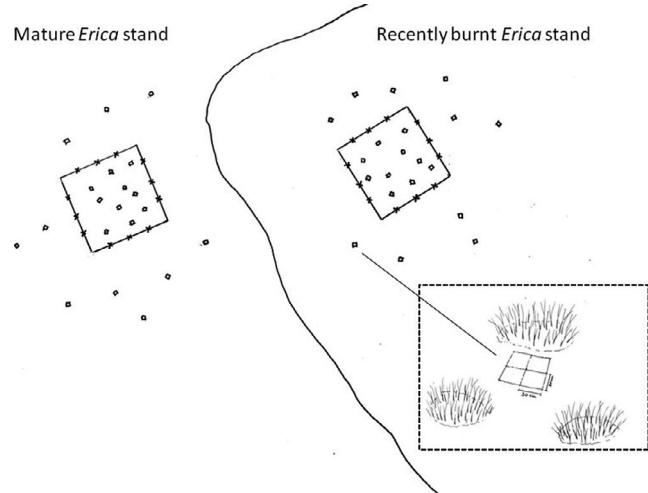
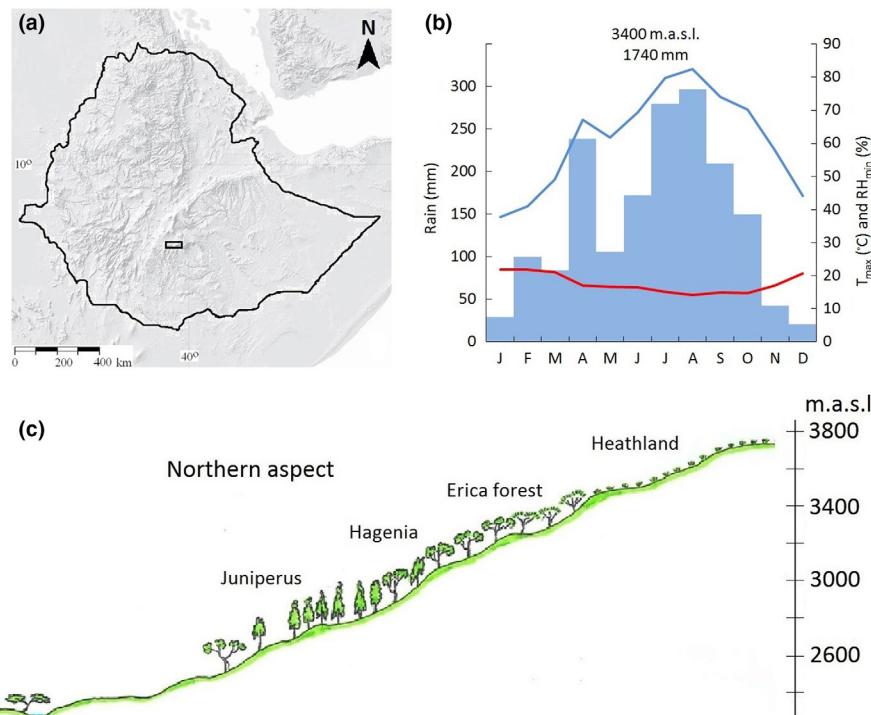


FIGURE 2 Split-plot design of paired *Erica* heathland exclosures in burnt, and in the adjacent unburnt stand, with line transects and blocked 30 × 30 cm vegetation plots, with scarified and control treatments

forest zone (Figure 1c). Higher up is a narrow belt of subalpine Ericaceous forest dominated by tree-formed *Erica arborea*, single-stemmed, or with few stems, ca 11–12 m tall, with a few emergent *H. abyssinica* and *H. revolutum* hereafter referred to as the *Erica* forest zone. At ~3,450 m.a.s.l., there is an abrupt transition to Ericaceous heathland (Figures 1c and 7a), dominated by mixed stands of multistemmed *Erica arborea* and *E. trimera* shrubs (hereafter collectively referred to as *Erica*) in different phases of post-fire regeneration, rarely exceeding 2–3 m in height before burning (Johansson et al., 2012). The heathlands are burnt on short rotation (average fire interval ~10 years, with stand sizes ranging from 0.5 to ~10 ha).

After each fire, the *Erica* shrubs quickly regenerate from large (~0.3–1.5 m diameter) buried lignotubers (spaced ~0.5–1.5 m apart) and young stands are dominated by a species-rich, grazed grass/herb field layer, hereafter referred to as the 'grass/herb lawn', in-between resprouting short *Erica* shrubs, creating a small-scale heterogeneity within stands (Figures 2 and 7d). Young stands are non-flammable the first four years because of the lack of fine fuels (Johansson and Granström, 2014). Throughout all zones, there is intense grazing by livestock, mainly cattle, with a few horses, sheep and goats (Johansson et al., 2012).

2.2 | Exclosure establishment

To quantify the effects of grazing, permanent livestock exclosures were erected in the three elevational zones: heathland, *Erica* forest and *Hagenia* forest. A summary of the set-up is found in Table 1. Sizes of exclosures differed (Table 1), but the construction was similar: a ~160 cm tall fence with six strands of barbed wire, 20 cm apart at the base, and 30 cm between the uppermost strands. Some sheep and goats were present close to habitations and here the exclosures were reinforced by vertical wood splints interwoven with the wire up to ~70 cm. Fences also excluded the Mountain Nyala (*Tragelaphus buxtoni*), but not rodents, monkeys or the high-jumping Bohor reedbuck (*Redunca redunca*). All exclosures were guarded and maintained by local staff, and no signs of grazing or browsing were observed inside exclosures. The basic experimental design of all exclosures is a split-plot design: we randomly selected the placement of the fence, which was surrounded on all sides by a larger area of similar vegetation used as the grazed treatment.

In the heathland zone paired grazing exclosures (10 × 10 m) were established at three sites, with one enclosure in recently burnt *Erica*

Vegetation	Experiment			Alt. (m.a.s.l.)	Slope (%)	Fenced (year ^a)	Exclosure size (m)
	1	2	3				
Above tree line							
Heathland	+	(+)	+	3,510	27	2005	10 × 10 ^b
"	+	(+)	+	3,530	34	2006	10 × 10 ^b
"	+	(+)	+	3,630	17	"	10 × 10 ^b
Below tree line							
<i>Erica</i> forest	+	+		3,400	15	2007	6 × 6
"	+	+		3,440	10	"	6 × 6
<i>Hagenia</i> forest	+	+	+	2,950	1.5	2006	30 × 30
"	+	+	+	3,210	3	"	30 × 30
"	+	+	+	3,350	2.5	"	30 × 3
Hagenia gap	+		+	3,230	3	"	5 × 5
"	+		+	3,370	2.5	"	5 × 5

Note: Experiment: 1) Vegetation development 2) Surface fuels (heathland fuels presented elsewhere) 3) Sowing/planting.

