

Research



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Global change biology

Long-term fire resilience of the Ericaceous Belt, Bale Mountains, Ethiopia

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Fire is the most frequent disturbance in the Ericaceous Belt (*ca* 3000–4300 m.a.s.l.), one of the most important plant communities of tropical African mountains. Through resprouting after fire, *Erica* establishes a positive fire feedback under certain burning regimes. However, present-day human activity in the Bale Mountains of Ethiopia includes fire and grazing systems that may have a negative impact on the resilience of the ericaceous ecosystem. Current knowledge of *Erica*–fire relationships is based on studies of modern vegetation, lacking a longer time perspective that can shed light on baseline conditions for the fire feedback. We hypothesize that fire has influenced *Erica* communities in the Bale Mountains at millennial timescales. To test this, we (1) identify the fire history of the Bale Mountains through a pollen and charcoal record from Garba Guracha, a lake at 3950 m.a.s.l., and (2) describe the long-term bidirectional feedback between wildfire and *Erica*, which may control the ecosystem's resilience. Our results support fire occurrence in the area since *ca* 14 000 years ago, with particularly intense burning during the early Holocene, 10.8–6.0 cal ka BP. We show that a positive feedback between *Erica* abundance and fire occurrence was in operation throughout the Lateglacial and Holocene, and interpret the Ericaceous Belt of the Ethiopian mountains as a long-term fire resilient ecosystem. We propose that controlled burning should be an integral part of landscape management in the Bale Mountains National Park.

1. Introduction

Burning triggers a variety of ecosystem responses depending on type, frequency, intensity and size of the fire [1–3]. This is particularly true in tropical montane ecosystems where fire exerts a critical role in controlling community

