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Factors determining the distribution of *Erica* patches on the Sanetti Plateau, Bale Mountains, Ethiopia

Betelhem Mekonnen[1,2] · Bruno Glaser[1] · Michael Zech[3] · Tobias Bromm[1] · Sileshi Nemmomisa[4] · Tamrat Bekele[4] · Wolfgang Zech[2]

Abstract

In the Bale Mountains, the ericaceous belt ranges between 3200 and 3800 m asl. Studies indicate an expansion on the Sanetti Plateau at the end of the Late Glacial and during the early Holocene. Currently, only patches of *Erica* growing between boulders are found on the Plateau, while most of the landscape above 3800 m asl is covered by afro-alpine plants. Driving factors for *Erica* patches above the upper ericaceous ecotone is a matter of debate. This study evaluates site variables and biogeochemical properties of soils under *Erica* patches and nearby *Erica*-free control to understand the environmental conditions responsible for the patchy occurrence of *Erica* on the Sanetti Plateau. Except for the boulder richness, *Erica* and control plots have comparable topography, soil texture, and electrical conductivity. However, soils below *Erica* patches have higher total organic carbon, nitrogen, carbon-to-nitrogen ratios, and black carbon contents than the control plots indicating fresh organic matter input and availability of combustible fuel. This implies that *Erica* did not fully cover the control plots in former times. Carbon and nitrogen stocks were slightly higher in control plots due to the lower stone contents of the profiles. In addition, soils of the *Erica* plots showed more positive $\delta^{13}C$ values than the control soils, possibly attributed to water stress. In general, the relief and soil conditions of control plots may support the growth of *Erica*. However, *Erica* growing between boulders seems to benefit from the favorable microclimate and physical protection against grazing and fire.

Keywords *Erica* patches · Environmental factors · Fire · Boulders · Sanetti Plateau · Ethiopia · Bale Mountains

Introduction

Defining the tree line ecotone of high-elevation vegetation is often problematic and debatable as it is difficult to unambiguously identify and quantify the factor that plays the most significant role (Körner 2007; Jacob et al. 2015). Such difficulties have been observed in the East African Mountains, which are vulnerable to climate change and anthropogenic impacts (Wesche et al. 2000; Jacob et al. 2015). *Erica*, also known as heathers or heath, is one of the most widely distributed plant genera in the Ericaceae family (Oliver 1989; Kron et al. 2002). Its geographical distribution covers Europe, the Middle East, South America, and Africa (Mcguire and Kron 2011). *Erica* species (*Erica trimera* and *Erica arborea*) dominate and characterize most high-elevation mountains in eastern Africa, forming the upper tree line forest (Hedberg 1951; Wesche et al. 2000; Fetene et al. 2006). Ericaceous vegetation is widespread in northern (Siemen Mountains) and southern Ethiopia (Bale Mountains, Mt. Chillalo, Mt. Kaka, Galama Mountains, and Arsi highlands) (Hedberg 1951; Miehe and Miehe 1994). In the Bale Mountains, the ericaceous belt covers an area of 90,000 ha and spans between 3200 and 3800 m asl (Miehe and Miehe 1994). According to Fetene et al. (2006), the ericaceous vegetation is grouped into three elevational subzones. The lower subzone is characterized by the *Erica*-dominated *Hagenia-Hypericum* forest, which spans between 3000 and 3400 m asl. The central part covers the elevation

✉ Betelhem Mekonnen
betymekonnen19@gmail.com

1 Institute of Agricultural and Nutritional Sciences, Soil Biogeochemistry, Martin Luther University Halle-Wittenberg, Halle, Germany

2 Department of Soil Science, University of Bayreuth, Bayreuth, Germany

3 Institute of Geography, Technical University of Dresden, Dresden, Germany

4 Department of Plant Biology and Biodiversity Management, Addis Ababa University, Addis Ababa, Ethiopia

between 3400 and 3600 m asl; dominated by *Erica trimera*, *Hypericum revolutum,* and *Alchemilla abyssinica*. In the upper subzone between 3600 and 4200 m asl, the Erica-ceous vegetation has a patchy appearance, especially at the Sanetti Plateau between 3800 and 4200 m asl. Such patchy appearance of *Erica* vegetation is also reported from other high-elevation African mountains such as Mt. Kilimanjaro, Mt. Elgon, Mt. Kenya, and the Rwenzori Mountains (Hedberg 1951; Beck et al. 1983; Wesche et al. 2000) and the Andes in South America (Kessler 2000). The presence of these *Erica* patches, mainly growing between big boulders, makes the demarcation of the upper limit of *Erica* difficult (Friis 1986; Miehe and Miehe 1994). The Sanetti Plateau is one of the largest afro-alpine areas in Africa (Hillman 1988; Groos et al. 2021). The area is mainly covered by afro-alpine plant species such as *Helichrysum*, *Alchemilla*, *Lobelia*, and grasses (Friis 1986; Miehe and Miehe 1994). However, big boulders, frequently present on slopes of the Plateau, serve as "refugee camps" for *Erica* above the upper ericaceous ecotone at ca. 3800 m (Miehe and Miehe 1994).

Climatic stress, fire, and overgrazing are postulated as potential drivers for tree line changes in the ericaceous vegetation of the Bale Mountains (Miehe and Miehe 1994; Wesche et al. 2000; Fagúndez 2013; Jacob et al. 2015; Johansson et al. 2018; Kidane et al. 2022). Similarly, the presence of *Erica* patches in the highest elevation east African mountains is explained by the impact of human-induced fire and climate change (Kessler 2000; Hemp and Beck 2001; Hemp 2005). For instance, Chala et al. (2017) suggested the downward shift of the tree line by 1000 m and the corresponding expansion of the afro-alpine habitat during the Last Glacial Maximum (LGM) in eastern Africa. Furthermore, paleoenvironmental studies in the Bale Mountains revealed the effect of climate fluctuation on vegetation (Umer et al. 2007; Gil-Romera et al. 2019; Groos et al. 2021; Mekonnen et al. 2022). Umer et al. (2007) reported that the ericaceous vegetation extended to the Sanetti Plateau during the beginning of the Holocene in response to the warm and humid climate, and they suggested that the vegetation expansion started to decrease during the mid-Holocene due to increasing aridity. Kidane et al. (2022) and Chala et al. (2016) assumed that the current climate warming might alter the spatial arrangement of the ericaceous vegetation in the Bale Mountains by supporting its expansion to the Plateau and simultaneously the extinction of afro-alpine vegetation.