^aAll fences were erected at the beginning of the year, in the dry season (January–February).

^bHeathland fences were built in pairs, one in a new burn and one in adjacent mature *Erica* stand (8–11 years old).

and one in the adjacent 'mature' *Erica* stand, both with adjacent control plots (Figure 2).

Experimental burning was not allowed, so we made use of fires set by locals just before enclosure set-up. Therefore no pre-fire measurements had been made, but judging from remnant fire-killed stem heights and annual ring counts, all burnt stands had been of the same pre-fire heights (140–180 cm) and age (8–11 years) as the adjacent mature stand. Slope, soil and water conditions were also judged to be similar within each pair of recently burnt and mature stands. At the first site, exclosures were built in February 2005 and at the other two sites in February 2006 (Table 1). Only the 2005 fire was directly observed by us, on February 23rd. All exclosures were installed shortly after fire, before new *Erica* shoots had emerged from the lignotubers. All sites had slightly sloping terrain (17%–34%) and contained both *Erica* species.

In the *E. trimera* forest zone, at ~3,400 m.a.s.l., at two sites, ~3 km apart, two exclosures (6 × 6 m) were built in February 2007. Sites were chosen to have moderate slopes and a closed *E. trimera* canopy, but a few *Hagenia* and *Hypericum* trees were present nearby. The trees were ~11 m tall and had two to six stems per tree. Counting of annual ring counts on six trees (diameter 30–35 cm) revealed an age of ~90 years. The basal area was 30 and 38 m² ha⁻¹ and canopy cover ~85%–95%. The field layer was an herb carpet cropped to 1.5–2.5 cm height by livestock (mainly cattle, horses and sheep). Control plots were surrounding the fences as described above.

At three *Hagenia* forest sites, ~14 and ~3 km apart, 30 × 30 m grazing exclosures were built in January–February 2006. Forest canopy and field-layer vegetation was similar inside and outside

exclosures at the start of the study. The sites had a closed canopy dominated by 18–20 m tall *Hagenia* trees (diameter at breast height, dbh, 60–100 cm), with a few *Hypericum* trees. Basal area ranged 27–75 m²/ha, and canopy cover was 80%–90%. The field layer was a herb/grass carpet grazed to a height of 1.5–2.5 cm. Control plots were placed as above. At two *Hagenia* sites, we built an additional 5 × 5 m exclosure in an adjacent forest gap, <300 m away, with similar altitude, slope and soil, but with full sunlight, with surrounding controls. The forest gaps were 100–200 m wide and appeared to have been tree-less for a long time (no tree-stumps or other signs of recent clearing). They were covered by a 1.5–2.5 cm tall intensely grazed grass/herb lawn, with 50%–65% herbs.

2.3 | Vegetation sampling

In the heathland, vegetation cover was sampled using line transects inside/outside exclosures in burnt/mature *Erica* stands, giving four treatments (Figure 2). Area cover of four different categories was measured using five 10 m long line-intercept transects oriented along the contour lines (Bauer, 1943): naked soil/humus, *Erica* shrub canopy, ground moss and grass/herb lawn. Vegetation transects were monitored annually from 2005/2006 to 2011. Measurements were done in January each year. Final measurements were done in January 2011 when burnt plots were 5 and 6 years old, respectively. Shrub biomass is reported in another paper (Johansson and Granström, 2014). All exclosures were revisited in 2012 and 2016, when tree heights were measured and shrub vegetation cover was reassessed by line transects.

TABLE 1 Overview of enclosure experiments and performed studies at the different sites

2.4 | Forest field layer and surface fuels

To quantify surface fuels in *Hagenia* and *Erica* forests, cover and biomass of field-layer vegetation and litter were sampled inside/outside exclosures in the dry season, and 1 year and 2 years after construction. Sample plots were placed at >5 m distance from the fence to avoid edge effects. Seven subplots were sampled inside/outside on all sides of the enclosure. Sampling was done on 1 × 1 m plots for the *Hagenia* leaf litter, which are large (~40 cm long) and curly, compound leaves. The herb layer and the small-sized litter layer (fragmented leaves, bark and twigs) were sampled in a 0.5 × 0.5 m subplot within the 1 m² plot. Biomass of the fractions was weighed in the field and later dried to constant weight in the laboratory to calculate dry weights and fuel moisture contents.

At the *Hagenia* and *Erica* forest sites, we recorded field-layer vegetation height and the depth of the litter layer at points every 1.3 m in three 30 m (6 m in *Erica* forest) line transects inside/outside grazing exclosures for 4 years. For the first two years after exclusion, herb species composition was also recorded. The last measurements were made in January 2011.

2.5 | Heathland succession

To analyse effects of grazing on herbaceous post-fire colonization and seedling establishment, we established permanent field-layer vegetation plots (30 × 30 cm) inside and outside the heathland exclosures described above (Figure 2). These were arranged in square blocks (2 × 2 plots) in-between the *Erica* shrubs or lignotubers, so that two plots were positioned directly adjacent to the lignotuber and two 30 cm out in the grass lawn. Plots were evenly distributed between the *Erica* shrubs, avoiding stones and tracks. To replicate the grazed controls (cf. Davies and Gray, 2015), the plots outside exclosures were distributed on three sides of the exclosures (Figure 2), and at a minimum distance of 3 m to the fence to avoid edge effects. In each block, one randomly chosen plot close to the lignotuber, and one further out, was scarified by mechanically removing the litter and upper 2 cm of the organic soil layer, including rooted herbaceous vegetation. Initial data analysis showed that position had little effect, and hence plot data from close/far from lignotuber were pooled. This gives a total of eight different treatments: 2 fire histories (recently burnt vs. mature *Erica*) × 2 grazing regimes (inside vs. outside enclosure) × 2 soil treatments (scarified vs. control), ($n = 10$ blocks at the 2005 site, $n = 7$ at the 2006 sites). All plots were marked by plastic sticks at the corners.