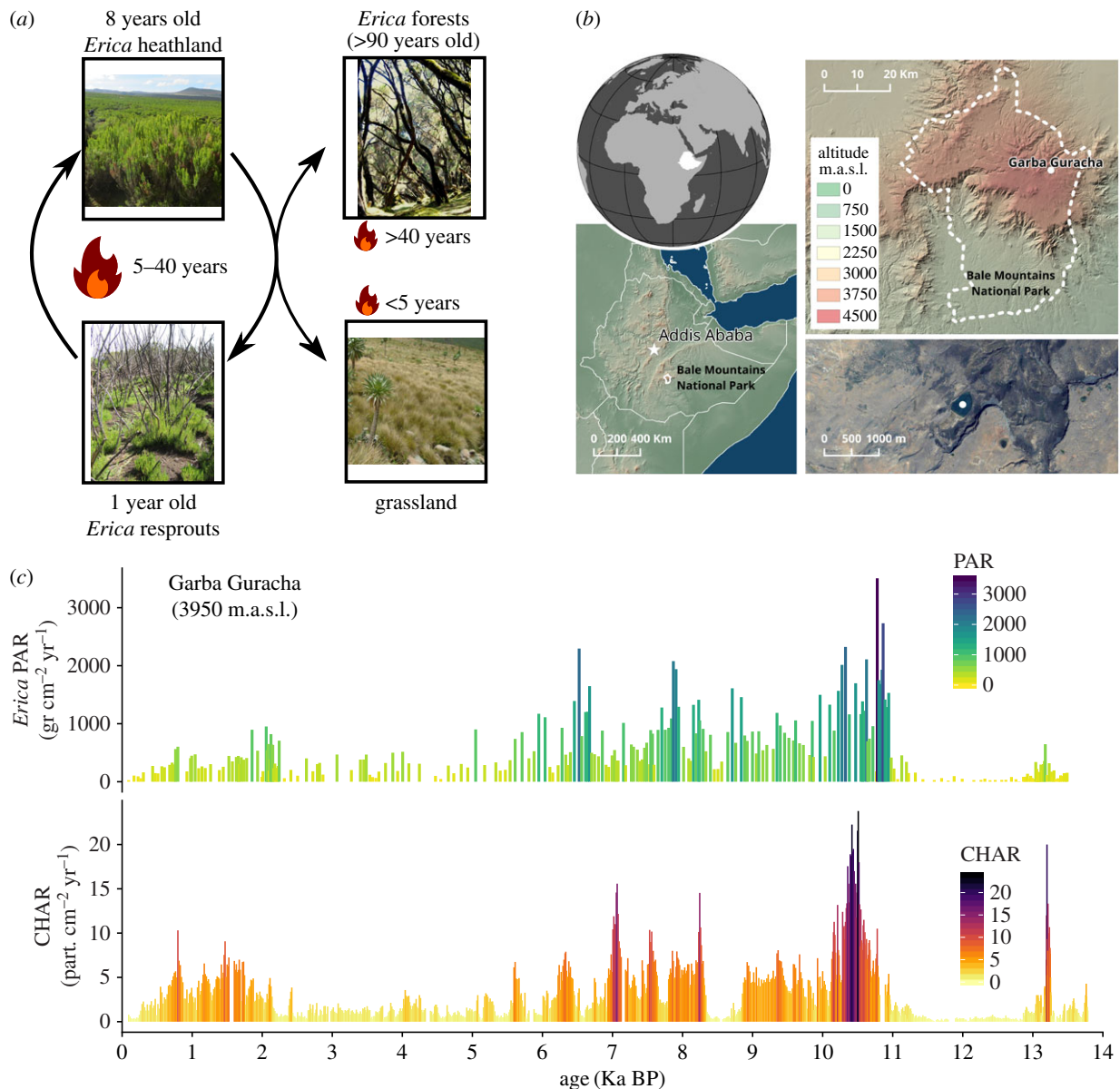


Figure 1. (a) Simplified fire trap dynamics in the Ericaceous Belt of the Bale Mountains. Fire regimes with a frequency between 4 and 50 years allows *Erica* to resprout creating a highly flammable landscape. Fire regimes above that range lead to *Erica* forests with reduced flammability and resprouting ability. More frequent fires lead to open landscapes with sparse less flammable stands and grassland. All photos are by M.U. Johansson but the 8 years old multi-stemmed landscape, which is by G. Gil-Romera. (b) Location map of Garba Guracha lake (3950 m.a.s.l.) in the BMNP. Source: Natural Earth and OpenStreetMap Contributors; DEM: ASTER GDEM (JPL-NASA) and satellite image Digital Globe via Google Satellite Imagery. (c) Top: *Erica* PAR. Bottom: CHAR. (Online version in colour.)

functionality, assembly and dynamics [4–6]. It is the case for the Ericaceous Belt of the Bale Mountains National Park (BMNP) of Ethiopia (figure 1), an African montane ecosystem in which woody vegetation is dominated by *Erica arborea* L. and *Erica trimera* (Engl.) [7,8] (*Erica* hereafter). It lies at the afro-montane–afroalpine ecotone between 3000 and 4300 m.a.s.l., and it varies from dense shrubland to open heathland to forest. This variation is driven by environmental factors such as temperature and moisture, but also by herbivory and fire frequency [9–11]. *Erica* shows a post-fire strategy in which lignotubers, partially underground carbon-storing structures, enable resprouting after fire under certain conditions [12,13]. This strategy sets a positive feedback between community flammability, understood as fire probability, and post-fire response, mediated by fuel accumulation and landscape age structure. In the multi-stemmed shrub phase (approx. 5–40 years), *Erica* is highly flammable [14]. In older phases, the flammable *Erica* canopy becomes vertically separated from surface fuels near

the ground, which creates a moister sub-canopy climate so flammability drastically decreases [4]. The relationship between *Erica* biomass accumulation, fire risk and post-fire response has been defined as a fire trap [14–16], i.e. the situation in which fire intervals between *ca* 5 and 40 years allow *Erica* to resprout and also provide enough time to accumulate biomass that may trigger new fire events [4,14,17] (figure 1a).

Fire in the Ericaceous Belt is often seen as a negative driver in terms of erosion, carbon storage or vegetation resilience [18,19]. However, we argue that through understanding timing and long-term impact of fire, conservation officers can sustainably manage montane ecosystems throughout Africa, especially in BMNP (figure 1b). The Ericaceous Belt is one of the most important ecosystems in the African mountains, and the BMNP holds the most extensive example in Africa [3], covering *ca* 90 000 ha at BMNP [20]. Intensive burning by local pastoralists is reported to negatively impact heathland conservation [16]. By contrast, traditional fire management aims at maintaining biodiversity

by creating vegetation mosaics, with young, non-flammable stands acting as fuel breaks [4].