At present, the growth of *Erica* on the Sanetti Plateau is mainly restricted to boulder-rich sites. In contrast, areas nearby without boulders are generally free of *Erica* and mainly covered by afro-alpine species such as *Alchemilla haumannii*, *Helichrysum splendidum* and *Festuca abyssinica*. These *Erica* patches are assumed to be relics of the ericaceous vegetation expansion during the humid Early Holocene (Miehe and Miehe 1994; Umer et al. 2007). Fire

has been prominent in the Bale Mountains for hundreds to thousands of years (Gil-Romera et al. 2019; Mekonnen et al. 2022). This is because the pastoralists in the Bale Mountains believe that fire stimulates the growth of new grass for cattle grazing, thus improving fodder quality, controlling insect pests, and protecting their cattle from predators (Miehe and Miehe 1994; Fetene et al. 2006; Belayneh et al. 2013). As a result, the spatial extent of different vegetation groups in the Bale Mountains, including the isolated patches of *Erica,* has drastically changed over time (Kidane et al. 2012). Grazing is also considered to play a significant role in controlling the expansion of *Erica*. According to Johansson et al. (2010), cattle, goats, and sheep are the main grazing domestic animals in the ericaceous vegetation. Furthermore, according to Gebremedhin et al. (2016), *Erica arborea* is a highly preferred diet by domestic goats in the Semien Mountains. In particular, goats and sheep intensively graze the *Erica* seedlings sprouting after fire, thus putting immense pressure on their regeneration. However, in addition to these biotic factors, temperature, precipitation, soil quality, and wind speed have determinant effects on the growth of trees (Jacob et al. 2015). Miehe and Miehe (1994) hypothesized that temperature and moisture availability could be factors limiting the growth of *Erica* on the Sanetti Plateau. Moreover, Groos et al (2022) have presented ground temperature data sets for the Bale Mountains high-elevation sites. However, up to now, except for observational descriptions, there has been no quantified evidence that can explain the patchy occurrence of *Erica* on boulder-rich slopes of the Sanetti Plateau above ca. 3800 m asl. $\delta^{13}C$ analyses of leaves and soils are used to determine historical alterations in the boundary between C3 woodland and C4 grasslands (Eshetu 2002). This is mainly due to the differences in the photosynthetic pathways between C3 and C4 plants. While C3 plants are characterized by $\delta^{13}C$ values of -22 to $-35‰$, C4 plants show $\delta^{13}C$ values of -11 to $-17‰$ (Marshall et al. 2007; Tiunov 2007). In addition, $\delta^{13}C$ is a prominent proxy for determining plant water status. It decreases the $\delta^{13}C$ value in dry tissue due to stomatal constraints on gas diffusion during periods of biomass production (Körner 2012a). Black carbon (BC) is a highly condensed carbonaceous product of organic matter combustion (Glaser et al. 1998; Brodowski et al. 2005). Due to its highly stable polycyclic hydrocarbons, black carbon is widely used as a proxy for fire history reconstruction (Kuzyakov et al. 2014). Applying this proxy in this study is promising because fire is a common incidence in the ericaceous vegetation of the Bale Mountains. In addition, the patchy distribution of *Erica* on the Sanetti Plateau is assumed to document fire disturbance (Miehe and Miehe 1994; Wesche et al. 2000; Gil-Romera et al. 2019).

In this study, we aim to contribute to a better understanding of the distribution of *Erica* on the Sanetti Plateau by comparing *Erica* and non-*Erica* plots (control plots) based

on different environmental and biogeochemical proxies such as topography and selected soil properties. Specifically, our research questions are: (i) Is topography (elevation, exposition, inclination) a limiting factor, and is stone cover a favoring factor for the growth of *Erica*? (ii) Do *Erica* sites have different soil properties than control plots (e.g., pH, TOC, N contents and stocks, stable isotopes, and BC contents)? Finally, (iii) Is there any evidence that *Erica* has previously occupied the control plots?

Materials and methods

Study area

Geology, vegetation, and climate

The Bale Mountains National Park is located in the Oromia National Regional State, south-east Ethiopia (6°29′–7°10′N and 39°28′–39°57′E; Fig. 1), covering an area of ∼ 2200 km² (Hillman 1988). The park was established in 1970 to conserve its endemic fauna and flora. The Bale Mountains were formed by volcanic eruptions during the Miocene and Oligocene, releasing large amounts of basalt, rhyolite, and ignimbrite (Mohr 1983). They rise from the eastern highlands (2500 m asl) alongside the Ethiopian rift valley to the Sanetti Plateau (3800–4000 m asl) and Tullu Dimtu (4377 m asl) (Miehe and Miehe 1994). Besides, the Bale Mountains were one of the most glaciated mountains in Ethiopia during the Late Pleistocene (Osmaston et al. 2005; Mark and Osmaston 2008; Groos et al. 2021).
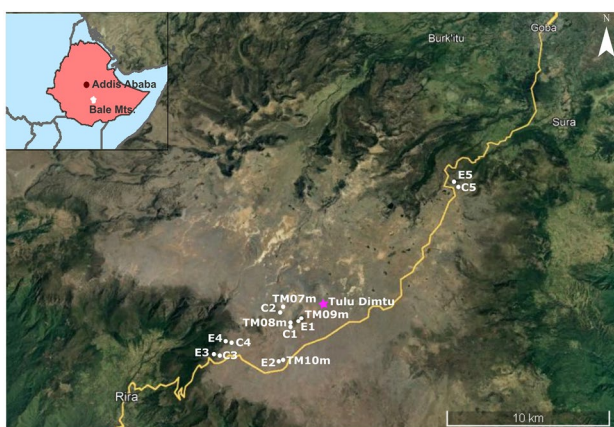

Fig. 1 Map showing the geographical location of the Bale Mountains in Ethiopia and the study sites; five covered by *Erica* patches (E1–E5) and five located nearby without *Erica* (Control sites C1–C5), covered by grass and *Helichrysum* and temperature loggers installed by Groos et al. (2022) at the site 1 (TM09m and TM08) and site 2 (TM07 and TM10)

Spatial and temporal variability prevailed in the different vegetation compositions of the Bale Mountains along elevation. The northern and southern declivities between 1450 and 3200 m asl are characterized as dry and moist Afromontane forests, respectively. One of the dominant vegetation types in the Bale Mountains is the Ericaceous belt mediating between Afromontane and afro-alpine vegetation (Miehe and Miehe 1994). It spans between about 3200 and 3800 m asl, dominated by *Erica arborea L.* and *Erica trimera* (Engl.) Beentje (Hedberg 1951) in the form of shrubland and moist forest along the northern and southern slopes, respectively. The afro-alpine vegetation dominates above 3800 m asl up to 4377 m asl, punctuated by patches of *Erica* (Miehe and Miehe 1994). The dominant plant species in each elevational zone are covered in depth elsewhere (Hedberg 1951; Friis 1986; Miehe and Miehe 1994).