In these 30 × 30 cm vegetation plots, area cover of all plant species and non-vegetated soil/humus was visually estimated annually (until burnt plots were 3 and 2 years old, and mature plots were 14 and 10 years old, respectively). *Erica* seedlings were recorded as part of the field layer, but resprouting *Erica* branches were not. Field-layer vegetation height was measured at four points and averaged per plot. Total numbers of species per plot were compared between treatments. Preliminary ordination analyses of species matrixes

revealed no obvious patterns regarding treatment or site, therefore, all vascular plants were grouped into six functional groups: woody + suffrutescent plants, nitrogen-fixing species, rosette plants, perennial herbs, annuals, graminoids (grasses, sedges, rushes). Large ground mosses (mainly *Breutelia diffracta*) were summed into one group. Area cover of each functional group was calculated for each year for the different treatments.

2.6 | Sowing and planting experiments

The same heathland 30 × 30 cm vegetation plots were also used for sowing experiments; 50 seeds each of *E. arborea*, *Hypericum* and *Hagenia* were sown on half the plot in March 2005 (2005 site) or March 2006 (other sites). Seeds were obtained locally, sorted under stereo-microscope and their viability assessed by germination tests in the laboratory 3 months later. Seed viability was >80%. *Hagenia* seeds are small (2 mm), with five wings, and are wind-dispersed, whereas *Hypericum* and *Erica* seeds are tiny (<1 mm) and have no special dispersal adaptations. Field germination is reported as proportion out of germinable seeds. Germination and seedling survival/growth was monitored annually during the first two years.

In the *Hagenia* zone (in both forest/gap exclosures) sowing experiments were done in March 2006, with the same seed batches. A total of 50 seeds of each species were sown on half of the plots of 1 × 1 m (but 0.5 × 0.5 in the gap exclosures, also sown with 50 seeds) with three different treatments, replicated five times: (a) control (no manipulation), (b) mechanical scarification (removal of herb/grass vegetation) and (c) fire (leaf litter, ~400 g/m² was added to the plot and then burnt, see *Hagenia* burning experiments in Supporting Information). The fire treatment was excluded from gap exclosures.

No seedling germination was observed in the seeded plots in the *Hagenia* forests (presumably owing to shading from the lush herb carpet that covered the scarified plots in less than 6 months). Additional planting was therefore done in June 2007 (rainy season) of 6 months old *Hagenia* seedlings, produced from our seed batches by a local nursery. At each *Hagenia* forest site, ~4 cm tall seedlings were planted along the fence ~2.5 m apart ($n = 45$ seedlings per treatment per site). At the two gap exclosures, nine seedlings were planted inside and outside. The herb carpet was then ~5 cm tall inside exclosures and ~2 cm outside exclosures. Seedling survival and height was monitored annually for 5 years and sapling height measured after 6 and 10 years.

2.7 | Soil sampling and *Hagenia* bioassay

To characterize soil properties (pH, bulk density, SOM [soil organic matter]), soil samples were collected at all sites, and from burnt and mature heathland stands (see Supporting Information). The same soil samples were used to perform a nursery soil bioassay with newly germinated *Hagenia* seedlings over a period of 18 weeks (see Supporting Information).

2.8 | Data analyses

To test effects of livestock exclusion on post-fire *Erica* canopy cover development, the line transect data (only from the recently burnt stands) was analysed by nested general linear models with four factors; age (time since fire), grazing (\pm livestock exclusion), transect and site. Transect was nested within treatment and site and so was the interaction age \times transect. Treatment and age were fixed factors while transect number and site were random. The unit of replication was the line transect.

For the 30×30 cm heathland vegetation plots, second-year area cover of plant functional groups was analysed by nested general linear models, with four factors; fire history (burnt/mature), fenced (\pm livestock exclusion), scarification (\pm soil scarification) and site. Plot was nested within site, fire history and fence. The unit of replication was the 30×30 cm plot. The third mature stand accidentally burnt in December 2007, and was thus excluded from final analyses. The same model was used for first-year seedling establishment in the same plots (seedling data ln-transformed, to meet ANOVA assumptions).

To test the effect of livestock exclusion on field-layer cover and biomass in the *Hagenia* forest, nested models with three factors were used: site, treatment (fenced/grazed) and transect/plot. Site and transect/plot were random and transects/plots were nested within site and treatment.

All statistical analyses were performed using the software package Minitab 16.

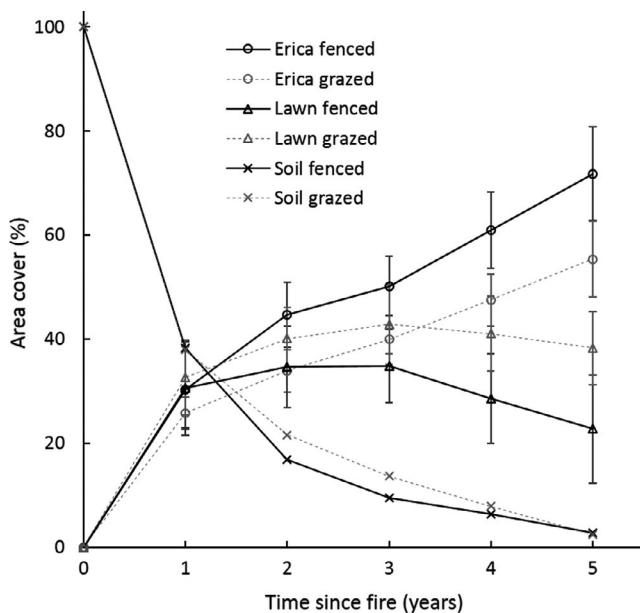


FIGURE 3 Heathland post-fire vegetation cover of *Erica* shrub canopy, the grass/herb lawn and bare soil/humus/naked lignotubers in fenced vs. grazed transects ($n = 5$ transects per treatment per site). Values are averaged for the three heathland sites (Error bars = 1SE) (see Appendix S1)

3 | RESULTS

3.1 | Heathland post-fire vegetation development

In the burnt heathland transects, there was rapid regrowth of *Erica* shoots from the lignotubers. *Erica* shrub cover outside exclosures was 21%–45% 1 year after fire (Figure 3). Within 5 years, it was 40–70%, nearly on par with adjacent mature stands. *Erica* shrub cover increased significantly faster inside exclosures ($p < 0.001$, Appendix S1). After 5 years, it was 13–20%-units higher inside exclosures than outside (Figure 3). Cattle browsed the top ~10 cm of the *Erica* shoots, at a bite diameter of ~1 mm. The resulting dense carpet of woody stem-pegs appeared to restrict consecutive cattle browsing further down into the shrubs, and thus offered some protection (Figure 7e). The proportional cover of the herb/grass lawn increased rapidly and culminated 1–3 years post-fire (Figure 3). Thereafter, herb/grass cover declined, faster inside exclosures. Non-vegetated soil/humus decreased rapidly in burnt plots, and was virtually nil after 5 years, both inside and outside exclosures (Figure 3).