The question is thus to what extent may short-term observations help in understanding ecosystem dynamics, and in formulating conservation policies. We hypothesize that fire has been in place over long timescales in the area and that resilience, understood as the capacity of a system to revert to a previous state after disturbance [21,22] is a defining feature of the Ericaceous Belt under certain fire regimes. We hypothesize that the fire trap is a resilient property of the Ericaceous Belt since it promotes and perpetuates the system's stability [15,23].

In this study, we provide a millennial to decadal temporal record, from the last deglaciation to the present, aiming: (1) to test the hypothesis that the Ericaceous Belt has long been subject to fire, by identifying and reconstructing past fire activity; and (2) to quantify the long-term fire–*Erica* feedbacks that may define the Ericaceous Belt's resilience. To address these goals, we present, to our knowledge, the most continuous, best-dated Lateglacial–Holocene charcoal record in the African continent from Lake Garba Guracha (GGU) in the BMNP.

2. Site description, material and methods

The Bale Mountains are composed of Miocene basalt and trachyte lava [24]. The BMNP was created in 1970 to protect parts of the unique Ethiopian afro-montane and afro-alpine ecosystems, extending from about 3200 m.a.s.l. in the upper montane zone, to 4377 m.a.s.l. at the peak of Tullu Dimtu in the afro-alpine zone, and including the afro-alpine Sanetti plateau [23]. GGU (06°52.679' N, 39°51.691' E, 3950 m.a.s.l.) has an area of 15 ha and a maximum water depth of 6 m (figure 1b). The regional climate has a pronounced rainfall seasonality; the south to north rainfall gradient and the altitudinal temperature gradient define the montane vegetation zonation [5]. Vegetation around the lake is dominated by afro-alpine communities with prevailing woody dwarf shrubs and various herbs forming a lakeshore marsh community, with isolated *Erica* shrubs and small *Erica* tree stands on the upper slopes of the lake catchment [5]. Palaeoenvironmental studies by Umer *et al.* [25] and Tiercelin *et al.* [26] provide detailed descriptions of the lake catchment geology, ontogeny and vegetation. We retrieved a new 15 m core from GGU in 2017 from which we took 1118 samples of macroscopic charcoal as proxies of past fire and biomass burning [27,28], and 275 fossil pollen samples to document *Erica* response to fire since 14 cal ka BP. Further details on core retrieval, chronology, proxy analyses and taphonomy are given in the electronic supplementary material.

To obtain a time-evenly distributed charcoal record, we modelled charcoal accumulation rate (CHAR) as a function of age with LOESS, by searching a value of the span argument maximizing the R^2 between predicted and observed CHAR. We predicted the result over a regular time grid of 10-year intervals, concurring with the average accumulation rates of GGU's record and with current knowledge of present-day *Erica* vegetation regeneration times [4,6].

Differences in resolution between CHAR and pollen samples prevented the application of cross-correlation [29] to better understand time-delayed and reciprocal links between both variables. Our alternative approach consists of fitting two sets of models: a *synchronous* model (electronic supplementary material, equation S1) fitted on CHAR and *Erica* pollen accumulation rate (PAR) samples with the

same age, and an *asynchronous* model (electronic supplementary material, equations S2 and S3), fitted on given response and time-delayed samples of the predictor. These were fitted once per *lag* on standardized data with generalized least squares (GLS) [30] by using the *gls* function of the R package *nlme* [31]. Pseudo R^2 and standardized coefficient estimates with their respective confidence intervals were used to assess goodness of fit. One thousand null models on permuted response variables were fitted for each equation to assess statistical significance. See electronic supplementary material, Section S6 for further details on numerical methods.