The climatic conditions of the Bale Mountains are defined by topography and the movement of the Intertropical Convergence Zone and the Congo air basin (Levin et al. 2009; Costa et al. 2014). As a result, the climate is characterized by a dry and bimodal rainy season. The dry season spans from November to February, and two rainy seasons prevail from March to June and from July to October, respectively. In Dinsho (the Bale Mountains National Park headquarters at 3070 m asl), the mean annual precipitation is 1069 mm, and the mean annual temperature is 11.8 °C. The southwestern part of the mountains experiences higher precipitation, with 1000–1500 mm per year, than the northern part, which exhibits annual rainfall ranging between 800 and 1000 mm per year (Hillman 1986; Tiercelin et al. 2008). The watershed of the Plateau is characterized by flat, swampy areas and many small, shallow lakes crucial for stream and river flow regulation (Belayneh et al. 2013). While the northern winds from the Arabian Peninsula dominate during the dry season, the southeasterly monsoon transports moisture from the Indian Ocean during the rainy seasons (Lemma et al. 2020). During the rainy season, snow can fall on the Plateau and highest peaks but usually does not persist for longer than a few hours or some days (Miehe and Miehe 1994).

Sample collection

Five sites were identified along a NE-SW transect over the Sanetti Plateau (Fig. 1). For each site two plots were identified; one covered by dense *Erica* patches (*Erica* plot) and the second one only by grass spp., *Helichrysum*, and a few *Alchemilla* plants (Figs. 1, 2) but without *Erica* (control plot). After testing the soil homogeneity using a soil auger, a total of ten representative soil profiles (five under *Erica* patches and five in adjacent control plots) were dug until the bedrock was reached, and the main topographic variables (elevation, aspect, and slope) and soil depth were recorded. Soil profiles were described (e.g., color, texture,
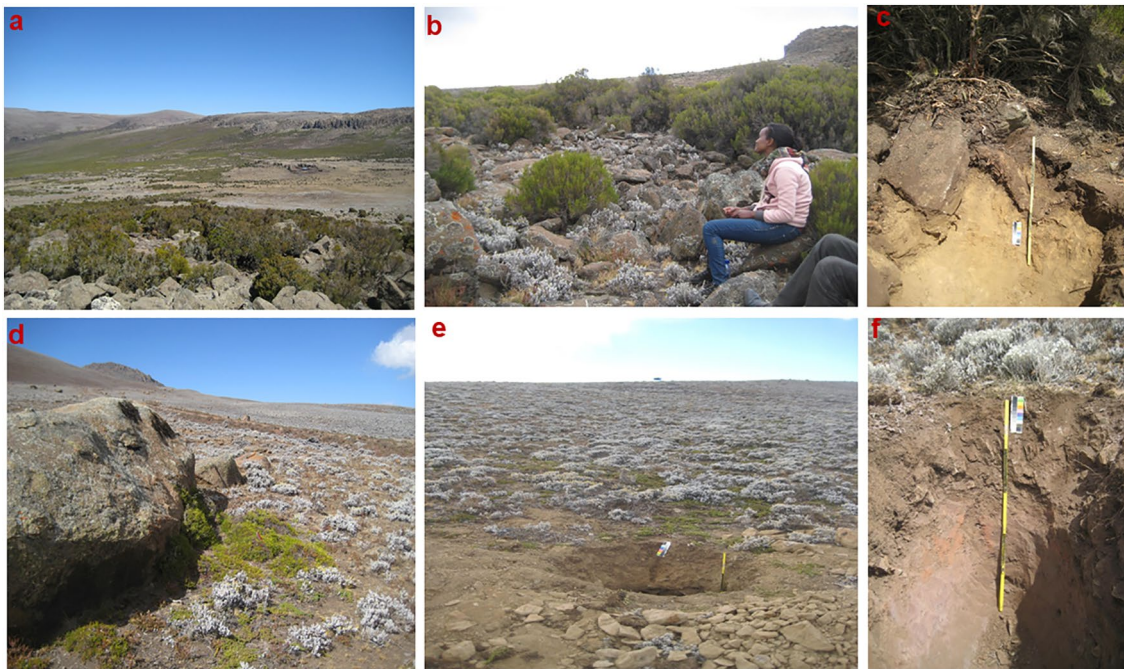
Fig. 2 Pictures showing sampling sites. **a** Site of *Erica* patch (E4) at 3970 m asl in north exposition **b** *Erica* patch E2 with *Erica* shrubs growing between stones and boulders. **c** Soil profile below *Erica* shrubs (E2). **d** *Erica* seedlings growing beside a single big boulder on a control plot. **e** Control plot (C1) covered by *Helichrysum* sp at 4150 m asl. **f** Soil profile below control plot (C3)

stone contents in vol.%, and root content, see Table S1 and Bodenkundliche Kartieranleitung (Ad-hoc-Arbeitsgruppe Boden 2005)), and samples were taken from each soil horizon, air dried, and stored in plastic bags. In addition to soil samples, leaves of *Erica*, grass (*Festuca*), and *Helichrysum*, the dominant afro-alpine species, were collected randomly from the study plots.

Laboratory analyses and statistical evaluation

pH and electrical conductivity were measured using 10 g of O-layer and 20 g of mineral soil samples. After placing the samples in containers, 25 ml of distilled water was added. The suspensions were shaken for 30 min and allowed to settle. Subsequently, electrical conductivity and pH were measured with a glass electrode. Soil texture analyses were done using PARIO Soil Particle Analyzer (METER Group, Munich, Germany). Before measurement, samples were treated using 50 ml of 30% H_2O_2 and 40 g/L solution of $Na_4P_2O_7$. Total organic carbon (TOC), total nitrogen (N), and the natural abundance of $\delta^{13}C$ and $\delta^{15}N$ were measured using an elemental analyzer coupled to an isotope ratio mass spectrometer (EL-IRMS). While sucrose (ANU, IAEA, Vienna, Austria) and $CaCO_3$ (NBS 19, TS limestone) were used as calibration standards for $\delta^{13}C$, IAEA 305A, IAEA N_2, IAEA NO_3, and USGS 41 were used for $\delta^{15}N$.

The precision of $\delta^{13}C$ and $\delta^{15}N$ measurements was 0.2‰ and 0.3‰, respectively.

Soil organic C and N stocks of each mineral soil horizon and the whole soil profile were calculated according to Batjes (Batjes 1996).

$$SOC_{stock} = \sum_{i=1}^{k} SOC \times BD \times t \times \left(1 - \left(\frac{S}{100}\right)\right), \quad (1)$$

where SOC_{stock} is the total amount of organic carbon (in kg m^{-2}), SOC is the proportion of organic carbon (kg Mg^{-1}) in layer i, BD is the bulk density (Mg m^{-3}) of layer i, t is the thickness of this layer (m), and S is the volume of the fraction of fragments > 2 mm.