In the 30×30 cm field-layer vegetation plots between the *Erica* shrubs, total herb and grass cover was on average 62% ($SD = 18$) 2 years after fire (Figure 4). Few seedlings were observed (mainly of *Alchemilla* spp., *E. arborea* and *Lobelia erlangeriana*) and most species instead colonized vegetatively from underground structures. For example, *Trifolium acaule* emerged from a thick rhizome 2–3 cm below soil surface, *T. cryptopodium* and *T. burchellianum* had both horizontal rhizomes and deep taproots, *Haplosporpha rueppellii* produced new shoots from a swollen taproot and *Thymus schimperii* produced new shoots from horizontal woody subsurface stems.

There were few treatment effects for most plant functional groups (Figure 4). However, large ground-covering mosses were dominant only in mature stands, and cover of N-fixing plants (mainly *Trifolium* spp.) increased in non-scarified plots and in burnt stands ($p = 0.046$, Appendix S2). Second-year field-layer vegetation was higher inside than outside exclosures (average 7.5 cm ($SD 3.1$ cm) vs. 2.0 cm ($SD 1.0$); $f = 322.99$; $p = 0.035$).

3.2 | Forest field-layer vegetation and surface fuels

In the *Hagenia* forest, herb/grass cover ranged from 80% to 90% outside exclosures. Inside exclosures the herb/grass cover increased to 100% after 1 year ($f = 1552.20$; $p = 0.001$). Herb/grass biomass was 3.2 times higher inside exclosures after 1 year and four times higher after 2 years ($f = 22.03$; $p = 0.042$) (Figure 5). The most common species at the start of the experiment were *Alchemilla abyssinica*, *Geranium arabicum*, *Parochetus communis* and *Trifolium semipilosum* v. *brunellii*, but after 2 years of livestock exclusion *Trifolium* had disappeared completely, while *Parochetus* had doubled in cover ($f = 127.60$; $p < 0.001$). Dry season moisture content of the herbs ranged from 300% to 450%.

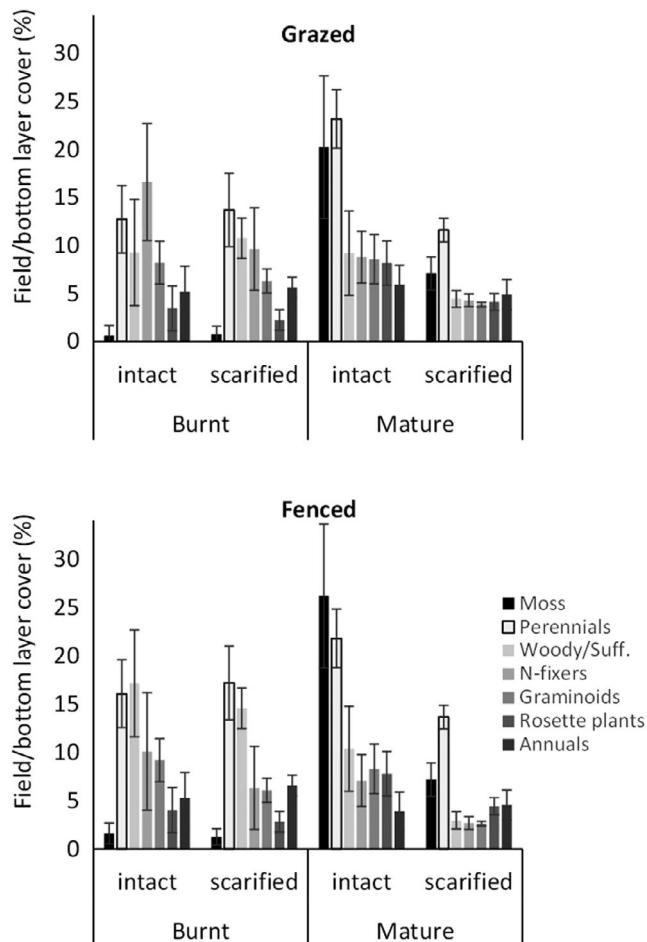


FIGURE 4 Area cover of field and bottom layer functional groups 2 years after experimental set-up involving livestock exclusion and soil scarification in newly burnt and mature *Erica* vegetation. Values are averages of three sites, ($\text{Error bars} = 1\text{SE}$, see Appendix S2). Functional groups are arranged according to abundance in mature intact treatment

Grasses were rare in the *Hagenia* forests; only at one site did grass cover reach more than 20% of the field-layer vegetation inside the enclosure 2 years after fencing. After 10 years grasses covered more than 60% in one enclosure, while the other surviving enclosure still had a herb-dominated field layer (the third *Hagenia* forest fence was broken after 6 years).

Hagenia leaf-litter biomass did not differ between treatments ($f = 0.00$; $p = 0.957$, Figure 5), but mass of small-sized litter (mainly fragmented *Hagenia* leaf litter and herb litter) was higher inside than outside enclosures after 2 years ($f = 32.74$; $p = 0.023$).

In the *E. trimera* forest enclosures, the herbaceous layer had a similar species composition and attained ~ 10 cm height with a biomass dry weight (DW) of 141.5 g/m^2 ($n = 8$, $SD = 31.8$) 1 year after fencing. Here, almost all surface fuels consisted of a mesophytic herb carpet and there was no large airy leaf litter because *Erica* needles are small and form a relatively compact litter layer. Thin *Erica* twigs fallen from the forest canopy comprised $\sim 18 \text{ g/m}^2$ DW fine

surface fuels ($n = 8$, $SD = 8.7$). Outside the fence, the herb sward was ~ 1.5 cm tall with a DW of 64.4 g/m^2 ($n = 8$, $SD = 12.3$).