3. Results and discussion: the Ericaceous Belt: a burning story

We have reconstructed the history of burning and ericaceous vegetation around Garba Guracha for the past 14 ka (figure 1c). The data show that fire activity has always been present since the Lateglacial–Holocene transition with varying magnitudes. There are remarkably continuous, intense fire phases during the early and mid-Holocene (10.8–6 cal ka BP) and over the last 2000 years. The long-term Ericaceae dynamics appear closely related to the burning patterns displayed in the GGU core. Thus PAR seems coupled to the higher charcoal abundances, indicating that more numerous and larger fires accompanied the spread of *Erica* around GGU as it dominated the landscape between 11 and 6 cal ka BP. Both *Erica* and burning increased slightly after 2 cal ka BP. We infer that the Ericaceous Belt extended significantly in the GGU catchment and across the adjacent Sanetti plateau, thus increasing fuel availability and supporting larger fires.

The synchronous model (electronic supplementary material, equation S1) show a positive relationship (pseudo R^2 0.16, electronic supplementary material, figure S4) between paired CHAR (hereafter called fire) and Ericaceae PAR samples (hereafter called *Erica*). The asynchronous model (electronic supplementary material, equation S2) fitted on time-delayed fire (i.e. the effect of past fires on current *Erica* value, figure 2a,c) showed that fire has a significant and increasing positive influence on *Erica* between 550 and 10 years (lag 55–1) before each *Erica* value, with a maximum pseudo R^2 value of 0.15 at lag 1, converging with the pseudo R^2 -squared of the synchronous model. These results suggest that the post-fire response to wildfires at multi-decadal timescales favoured heathland, rejuvenating the system, fostering vegetative resprouting (i.e. maintaining the fire-trap) and strengthening its resilience. This process took place for most of the Holocene in the Bale Mountains.

The output of the asynchronous model (electronic supplementary material, equation S3) fitted on time-delayed *Erica* samples (i.e. the effect of past *Erica* values on current fire occurrence, figure 2b,d) showed that *Erica* has an increasingly strong positive correlation with fire across all lags, starting with a pseudo R^2 value of 0.20 at lag 1 (also converging with the pseudo R^2 of the synchronous model) reaching 0.35 at lag 40 (400 years).

A thought-provoking result is that the positive effect of *Erica* on fire occurrence over such a large time interval implies a period of longer fuel accumulation than that of the modern fire-trap system (5–40 years). Old *Erica* trees are not able to resprout; once burnt, large trees die, thus