The carbon stock of the O-layers was calculated differently from that of the mineral soils:

$$C - stockO - layer = \left(\left(\frac{weight}{40}\right) \times SOC\right)/100, \quad (2)$$

The organic material has been sampled using a 20 cm × 20 cm metal frame. This procedure provides the weight of all the organic material sampled per unit area, independently of its depth.

BC was analyzed using benzene polycarboxylic acids (BPCAs) as molecular markers, following Glaser et al. (1998) with modifications by Brodowski et al. (2005). Five

hundred mg of each sample were hydrolyzed with 10 ml 4 M TFA for 4 h at 105 °C. The hydrolyzed samples were filtrated on glass fiber filters and rinsed several times with de-ionized water to remove polyvalent cations. Subsequently, the samples were digested with 65% nitric acid for 8 h at 170 °C in a high-pressure digestion apparatus. The solution was passed through Dowex 50 W resin columns (200 to 400 meshes) to remove polyvalent cations. After derivatization, the BPCAs were separated using gas chromatography (SHIMADZU, GC-2010, Kyoto, Japan) and detected using a flame ionization detector (FID) with an injection temperature of 300 °C. All statistical analyses were done using R software.

Results

Environmental features and soil properties

Erica and control plots of a given site generally have comparable topographic features; they are located in southern (sites 1, 2, and 3) and north-eastern (sites 4 and 5) expositions between 3850 and 4150 m asl (Table 1).

Except for E4, usually, the inclination is weak. *Erica* plots are generally covered by big boulders (average 60%), with *Erica* shrubs (~ 1.5 m tall) growing between the boulders (Fig. 2a, b). In contrast, control plots are completely covered by grass and afro-alpine plant species with no visible big stones/boulders on the surface (Fig. 2e, f).

The soils under study are characterized by thick Ah horizons (up to 75 cm), which were further subdivided into Ah1, Ah2, and Ah3. Additionally, B, C, and transitional horizons could be identified based on morphological properties such as color, stone content, roots, etc. (Fig. 2c, f; Table S1). Due to the very high stone contents of the C horizons, the comparison between *Erica* plots and the corresponding control plots was restricted to O, Ah, and Bw horizons; only the

SOC stocks were calculated for the whole soil profile. Since the percentage of stones is a very influential factor for root penetration, water storage capacity, carbon, and nutrient accumulation, stoniness was determined per horizon. The results showed that, even though not statistically significant, stone contents are often higher below *Erica* than in soils of control plots (Fig. 3). For instance, the Ah1 horizons of control and *Erica* plots have an average stone content of 36 and 45, respectively. In the Bw horizons of *Erica* and control plots, stone contents increased to ca. 90 (Fig. 3). Bulk density of control soils was significantly higher than that below *Erica* (Fig. S1, $p = 0.002$).

Soil texture fractions are highly variable along the soil depth of *Erica* and control profiles (Fig. S2). However, no significant difference is obtained between *Erica* and the
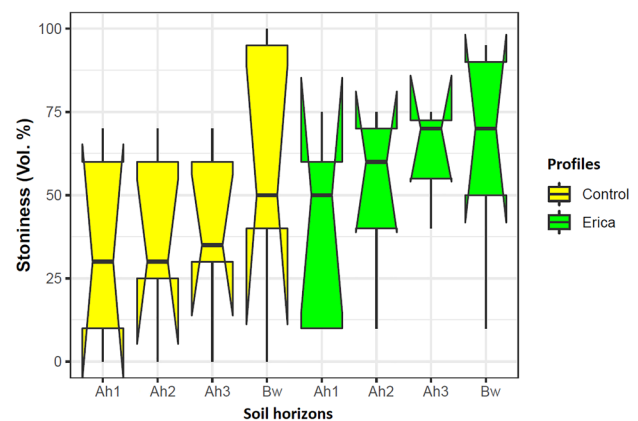

Fig. 3 Stone content in soil horizons of all *Erica* and control sites, estimated according to Bodenkundliche Kartieranleitung (2005). The notched box plots indicate the median (solid lines between the boxes) and interquartile range (IQR) with upper (75%) and lower (25%) quartiles. The notches display the 95% confidence interval of the median. The lines extending outside the box (whiskers) show variability outside the quartiles

Table 1 Topographic features and estimated surface stone cover of (**a**) the *Erica* plots (E1–E5) on the Sanetti Plateau, and (**b**) *Erica*-free control plots (C1–C5) on the Sanetti Plateau

| Sites	Latitude	Longitude	Elevation m asl	Exposition	Inclination	Stone cover of surface (vol. %)
(a) (E1–E5) on the Sanetti Plateau						
E1	6.8133	39.81968	4140	SE	5°	80
E2	6.79183	39.81035	3900	S	3°	80
E3	6.78887	39.77353	3850	S	3°	25
E4	6.802583	39.78088	3940	NNE	30°	50
E5	6.8956	39.90972	3975	N	2°	60
(b) (C1–C5) on the Sanetti Plateau						
C1	6.8193	39.81148	4150	SE	5°	0
C2	6.826067	39.8049	3920	S	3°	0
C3	6.78827	39.77207	3850	S	2°	0
C4	6.80228	39.78257	3900	N	3°	0
C5	6.89313	39.9092	3990	E	1°	0

control plots. pH values range between 5.6 and 6.8 in *Erica* and control soils (Fig. 4). However, the pH values do not vary significantly between *Erica* and control plots, except for the O layers below *Erica*, which show a slight decrease in pH values ($\bar{x} = 5.6$). EC values vary between 45 and 198 µS cm^{-1} below *Erica* and between 31 and 488 µS cm^{-1} in control soils (Fig. 4). Moreover, EC values decrease with increasing soil depth in both *Erica* and control soil profiles.