3.3 | Tree seedling establishment in heathland and forest

In the heathland sowing experiments, seedlings of all three tree species emerged (*E. arborea*, *Hagenia*, and *H. revolutum*) but in highly variable numbers (Figure 6). *Hagenia* seedlings had significantly greater establishment in scarified plots ($f = 0.125$ $p < 0.001$): ~10% and 36% ($SD = 15$ and 36) out of germinable sown seeds, for burnt and mature fenced plots, respectively. *Hagenia* first-year establishment was also significantly higher in mature stands ($f = 138.49$; $p < 0.001$).

Germinants of all species developed slowly. Two years after seeding, *Hagenia* seedlings were only 2–4 cm tall and discoloured (reddish) *Erica arborea* and *Hypericum* seedlings also developed slowly, attaining maximum heights of 7.5 and 15 cm, respectively, after 2 years. Second-year survival of the established first-year seedlings in the heathland was higher inside the exclosures than outside; on average 53% vs. 15% for *Hagenia*, 90% vs. 67% for *Hypericum* and 86% vs. 50% for *E. arborea*, respectively. Differences were, however, significant only for *Hagenia* ($f = 3.621$ $p = 0.034$). After 5 years, all tree seedlings were gone.

In the *Hagenia* forest plots, there were no tree seedlings in seeded plots 8 months after seeding, or any time later. We did not observe any spontaneous seedlings either, despite an evidently large seed rain from *Hagenia*.

For planted *Hagenia* seedlings, first-year mortality was higher outside exclosures ($f = 26.68$; $p = 0.014$). Within 2 years, all unfenced seedlings had disappeared, presumably consumed by livestock. Inside forest exclosures, *Hagenia* seedlings grew slowly and were embedded in the dense ~15 cm tall herb layer, and here losses were also high. Six months after planting, fenced seedlings were etiolated, with yellow leaves under the thick herb layer, but most just disappeared, and fence guards suggested they might have been consumed by colobus monkeys. After 18 months, only 10% of the planted seedlings were alive, with heights of 33–65 cm (Appendix S3b). After 4.5 years, no *Hagenia* seedlings were alive in the forest exclosures.

In the gap exclosures, however, five and four (out of nine planted per exclosure) *Hagenia* seedlings survived. Some seedlings were evidently harmed by mole-rat digging the first years. Ten years after planting the largest surviving *Hagenia* trees were 5 m and 10 m tall (Figure 7f) in the two gap exclosures, respectively.

In the *Hagenia* gap-exclosure seeding experiment, first-year establishment of seedlings (out of germinable sown seeds), was for *Hagenia* 1.6% and 0.6% ($n = 4$, $SD = 1.3$ and 0.9) for scarified and control plots, for *Hypericum* 10.4% and 5.5% ($n = 4$ $SD = 11.1$ and 7.8) and for *E. arborea* 1 and 0% ($n = 4$ $SD = 5.2$ and 0). Survival until the second year was 50%, 100% and 50% for *Hagenia*, *Hypericum* and *E. arborea*, respectively. However, after 5 years only four sown

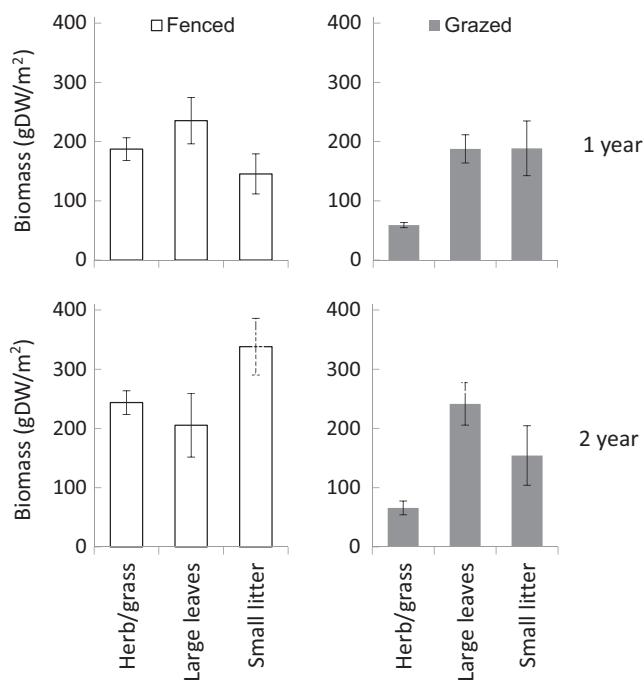


FIGURE 5 Dry-season biomass (dry weight) g/m² of the herb/grass field layer, large leaves (mainly *Hagenia* leaves) and small-sized litter in fenced and grazed *Hagenia* forest plots, (a) 1 year and (b) 2 years after grazing exclusion. Data are averages for the three *Hagenia* forest sites (Error bars = 1 SE)

seedlings were still alive. Maximum heights were then 30 cm and 24 cm for *Hagenia* and *Hypericum*, respectively.

3.4 | Soil status

Soil pH was lower in the mature heathland than in *Hagenia* forest. There was an overall negative relation between SOM and pH and SOM and bulk density, and fire only marginally reduced SOM and increased bulk density and pH (Figure 8a,b). In the bioassay, *Hagenia* seedling growth was lower in the heathland soils (Figure 8c). Average seedling heights were ~50% higher per 1 unit increase in soil pH.

4 | DISCUSSION

In the present study, manipulation of two putatively important factors, fire and livestock grazing, resulted in surprisingly small effects on the vegetation, and thus on flammability. Fire disturbance in the heathland caused only minor shifts in species composition, and a quick return to a closed, flammable *Erica* canopy within 5–6 years, with or without grazing. Livestock exclusion in the forests had little effect on surface fuels, and possibly even increased leaf-litter decomposition rates. Below the tree line, *Hagenia* seedlings only survived inside exclosures, and in full sunlight. Above the tree line, *Hagenia* seedlings did not survive, not even with livestock exclusion and full sunlight, probably because of the acidic heathland soils. The

combination of these mechanisms would, over a long time, have acted to stabilize the tree line.

4.1 | Heathland vegetation dynamics under fire and grazing

In the heathlands, fire was followed by fast recolonization from surviving vegetative structures in the soil, notably from the *Erica* lignotubers, but also from extant herb and grass rhizomes and roots. Two characteristics of the fire regime might contribute to this: the relatively short fire intervals, allowing for a rich herb and grass component also surviving under maturing *Erica* shrub, and the typically shallow depth of burn (Johansson et al., 2012), allowing survival of regeneration buds in the humus layer. Similar patterns have been reported earlier for shrublands under regimes of short-interval fire (Céspedes et al., 2014; Parra and Moreno, 2017). Excluding livestock resulted in a faster recovery to closed-canopy *Erica* shrub, but livestock browsing of *Erica* outside exclosures was not able to completely arrest height growth. Similarly, there were hardly any effects of livestock exclusion on the abundance of early-successional plant species. Small mammals were not excluded and might possibly have had a moderating effect if, for example, grass rats, which consume large quantities of grass (Vial et al., 2011), were attracted to taller grass vegetation inside exclosures. However, we did not observe any obvious signs of rodent grazing.

