Global Ecology and Conservation 19 (2019) e00670

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

# Dead end for endemic plant species? A biodiversity hotspot under pressure

Yohannes O. Kidane [a, *], Manuel Jonas Steinbauer [b], Carl Beierkuhnlein [a, c, d]

[a] *Department of Biogeography, Bayreuth, University of Bayreuth, Germany*
[b] *GeoZentrum Nordbayern, Department of Geography and Geosciences, Friedrich-Alexander University of Erlangen-Nürnberg (FAU), Loewenichstr. 28, 91054, Erlangen, Germany*
[c] *Bayreuth Center of Ecology and Environmental Research (BayCEER), Bayreuth, Germany*
[d] *Geographical Institute Bayreuth (GIB), Bayreuth, Germany*

ARTICLE INFO

*Article history:*
Received 28 December 2018
Received in revised form 18 May 2019
Accepted 18 May 2019

*Keywords:*
Elevational gradients
Tropical mountains
Sky islands
Range shifts
Endemism
Extinction

## ABSTRACT

Tropical high mountains are hosting important hot spots of biodiversity on small mostly remote areas. Recently, these precious ecosystems are under threat from land use change and climate change coupled with other local drivers of biodiversity loss. Along the East African Afroalpine ecosystems, area above the treeline have experienced long-term spatial isolation and extreme climatic conditions (climatic factors such as low mean temperature, diurnal freeze-thaw cycles and other energy-related factors) which lead to the formation of "Sky Island" like ecosystems that are rich in endemics and unique. The Bale Mountains of Ethiopia are home to the largest tropical alpine plateau in Africa, with no spacious high summits that provide space for upward shift of species. Here, we studied plant species diversity and distribution patterns and tested potential future impacts of climate change induced warming on those patterns. This study is based on distribution data acquired from nested circular plots along an elevational gradient ranging from 2000m asl to the highest elevation (4385 m asl). We find hump shaped species richness patterns on both aspects, i.e. the dry north-eastern and the wet monsoon exposed south-western escarpment. In addition, the proportion of endemic species increases monotonically towards the summit on all slopes. Based on our data and literature, we project future climate impact for three regional warming scenarios (+2 °C, + 3 °C and + 4 °C). We quantify the future range of 114 endemic plant species based on their current occurrence records applying a lapse rate of 0.6 °C per 100 m of elevation. We find that future climate change would significantly alter species distribution patterns with pronounced impact on the unique ecosystems and endemic species restricted to the afroalpine plateau. Very likely this will be leading to the extinction of many endemic species.

## 1. Introduction

Ethiopia is characterized by the largest montane areas in tropical and subtropical Africa, which are at the centre of East Africa's hotspot of diversity (Mutke et al., 2001). Especially, the afroalpine ecosystems on isolated mountains (the Ethiopian

---

* Corresponding author.
*E-mail addresses:* Yohannes-kidane@hotmail.com, yohannes.kidane@uni-bayreuth.de (Y.O. Kidane).

https://doi.org/10.1016/j.gecco.2019.e00670

"sky islands") harbour a large number of unique endemic species (Hillman, 1988; Friis et al., 2005). The significance and influence of these mountains, in terms of biodiversity conservation and other ecosystem services, exceed their spatial limits reaching further beyond surrounding lowlands. Owing to their agricultural productivity, favourable climate, safety and rich natural resources, Ethiopia's mountains are centres of ancient human residence, sources of livelihood and socioeconomic activities. Besides these mountains are endow with immense plant diversity, that has spectacular altitudinal patterns.

Systematic approaches to defined and understand plants diversity and distribution patters across spaces and time has been central concern of biogeographers. Yet, the relation between elevation and species richness patterns and the underlaying causes are poorly understood and/or are immature (Rahbek, 2005; Sanchez-Gonzalez and Lopez-Mata, 2005). Especially with climate change understanding these richness patterns and relationships and analysing their underlying mechanisms is crucial (Jentsch and Beierkuhnlein, 2003). Generally, species richness tends to decrease with altitude (Grytnes, 2003; Bruun et al., 2006). Several studies have also documented a nonmonotonic pattern of species richness (Grytnes, 2003; Bhattarai and Vetaas, 2003). The most commonly observed pattern of diversity is a midaltitude bulge (Lomolino, 2001; Rahbek, 2005; Steinbauer et al., 2018).

Climate change induced warming is expected to impact plant diversity and distribution at all levels starting from single species to biomes (Parmesan, 2006). Increase in temperature will result in habitat quality deterioration and instability which could lead to the loss of species, alteration of species diversity, abundance and distribution (Enquist, 2002; Davis et al., 2005; Malcolm et al., 2006; Lovejoy, 2008; Jump et al., 2009; Kreyling et al., 2010). It will also result in alterations in population dynamics of native species that may enhance climate mediated biological invasion, alter community interactions and structure, and ecosystems functions (Walther et al., 2002). Small shifts in the thermal isotherm shift along altitudinal gradients may allow species to adapt and remain within their tolerance limits or may be compensated by adaptation, and/or compel them to move to novel environmental conditions. However, considerable warming is likely to result in altitudinal range shifts via dispersal or migration and local loss of populations which means extinction in the case of spatially restricted endemic species (Enquist, 2002; Davis et al., 2005; Malcolm et al., 2006; Steinbauer et al., 2018).

Africa's tropical alpine ecosystems are experiencing the direct and indirect impacts of climate change, human population growth and socioeconomic development (Buytaert et al., 2011; Jacob et al., 2014). Climate change perhaps is one of the most pervasive and serious of the various threats to biodiversity (Malcolm et al., 2006; Jump et al., 2009). More specifically, for East African mountains, climate change is expected to result in altitudinal range shift and range contraction (Kreyling et al., 2010).