Soil organic carbon and nitrogen contents

TOC values of *Erica* plants show significantly higher values than *Helichrysum* and *Festuca* ($p = 0.009$) (Fig. 5). However, there is no significant difference between the TOC contents in the soils of *Erica* and control plots. Nevertheless, the mineral soil horizons of the *Erica* plots tend to have higher TOC contents than the control profiles. TOC values of organic
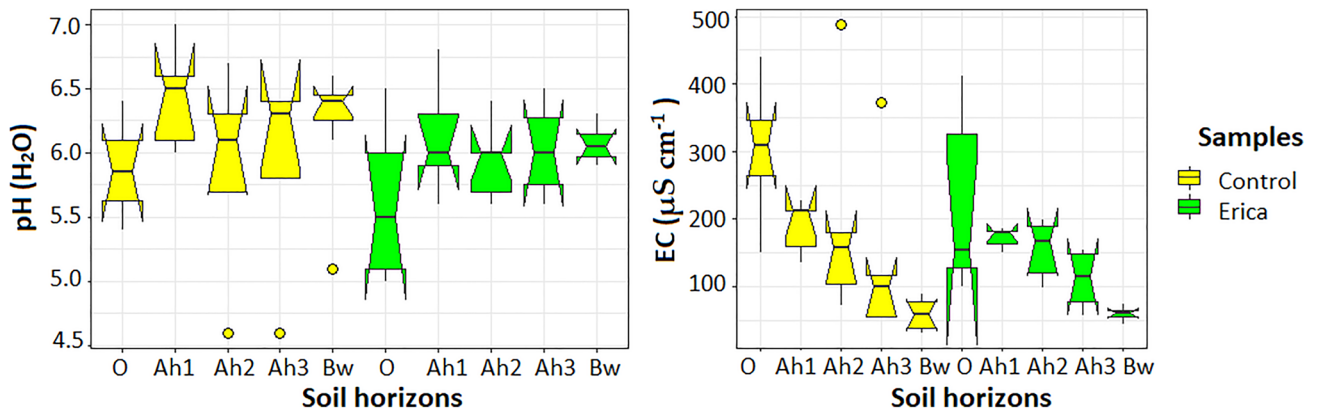
Fig. 4 Electrical conductivity (EC) and pH in soil horizons of *Erica* and control sites. The notched box plots indicate the median (solid lines between the boxes) and interquartile range (IQR) with upper (75%) and lower (25%) quartiles. The notches display the 95% con- fidence interval of the median. The lines extending outside the box (whiskers) show variability outside the quartiles. The circles repre- sent outliers
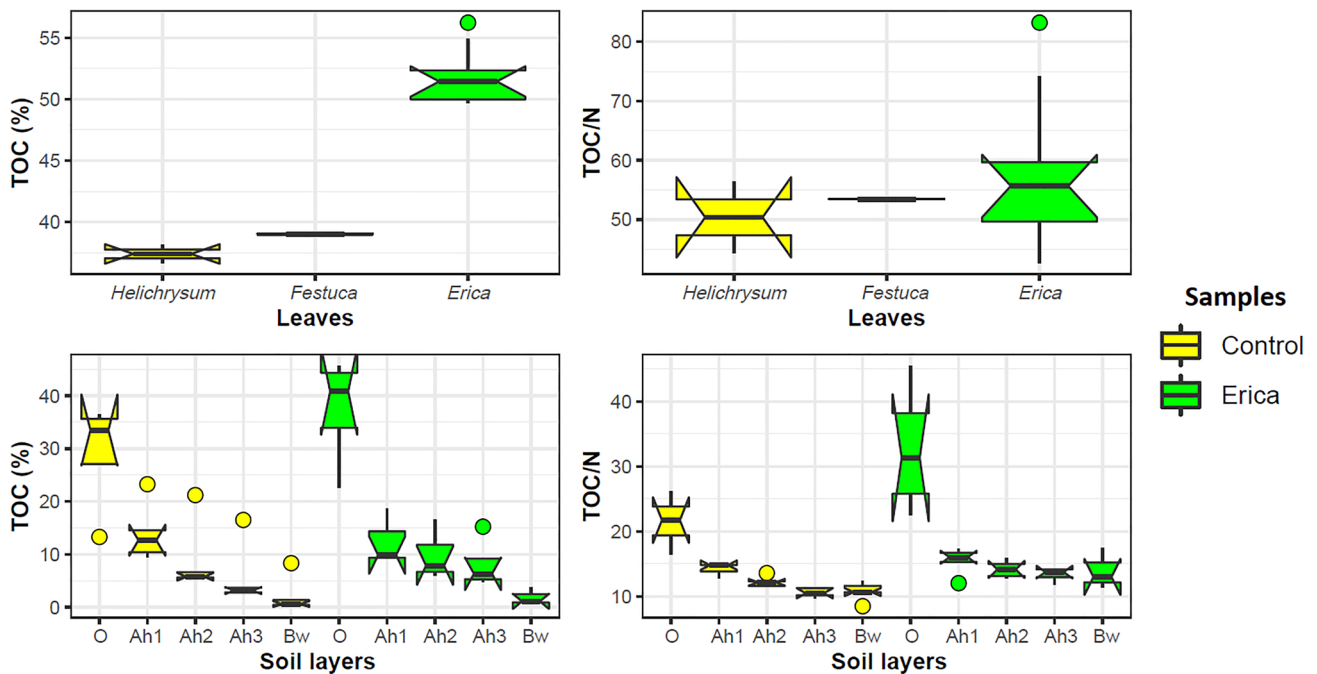
Fig. 5 Total organic carbon (TOC) and TOC/N ratio of plant leaves and soil horizons of *Erica* and control sites. The notched box plots indicate the median (solid lines between the boxes) and interquartile range (IQR) with upper (75%) and lower (25%) quartiles. The notches display the 95% confidence interval of the median. The lines extend- ing outside the box (whiskers) show variability outside the quartiles. The circles represent outliers

layers vary between 13 and 33% in control plots and range from 23 to 46% in *Erica* plots. Moreover, the TOC values of the Ah3 layers below *Erica* are higher ($\bar{x} = 8.2\%$) than those of the control plots ($\bar{x} = 5.7\%$). Similar to TOC, the N contents of *Erica* leaves are higher than those of *Festuca* and *Helichrysum* (Fig. S3). In the organic and Ah1 horizons of control plots, N contents are slightly higher than below *Erica*, while N in the other horizons is somewhat enriched below *Erica*. N values, like TOC values, decline with increasing depth in all soil profiles.

In soils, TOC/N ratios range from 10 to 45 below *Erica* and 9–26 in control plots (Table S2). They are, in general, significantly higher in *Erica* plots than in control plots ($p = 0.006$). While TOC/N ratios in control soils drastically decrease with increasing soil depth (from Ah1 to Ah3), they remain significantly high in Ah2 ($p = 0.03$) and Ah3 ($p = 0.01$) soil horizons under *Erica* (Fig. 5).

Soil organic carbon and nitrogen stocks

Figure 6 depicts soil organic carbon stocks restricted to soil depths of 0–30 cm, 0–50 cm, and the whole profile that considers the profile's maximum depth in each plot. The results show that, even if not statistically significant, SOC stocks are slightly higher in control plots than in *Erica* plots (Fig. 6).