Livestock impacts on shrubland dynamics are highly variable and depend both on vegetation composition, livestock species and the duration of the land use. In Australian heathlands, introduced cattle had little effect on shrub fuels because the cattle avoided mature stands (Williams et al., 2006). In Patagonia, introduced cattle reduced *Nothofagus* shrubland flammability by reducing the amounts of fine dead fuels, but at the same time they prevented succession into less-flammable forest (Blackhall et al., 2017).

Incidentally, the same plant traits that allow for survival after fire, such as effective vegetative regrowth, common in our dominant species, would also promote high grazing tolerance (Canadell and Lopez-Soria, 1998; Bond and Keeley, 2005). Although we mainly observed vegetative regrowth, there was some seedling establishment of herbs, grasses and *E. arborea*, evidently from the large and species-rich seed bank (unpublished data).

In the present study, there were a few naturally germinated seedlings of *E. arborea* in the small plots, but they were efficiently removed by the cattle. Even inside the exclosures, *Erica* seedlings did not exceed a height of 5 cm after 5 years, probably owing to intense competition from the old *Erica* individuals, which had a head start resprouting from lignotubers. In facultative resprouters, there can be a trade-off between resprouting capacity, increasing competitive success under a frequent-fire regime, and a large seed production, increasing success after infrequent, but more severe fires (Paula and Pausas, 2008; Maia et al., 2016). In the Bale Mountain heathlands, *Erica* seedling recruitment is evidently minor owing to heavy grazing pressure and the fact that

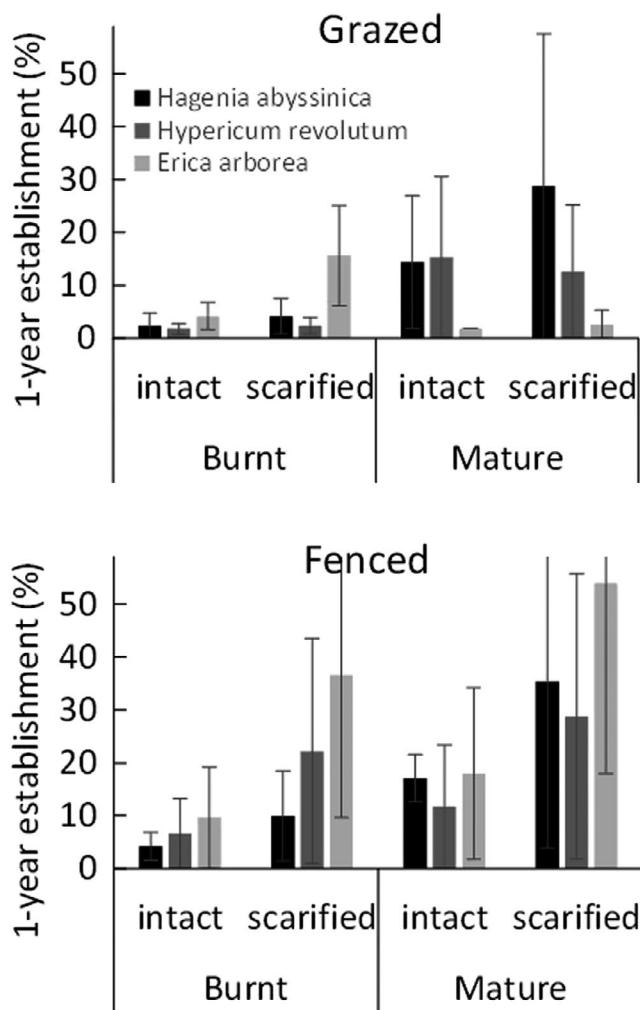


FIGURE 6 Seedling establishment in the heathland sowing experiment, 1 year after sowing. First-year establishment expressed as the proportion observed seedlings out of germinable sown seeds of *Hagenia abyssinica*, *Hypericum revolutum* and *Erica arborea* in the 30 × 30 cm plots. Germination was higher on bare soil (burnt and scarified), survival was higher in mature stands (Error bars = 1 SE, n = 3 sites)

most lignotubers survive repeated fires. The *E. trimera* lignotubers are old and frequently more than 1 m in diameter. We did not observe mortality resulting from decaying lignotubers except after the extreme drought in April 2008, when deep humus smouldering caused some mortality.

4.2 | Fire and the formation of the tree line

There is a stark contrast in flammability between shrub-shaped *Erica* in the heathlands, and tree-shaped *E. trimera* in the zone below. Excluding livestock for 5 years in the *Erica* forest did not increase surface fuel flammability. Even 10 years after fence construction the field layer was still dominated by non-flammable mesophytic herbs.

We suggest that the mechanism behind the formation of a distinct forest–heathland border is the reduced *Erica* growth rates with

increasing altitude, owing to the harsher climate. This increases the time needed for the *Erica* shrubs to grow into tall trees and thereby escape ‘the fire trap’ (cf. Bond and Midgley, 2001). Once established, the tree line has been maintained at its current position because of the contrasting flammability of the heathland and forest zones. It is probable that the tree line has been stable for a considerable time, perhaps since anthropogenic fire commenced, likely more than 2000 years ago (Umer et al., 2007; Gil-Romera et al., 2019).

4.3 | *Hagenia* regeneration and potential for colonizing the heathland

Hagenia abyssinica is the potentially dominating species with capacity to colonize upwards into the Ericaceous zones in a warming climate. The observed overall regeneration failure for *Hagenia* in all zones is not caused by a lack of viable seeds, or by livestock grazing only. Clearly, current grazing pressure is intense enough to remove any emerging seedling, as *Hagenia* leaves are highly palatable to livestock and wild herbivores. But even inside exclosures, both above and below the tree line, regeneration was unsuccessful. In the closed forest habitats, competition, notably for light, should be restricting. At 50 cm height, the light levels relative to the open field averaged 17% (Appendix S3), which is low for a light-demanding species such as *Hagenia* (Fetene and Feleke, 2001). If grazing would cease, germinants would have to start from under a dense herb field layer where there is even less light.