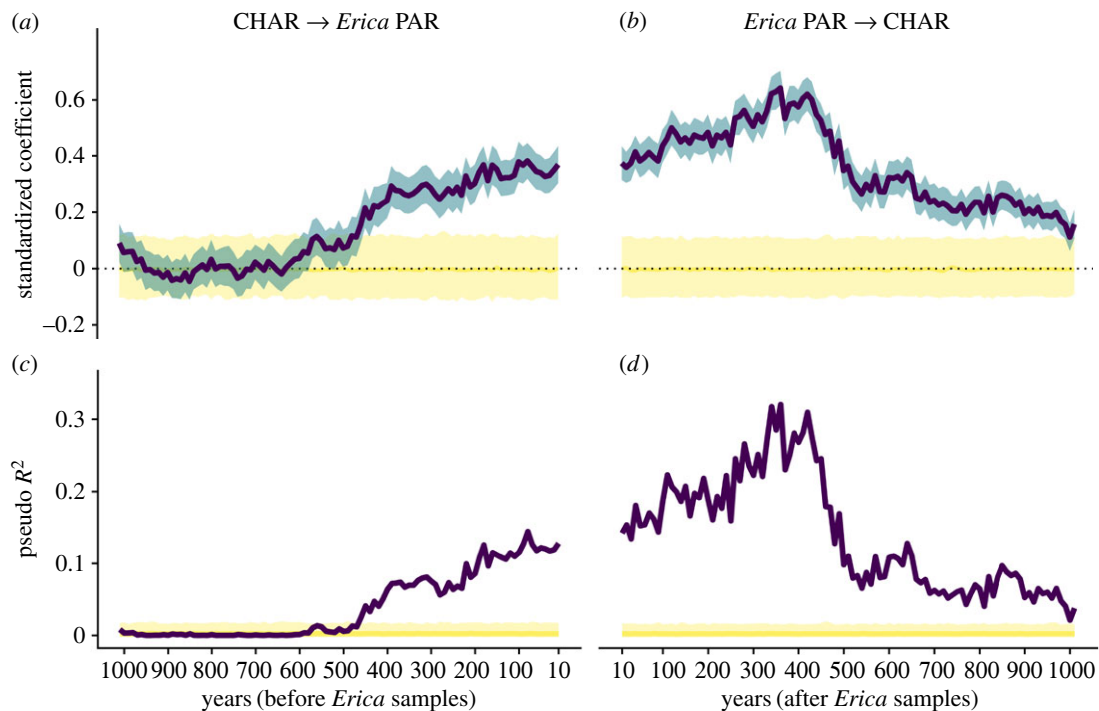


Figure 2. Standardized coefficients (a,c) and pseudo R^2 (b,d) results from the GLS models fitted on lagged data to assess the effect of fire on *Erica* (a,b), and *Erica* on fire (c,d). Yellow lines represent coefficients and pseudo R^2 for the null model, so data not intersecting yellow lines are interpreted as statistically significant. (Online version in colour.)

disrupting the fire trap [32]. Rather than a contradiction, we understand this to be a non-analogue situation; i.e. there are no equivalent dense old *Erica* forests in the present-day *Erica* heathlands. The multi-stemmed *Erica* shrubs (5–40 years old) have a higher flammability than *Erica* forests [14]. However, landscape flammability does not correlate with quantity of fuel after passing the forest threshold; although *Erica* forest has higher fuel abundance, it is less flammable than *Erica* shrubs. Fuel amount is undoubtedly one of the most relevant parameters controlling charcoal amounts deposited into a lake. This means that intense, large *Erica* forest fires left a larger imprint in the lacustrine sequence than fires in the dense, shorter heathland thickets. Therefore, biomass accumulating over centuries without fires could lead to increased fire intensity—recorded as charcoal amounts in the sedimentary archive—when a fire eventually occurs.

We thus interpret the current Ericaceous Belt on the Bale Mountains as a legacy of a long history of fire, where *Erica* heathland resilience built up under short and medium time-scale fire regimes. There are no other quantitative studies on the long-term effect of fire in the African Ericaceous Belt, but our findings concur with evidence from Ericaceae communities in other biomes, such as the Mediterranean biome, and their post-fire responses [33,34]. Our results support the conclusion that controlled burning is indeed necessary to favour mosaic *Erica* landscapes where a variety of community ages prevents very large, destructive wildfires.

4. Conclusion

We confirm that the Ericaceous Belt of the Bale Mountains is a historically fire-dominated landscape where fire has been particularly intense during the early Holocene and over the last 2000 years. Our results indicate that the Ericaceous Belt has

long-term resilience to burning, as past montane *Erica* communities at these altitudes underwent intense burning without reducing their dominance. Our asynchronous GLS model indicates that the bidirectional relationship between fire and *Erica* is positive. The model indicates that a long history of fire occurrence at decadal to multi-centennial scales had a positive effect on today's *Erica* heathlands. Similarly, *Erica* fuel accumulation over timescales of tens to hundreds of years has played an important role in fire occurrence and behaviour. These results support the integration of fire as a tool for landscape conservation in the Ericaceous Belt of the BMNP.

Data accessibility. The code and data are temporarily archived in the Zenodo repository: <https://zenodo.org/record/3245377> but data will also be available at the Global Charcoal Database: <https://www.paleofire.org/> and the Neotoma palaeo data archive <https://www.neotomadb.org/>, upon publishing this manuscript. The code is likewise available in the first author's github: <https://github.com/ggilromera/BaleFire>.

Authors' contributions. G.G.-R., M.U.J. and G.M. conceived the study, G.G.-R., H.F.L., M.Z., L.B., B.L., D.A.G. and M.F. performed the coring campaign. L.B. coordinated the dating process and performed the depth-age model and G.G.-R. analysed pollen and charcoal. G.G.-R., B.M.B. and C.A. performed numerical analyses, wrote the code and discussed results. G.G.-R. led the writing process, M.U.J., G.M., B.M., B.G. and W.Z. discussed the role of fire and the relationship with *Erica*, M.S.-C. contributed with art work and all authors made important contributions to the final manuscript revising it critically adding important intellectual content. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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