Black carbon

Our results demonstrate significantly higher BC contents (related to sample: $p = 0.01$ and related to TOC: $p = 0.02$) in *Erica* soils than in control soils (Fig. 7a, b). Moreover, the BPCA pattern shows a higher contribution of B4CA, B5CA, and B6CA and a lower percentage of B3CA in both
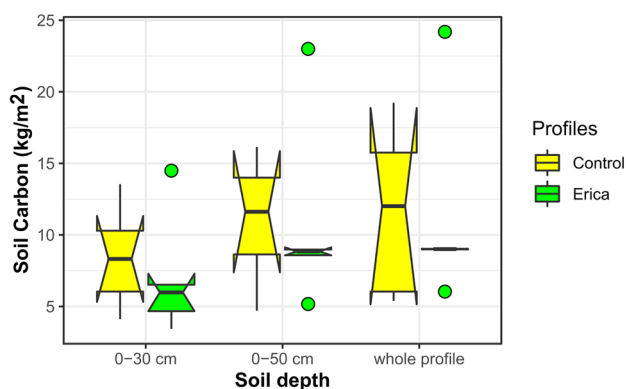

Fig. 6 Soil organic carbon (SOC) in soil profiles under *Erica* and control sites. The notched box plots indicate the median (solid lines between the boxes), and interquartile range (IQR) with upper (75%) and lower (25%) quartiles. The notches display the 95% confidence interval of the median. The lines extending outside the box (whiskers) show variability outside the quartiles. The circles represent outliers

Erica and control plots (Fig. S4). The B5CA/B6CA ratios range from 0.63 to 1.39 below *Erica* and from 0.74 to 2.51 in the control plots (Fig. 7c). Topsoils of control plots have significantly higher B5CA/B6CA ratios ($p = 0.02$) than the *Erica* profiles. The Bw horizons of the control soils always have lower BC and B6CA contents than those below *Erica*.

Stable isotopes

$\delta^{13}C$ values of leaves sampled from the *Erica* and control plots range between -28.6 and $-23.8\permil$. *Erica* leaves have significantly higher values than *Festuca* and *Helichrysum* ($p = 0.03$) (Fig. 8). $\delta^{13}C$ values vary between -24.7 and -22.3 in soils of *Erica* plots and from -27 to $-22\permil$ in control plot soils, with the highest values recorded in Bw horizons (Fig. 8). In general, $\delta^{13}C$ values are significantly higher in soils under *Erica* ($p = 0.02$) than in control profiles, and they increase with increasing soil depth in both *Erica* and control plots. $\delta^{15}N$ values vary between -6.5 and 0.1 in leaves (Fig. 8). *Helichrysum* and *Festuca* show higher $\delta^{15}N$ values than *Erica* leaves. Similarly, soils under *Erica* shrubs reveal $\delta^{15}N$ values ranging from -3.4 to $7.0\permil$, with the highest values recorded in Bw horizons. Control plot soil exhibits $\delta^{15}N$ values between -2.7 and $9.0\permil$, with the highest value recorded in Ah3 horizons (Fig. 8).

Discussion

Our results illustrate similarity in site exposition and environmental features of *Erica* and control plots established per site. The most striking difference is the high amount of boulders covering the *Erica* plots. The Sanetti Plateau is characterized by harsh climatic conditions with strong winds, extreme solar radiation, heating, desiccation, and frequent frost at night (Miehe and Miehe 1994; Wesche 2003; Groos et al. 2022). Alpine plants adapt to such extreme conditions, whereas woody plants face difficulties regulating the ambient temperature (Wesche 2003; Wesche et al. 2008; Körner 2012b). According to Körner (2012a, b), the upper tree line is globally seen as controlled by the mean temperature during the growing season. Therefore, we assume that the big boulders positioned above the upper timber line of the *Erica* belt protect the *Erica* patches against wind and provide warmth and shade, particularly for the *Erica* seedlings (Wesche et al. 2008). On the other hand, afro-alpine plants are rather shade-intolerant due to their high photosynthetic light-compensation points (Billings and Mooney 1968; Johansson et al. 2018). Therefore, *Erica* seedlings growing beside boulders may outcompete the afro-alpine plants and mature into shrubs. This interpretation is supported by Fig. 2d, which depicts *Erica* seedlings growing in the south exposition alongside a single big boulder on a control plot.
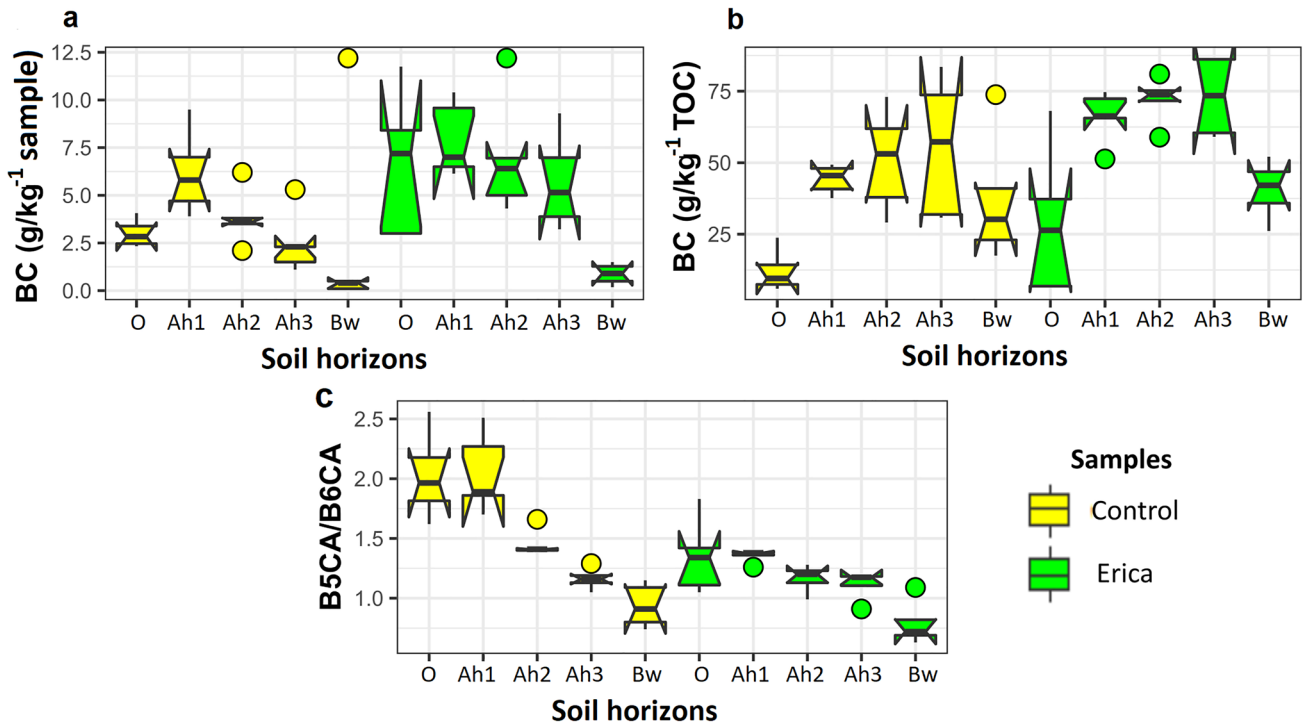
Fig. 7 Black carbon contents (BC) (**a**), black carbon contribution to TOC (**b**), and B5CA/B6CA ratios **c** of *Erica* and control sites soils. The notched box sites indicate the median (solid lines between the boxes), and interquartile range (IQR) with upper (75%) and lower