In the heathland, where *Hagenia* seedlings indeed did emerge after seeding (mainly in scarified and burnt plots), the poor nutrient status, or the low soil pH, is instead the likely reason for their poor performance in the fenced plots as well. The nursery bioassay showed poor *Hagenia* growth in the acidic heathland soils, even at a more favourable climate at a lower elevation. In the heathland, *Erica* and mosses form a recalcitrant litter, producing a thick and acidic humus layer. This is in accordance with the scheme suggested by Read and Perez-Moreno (2003) of long-term soil–plant interactions in areas dominated by ericaceous plants. Most heathland fires in Bale occur when the humus is too moist to smoulder, and thus fire has little effect on the humus layer below the surface litter (Johansson et al., 2012). Of course, the harsh climate in the heathland might also contribute to poor *Hagenia* growth, but we have observed individual vigorous *Hagenia* trees well above the tree line, but always in fire-protected habitats with atypical soils: road banks or rocky outcrops (Figure 7b,c). The lack of basal resprouting in *Hagenia* (personal observation) would in any case eliminate the species under a regime of short-interval fire because natural fire refugia are rare in the heathlands.

It has been suggested that *Hagenia* would efficiently regenerate in the forest zone only after wildfire (Lange et al., 1997) because of its shade-intolerance (Fetene and Feleke, 2001), high palatability and efficiently wind-dispersed seeds. After wildfire, there would be more sunlight and perhaps also grazing protection from fallen fire-killed tree stems (cf. de Chantal and Granström, 2007)

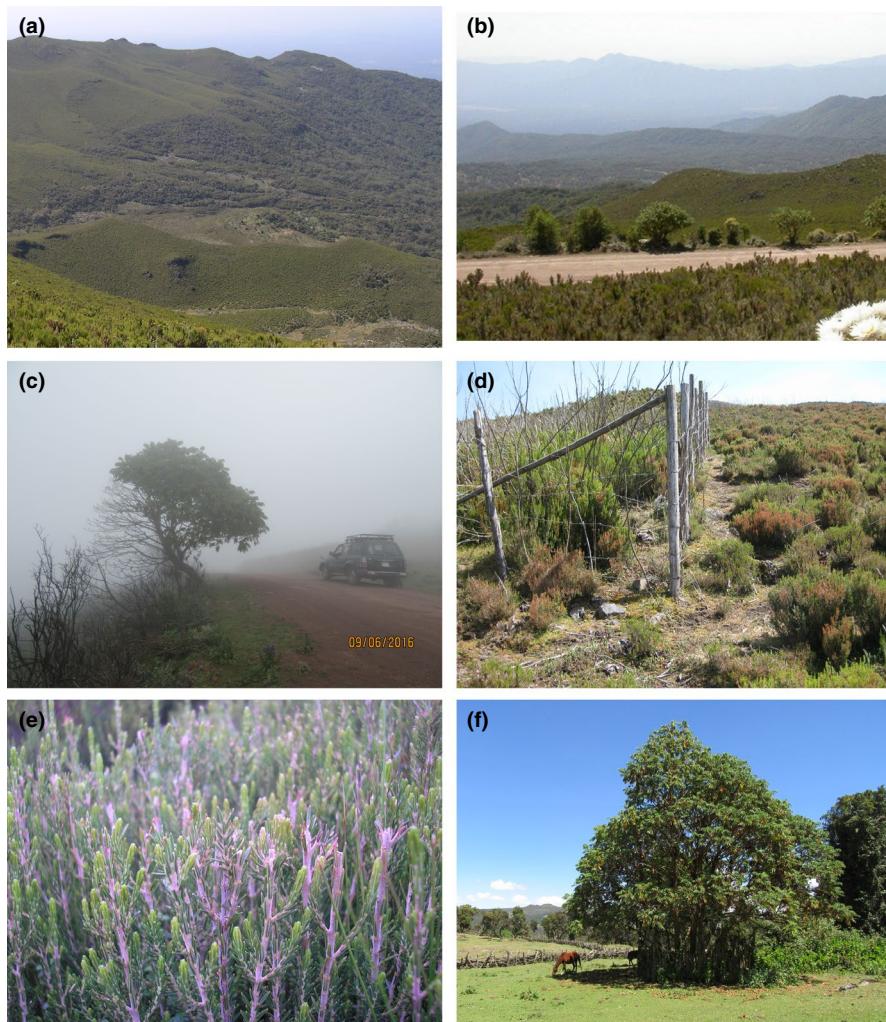


FIGURE 7 Photographs of landscapes and experiments (a) The border between the *Erica* forest and the heathland at ~3,450 m.a.s.l., (b) and (c) young *Hagenia abyssinica* trees in the heathland, ~100 m above the current tree line, standing along a gravel road that was built in the 1980s. Trees are rooted in mineral soil and slightly fire-protected. Note in (c) the lower left part of the tree crown damaged by fire burning the *Erica* shrubs below the road. (d) One of the heathland enclosures, 4 years after fire and grazing exclusion. (e) *Erica trimera* shoots recently browsed by livestock; the bite diameter is ~1 mm and the dense carpet of hard woody pegs prevents cattle browsing further down in subsequent browsing episodes. (f) Five *Hagenia abyssinica* trees 10 years after planting in one of the *Hagenia* forest gap enclosures. Height of the tallest tree was ~10 m [Colour figure can be viewed at wileyonlinelibrary.com]