(25%) quartiles. The notches display the 95% confidence interval of the median. The lines extending outside the box (whiskers) show variability outside the quartiles. The circles represent outliers
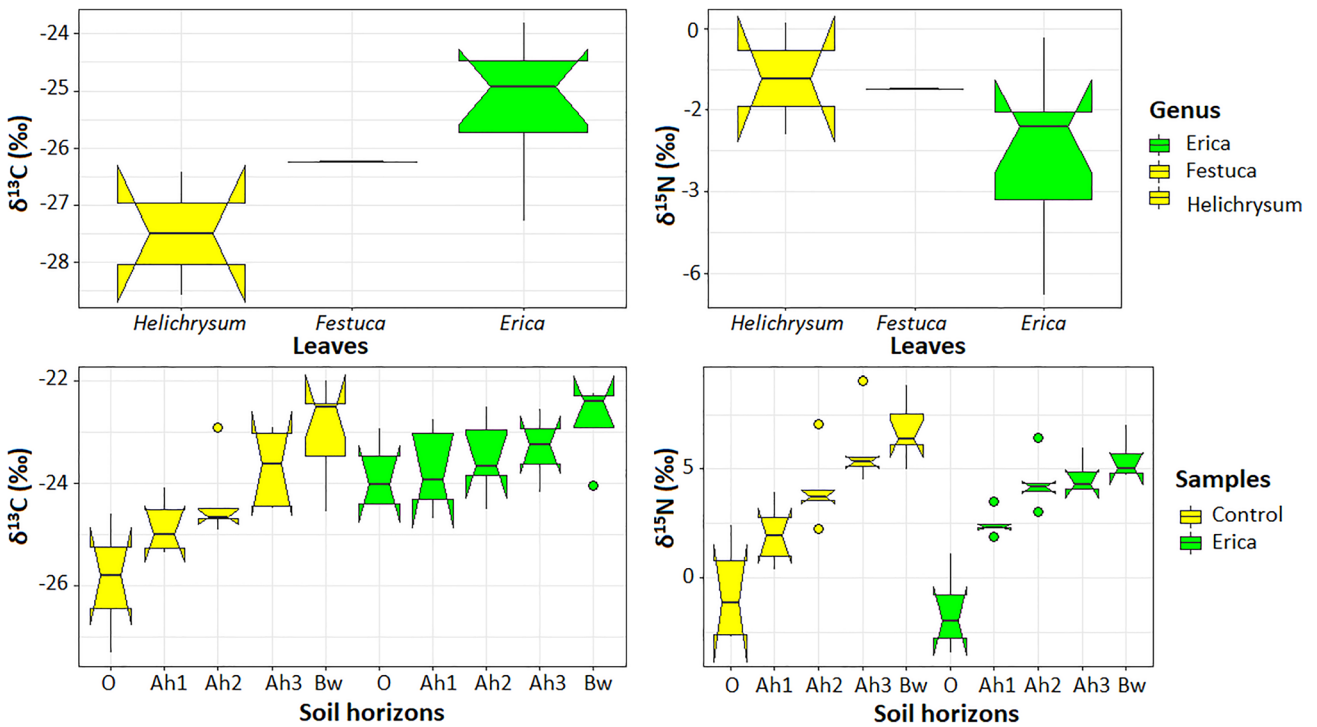
Fig. 8 $\delta^{13}C$ and $\delta^{15}N$ values of leaves and soil layers of *Erica* and control plots. The notched box plots indicate the median (solid lines between the boxes) and interquartile range (IQR) with upper (75%)

and lower (25%) quartiles. The notches display the 95% confidence interval of the median. The lines extending outside the box (whiskers) show variability outside the quartiles. The circles represent outliers

However, the *Erica* plants were confined to short stature due to intensive grazing.

Groos et al. (2022) installed temperature data loggers at the elevation range from 3493 to 4377 m asl. From these temperature data loggers, four were installed at 10 cm depth at our *Erica* (E1 and E2, TM09m and TM10m) and control (C1 and C2, TM08m and TM07m) plots (see Fig. 1). The results show no difference in the temperature pattern between *Erica* and control plots (Fig. S5). At site 1, a high temperature was recorded during the dry season, decreasing during the rainy season at both *Erica* and control plots. In contrast, at site 2, the temperature decreased during the dry season and increased during the rainy season at both the control and *Erica* plots. According to Groos et al. (2022), the temperature difference between the sites can be attributed to a difference in exposition. Nevertheless, since the number of data loggers installed at our study sites was very low, further studies are required to check whether there is a difference in microclimate between *Erica* and the control plots.

Except for bulk density, TOC, TOC/N and BC, other biogeochemical proxies do not show a significant difference between *Erica* and control plots. The significantly lower soil bulk density under *Erica* could be caused by a high organic matter content and increased stone contents (Fig. 3). Even though statistically not significant, the lower pH values recorded in soils of *Erica* plots (Fig. 4) can be explained by the acidifying effects of the thick, slowly decomposing *Erica* litter (Dahlgren et al. 1997). Nevertheless, pH values recorded in our *Erica* profiles are slightly higher than those reported by Johansson (2013) from the *Erica* belt in the Bale Mountains. These high pH values might be caused by increased alkaline dust inputs from the surroundings on the Sanetti Plateau. Moreover, the decrease of EC values along soil depth in both *Erica* and control soil profiles might be due to the ascendance of water and ions during the dry period.

Higher soil TOC and N contents of *Erica* plots compared to the control plots can be attributed to differences in quality and quantity of the litter input (see Fig. 5 and S3, high TOC and N values of *Erica* leaves) (Andrén and Kätterer 1997). Furthermore, increased insolation on control plots (Miehe and Miehe 1994) might support organic matter degradation, whereas soils under *Erica* benefit from the shade provided by large rocks and the *Erica* canopy. Moreover, the Ah3 and Bw horizons at the bottom of the soil profiles of the control plots contain less TOC and N than the control soils, which may indicate that *Erica* was not a common vegetation component on these plots in the past. Despite lower N values of plant species growing on control plots, their O and Ah layers show higher N values (Fig. S3), likely due to fecal N input from grazing cattle (Baron et al. 2002; Johansson et al. 2012). High TOC/N values recorded in our *Erica* plots agree with Mekonnen et al. (2019) and Zech (2006), reporting

that such high values characterize the *Erica* vegetation and its soils at high elevations in other African Mountains. The low TOC/N ratios, especially of the Ah3 and Bw horizons of control plots, also support the interpretation that the control plots have never been fully covered by *Erica*. Besides, the higher TOC/N ratios of the mineral soils below *Erica* reflect that *Erica* litter is less decomposed by soil microorganisms (Jacob et al. 2015).