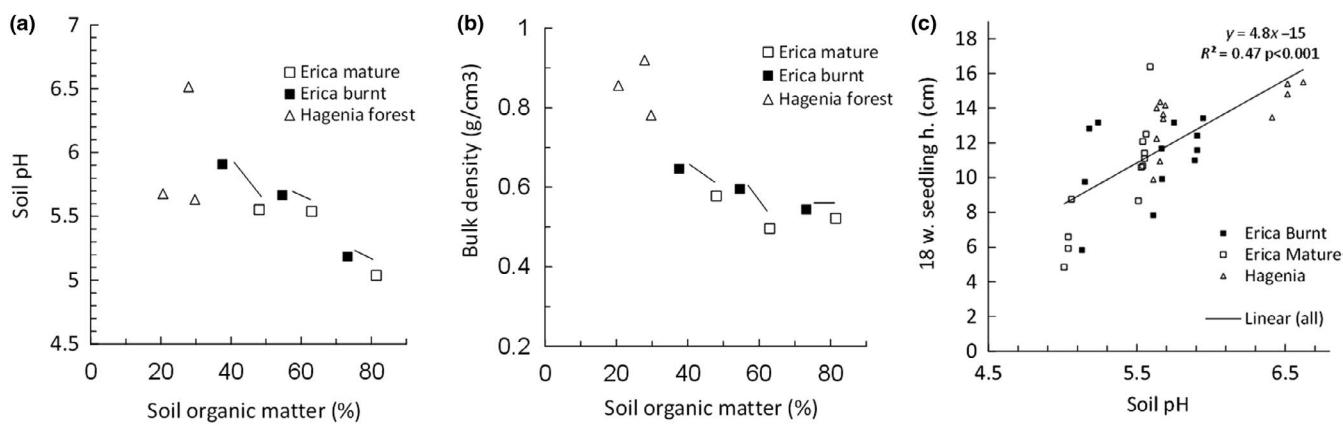


FIGURE 8 Soil analyses (see Supporting information) (a, b) soil sample average pH, soil organic matter and bulk density for recently burnt (filled squares) and mature (open squares) *Erica* stands (values from the same sites connected with a line) and *Hagenia* forests (triangles). (c) Results of *Hagenia* seedling soil bioassay (see Supporting information): *Hagenia* seedling 18-weeks average heights for each soil sample ($n = 12$ soil samples per site, averages of 10–24 seedlings per soil sample)

as well as less competition from a field layer. However, this theory has not been substantiated by any evidence of fire potential in *Hagenia*-dominated forest. Our study does not provide conclusive evidence in either direction. The data suggest that surface fuels in the *Hagenia* forest are poor, whether or not there is grazing. The

total annual leaf-litter fall under closed-canopy *Hagenia* (~430 g/m², Supporting Information) might seem sufficient to allow surface fire (judging from our ignition tests in arranged fuel beds, where the limit for successful fire propagation was ~320 g/m², Supporting Information). However, litter fall was distributed throughout the

year, which reduces the standing surface fuel mass in the dry season. At that time, when pasture is poor, livestock actually consume the fallen *Hagenia* litter. In addition, cattle trampling breaks the brittle leaves, further reducing the standing leaf-litter fuel. In contrast, when livestock was excluded, the forest floor became covered with a dense carpet of mesophytic herbs that possibly increased litter decomposition rates (personal observation of partly decomposed leaves) by keeping it moist (leaf-litter biomass was not greater inside exclosures despite the fact that the cattle eat them outside). In any case, the herb-dominated field layer would inhibit fire as long as it is green. The field layer under closed *Hagenia* forest was never observed to cure, not even during the severe drought in 2007/2008 (cf. Mokria *et al.*, 2017).

Our data show that relaxed grazing pressure is an absolute requirement for the regeneration of *Hagenia*, but this would also have to be accompanied by canopy opening. The few surviving *Hagenia* saplings in our gap exclosures (up to 10 m tall in 10 years, Figure 7f) testify to excellent growth potential in sunny sites, if grazing is excluded and the seedlings can escape competition with the field layer.

4.4 | Effects of livestock exclusion on stability of the tree line

Our results suggest that the distinct tree line, once established, is maintained by several factors which in turn stabilize a clear boundary with respect to flammability. The heathland is highly flammable, in contrast to the forest below because of differences in fuel structure and vertical fuel connectivity (Johansson and Granström, 2014). These contrasts could potentially erode if dominance among the woody plant species is altered, for example if the taller *Hagenia* would be able to colonize the heathland. But three main factors seem to prohibit this: (a) poor *Hagenia* growth in the acidic heathland soils, (b) frequent fires that give competitive advantage to the vegetatively regenerating *Erica* and (c) intense grazing.

As for the highly flammable heathland, removing both livestock and fire would only slowly alter the fuel situation, or the chances for *Hagenia* colonization. It takes more than 20 years before the canopy fuels start separating from the surface fuels (Johansson and Granström, 2014) and substantially longer before flammability decreases. The other *Hagenia* barriers, the soil status and competition from resprouting *Erica*, are more long-term legacies that will remain, even if fire could be excluded (Read and Perez-Moreno, 2003). Similarly, excluding livestock from the forest will not alter flammability much. The poor surface fuels in both *Erica* and *Hagenia* forests will probably remain, as long as the forest canopy is closed, restricting the fuel bed to mainly leaf litter. In many forest habitats reduced grazing of the field-layer results in increased surface fuel mass (Belsky and Blumenthal, 1997; Raffaele *et al.*, 2011; Blackhall *et al.*, 2015), but in our case the denser herb-dominated vegetation that followed on from livestock exclusion even resulted in decreased flammability, given the short dry period and low chances for field vegetation to cure.

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Repeated heathland burning over centuries has created a mosaic of *Erica* stands of different height and cover, resulting in rich biodiversity and extended habitat for Afro-alpine species (Johansson *et al.*, 2018). There is palynological evidence of heathland dominance and anthropogenic fire during the last 2,000 years (Umer *et al.*, 2007; Gil-Romera *et al.*, 2019). Owing to a long history of burning and grazing, the Bale Mountains heathlands have remained in a fire trap. The tree line has not advanced upslope, as would be expected from the long-term warning trend in Africa (cf. Jacob *et al.*, 2015). Within the framework of the new REDD + project in Bale Mountains, there are currently efforts to stop the burning and to impose stronger grazing restrictions (Watson *et al.*, 2013). However, attempts to reduce livestock grazing are not likely to substantially change the present situation either with regard to fire potentials, or with regard to forest regeneration. The old forests will remain highly non-flammable and non-regenerating, and the tree line will remain in place. Heathlands will still be dominated by resprouting *Erica* and high flammability is likely to persist over the foreseeable future. Even without fire and grazing, the acidic soils, a legacy of centuries of *Erica* dominance can further prevent *Hagenia* advancing uphill into the heathlands.

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AUTHOR CONTRIBUTIONS

Both authors were responsible for the conception of ideas and the study design. M.J. did most data collection, analysed the data, and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY

All data are submitted for archiving in Dryad with <https://doi.org/10.5061/dryad.7wm37pvq7>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Summary statistics for *Erica* shrub cover vs. time (for Figure 3)

Appendix S2. Summary statistics for herb functional group cover (for Figure 4)

Appendix S3. Light levels in heath and *Hagenia* forest

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