SOC and N stocks of *Erica* plots are partly lower than those of control plots (Fig. 6; Fig. S3). This is mainly due to their higher stone contents which are negatively correlated with the SOC and N stocks ($R = -0.5$). Furthermore, the PCA results demonstrate the impact of stone contents on the carbon and nitrogen stock accumulation (Fig. S6). Similarly, Gebrehiwot et al. (2018) found higher SOC stocks in the afro-alpine grassland soils of the Abune Yosef Mountain in Northern Ethiopia compared to soils below the ericaceous forest. In a study about soils under different vegetation in the Bale Mountains, Yimer et al. (2006) noted higher carbon stocks in 0.3–1 m soil depth below *Erica*. However, this difference can be explained by the variability of climatic conditions and environmental factors between the lower elevation of the *Erica* belt and our high-elevation sites on the Sanetti Plateau.

Our results further show that soils under *Erica* are enriched in BC compared to soils of the control plots (Fig. 7a, b). This indicates a higher amount of combustible fuel on *Erica* plots than on control plots. Furthermore, the significantly increased BC contents, especially of Ah2 and Ah3 horizons in soils below *Erica* (Fig. 7a, b), support our interpretation that *Erica* did not intensively cover these plots previously. Otherwise, a higher accumulation of recalcitrant BC would have been preserved during the burning of former *Erica* shrubs.

In addition to BC contents, the relative contribution of benzene polycarboxylic acids (BPCA) provides information on fire temperature and fuel source (Schneider et al. 2010; Wolf et al. 2013). For instance, benzene rings with four and five carboxylic groups (B4CA and B5CA) are primarily produced at low temperatures ($\sim 300\ °C$), whereas benzene rings with six carboxylic groups (B6CA) are mainly produced at high temperatures (600 °C). Moreover, the B5CA/B6CA ratio is supposed to indicate the type of vegetation burned in the area. According to Wolf et al. (2013), forest ground and grass fires have B5CA/B6CA ratios of 1.5–2.0, whereas shrub fires have B5CA/B6CA ratios of 0.8–1.7. Our result correlates with the range suggested by Wolf et al. (2013) for shrubs and grassland fires. Moreover, significantly high B5CA/B6CA values in control plots indicate low temperature, while low B5CA/B6CA values in *Erica* plots indicate high combustion temperature. The latter is attributed to the high flammability of *Erica* twigs due to low moisture content and high concentrations of oils, waxes,

and terpenes, which are readily volatile and contribute to the energy released by burning. In contrast, *Helichrysum*, the main vegetation constituent of the control sites, is naturally less flammable (Johansson et al. 2012).

The δ¹³C values of plants from our *Erica* and control plots are within the range reported for C3 plants (Marshall et al. 2007; Tiunov 2007) (Fig. 8). This is consistent with results of our previous transect study in the Bale Mountains reporting that the dominant plants including grasses, growing between 2550 and 4377 m asl are characterized as C3 plants (Mekonnen et al. 2019). However, the significantly high δ¹³C values of *Erica* plants (Fig. 8) seem to contrast with the finding of the transect study (Mekonnen et al. 2019), where no significant difference between *Erica* and other dominant plants could be identified. This discrepancy might be due to the effect of elevation on δ¹³C values and the different ways plants adjust their gas exchange to mitigate the decline in atmospheric CO_2 pressure along elevation (Körner et al. 1991). To prove this, we ran a correlation analysis between elevation and δ¹³C values of dominant plants from the transect study. The results showed that elevation correlates positively with δ¹³C of *Erica* leaves ($R = 0.5$) but negatively with *Festuca* ($R = -0.7$), whereas δ¹³C of *Alchemilla* leaves did not change with elevation. The isotope pattern found for *Erica* in this study is in agreement with the elevation effect (Körner et al. 1991), whereas the isotope pattern of *Festuca* does not. A similar statistical test was not possible for *Helichrysum* due to limited data. Moreover, the relatively positive δ¹³C values of *Erica* leaves from our *Erica* plots on the Sanetti Plateau might suggest temporary water stress, e.g., during the dry season. In contrast, *Festuca* does not respond similarly, most likely due to distinct physiological conditions that enable it to mitigate water scarcity (Hedberg 1964). Moreover, the high stone content of the soil profiles under *Erica* patches reduces the plant-available water storage capacity. δ¹³C values of the O, Ah1, and Ah2 horizons under *Erica* correspond to the values of the *Erica* leaves. The more negative δ¹³C values of these horizons from control soils correlate with the negative δ¹³C values of *Helichrysum* and *Festuca*. The increase from O to Bw shows progressing organic matter mineralization with increasing soil depth in both plots. This interpretation is supported by the negative correlation between δ¹³C and carbon stocks (Fig. S6). Generally, higher δ¹⁵N values in control profiles correlate with high δ¹⁵N values of *Helichrysum* and *Festuca*. The continual increase of δ¹⁵N along soil depth is attributed to the loss of δ¹⁴N during microbial decomposition of organic matter (Natelhoffer and Fry 1988; Eshetu 2004; Andersson et al. 2012). Besides, the frequent vegetation fires at the high elevations of the Bale Mountains could also be responsible for increased δ¹⁵N values, recorded in both *Erica* and control plot soils (Zech et al. 2011; Johansson 2013). Generally, higher δ¹⁵N values in control profiles

likely correlate with the high δ¹⁵N values of *Helichrysum* and *Festuca*, implying that control plots were previously dominated by afro-alpine vegetation.

Conclusions

In this study, we examined potential factors responsible for the patchy occurrence of *Erica* above the upper ericaceous ecotone on the Sanetti Plateau, Bale Mountains. Apart from the boulder cover, topographic features, soil texture, and EC did not show significant differences between *Erica* and control plots. High TOC and TOC/N values were recorded below *Erica* and can be attributed to increased fresh organic matter input. Still, slightly higher SOC stocks were calculated for the control plots due to their lower stone contents. *Erica* leaves on the Sanetti Plateau were characterized by more positive δ¹³C values compared to leaves of *Helichrysum* and grass growing on the control plots. This difference is also reflected in the soils, probably influenced by water stress on the *Erica* plots. In addition, *Erica* sites are characterized by high BC contents indicating a high amount of combustible fuel at *Erica* plots. Low TOC, TOC/N ratio, and BC contents but high B5CA/B6CA ratios in the control plots indicate that *Erica* did not occupy the control plots in former times. However, *Erica* shrubs growing between the surface boulders appear to benefit from the improved microclimate created by the big dark basal rocks and from physical protection against grazing and fire. We conclude that, in general, the soil conditions of most control plots would allow the growth of *Erica*, but in the absence of boulders, the microclimatic conditions above 3800 m asl are too severe. Therefore, further investigations should focus on a detailed assessment of the microclimate conditions, soil moisture availability, and water potential of the *Erica* patches on the Sanetti Plateau.

Declarations

Conflict of interest The authors declare no conflict of interest.

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