The Bale Mountains of south-central Ethiopia form the largest continuous area above 3000 m in Africa, supporting the most extensive area of afroalpine and subalpine ericaceous vegetation on the continent (Miehe and Miehe, 1994). The contiguous mountain massifs were one of the most extensively glaciated mountains during the Pleistocene, which shaped their recent geomorphology (Bonnefille, 1983; Osmaston et al., 2005). Consequently, only three small peaks (Tullu Dimtu 4385 m asl, Batu 4307 m asl, and Konteh 4132 m asl.) of total area 99.1 km$^2$ reach elevations beyond 4100 m asl, while the largest part of the plateau is characterized by homogenous topography. The area of the plateau which extends between 3100 and 4385 m asl is 2020 km$^2$. Nevertheless, the area above the treeline at approximately 3800 m asl is very spacious and extents up to 480.5 km$^2$ forming the largest area of afro-alpine ecosystems.

The Bale Mountains are hosting a high priority conservation area of global significance. They represent one of the 34 biodiversity hotspots and are listed by UNESCO as tentative world heritage site and biosphere reserve (Mittermeier et al., 2004). Further, they are within the range of Endemic Bird Areas analysis of BirdLife International (Stattersfield et al., 1998). Nevertheless, given their significance, they have received little international attention.

Along the altitudinal gradients of the Bale mountains, from the tropical rainforest to the treeless Afroalpine meadows, an orderly sequence of vegetation zones are visible. Like many other tropical mountains in Africa and Asia (Parmesan, 2006), no study has so far systematically analysed these altitudinal biotic patterns along the Bale Mountains. In addition, to their significance in providing more information to evaluate impact of future climate changes, such elevation gradients on isolated mountains also pose unique opportunities to study the effect of ecological and evolutionary processes (Steinbauer et al., 2016a, 2016b). The Island-like nature of these ecosystems permits study of how isolation and habitat area affect community structure and dynamics (Itescu, 2018). Moreover, major advances in the understanding of patterns in species composition and diversity are acquired from such gradient analysis (Schweiger et al., 2016).

There are few ecological studies that focus on the biogeography of the area, studies that explore vascular species richness, especially endemic species richness along altitudinal gradient and climate change impacts on future species distributions do not exist. Such studies are important, because (1) the Afroalpine plateau is significantly and uniquely representative. The Sanetti plateau on the Bale mountains is one of the largest continuous Afroalpine habitats. The total area of Africa's tropical afroalpine ecosystems is less than 5000 km$^2$ (Körner et al., 2017; Gehrke and Linder, 2014), of which as much as 27% is in the Bale mountains (1354 km$^2$, area above 3400 m asl, own calculations); and (2) unique diversity is under immediate threat from coupled impact of local intensification of human activities and climate change.

Therefore, our study will: (1) analyse plant species-diversity-richness and endemic-diversity-richness relationships along elevation gradient of the Bale Mountains aiming at a better understanding of spatial patterns in diversity within the hotspot area; and (2) demonstrate direct consequences of warming induced thermal isotherm shift for the diversity, abundance and distribution of endemic species. Our findings may contribute (1) to frame conservation management strategies for biodiversity in face of climate change and increasing human activities; and (2) to add a voice to the calls for bringing international attention in recognizing the Afroalpine habitat as a global significant biodiversity hot spot.

## 2. Material and methods

### 2.1. Study area

The Bale Mountains are located 400 km south of Addis Ababa among those Ethiopian high mountain chains located on the South-eastern flanks of Great East African Rift Valley (Fig. 1). The Bale Mountains National Park (hence forth BMNP) covering above 2200 km$^2$ of afromontane and afroalpine habitats is located within the mountains. These mountains are one of the last remaining pristine afroalpine biodiversity hotspots in the tropics and one of the last remaining habitats for most Bale Endemic plants. Generally, Africa's afroalpine ecosystems exclusively occur along the Great Rift Valley as small and isolated patches (Buytaert et al., 2011).

The Bale Mountains are located at the convergence of the wet East African and dry northeast African mountains of southeast Ethiopia. They are important water sources for the dry lowlands feeding many perennial mountain springs and more than 40 small rivers discharging into the five major rivers Web, Wabe Shebele, Welmel, Dumal and Genale (Hillman, 1986; Dullo et al., 2015). Historically, the Mountains have experienced a high degree of climate variability and change (Peyron et al., 2000; Umer et al., 2007; Kuzmicheval et al., 2013; Kuzmicheval et al., 2014). Contemporary climate within the area varies from northeast to southwest mainly due Orographic effects (Uhlig, 1990; Miehe and Miehe, 1994). The south and southwest facing slope is more humid with subtropical climate, high annual rainfall (up to 1500 mm/year), and with the dry season lasting only about two months. While the north and northeaster parts receive from 800 to 1100 mm/year of annual rainfall and a wet season from June to September. Along altitude, precipitation increases up to an elevation of 3,850 m asl, but then decreases towards the summits (Hillman, 1986). In the region the rainfall pattern is slightly bimodal, with a peak from April to May followed by a second peak from August to October.

The Afroalpine habitats are characterized by strong seasonal and diurnal temperature fluctuations and night frost. On the Plateau, an extreme diurnal temperature range of about 40 °C (−15 °C to + 26 °C) has been recorded during the dry season (Hillman, 1986). Night frost is common year-round above 4000 m asl. Consequently, the biota experience extreme diurnal

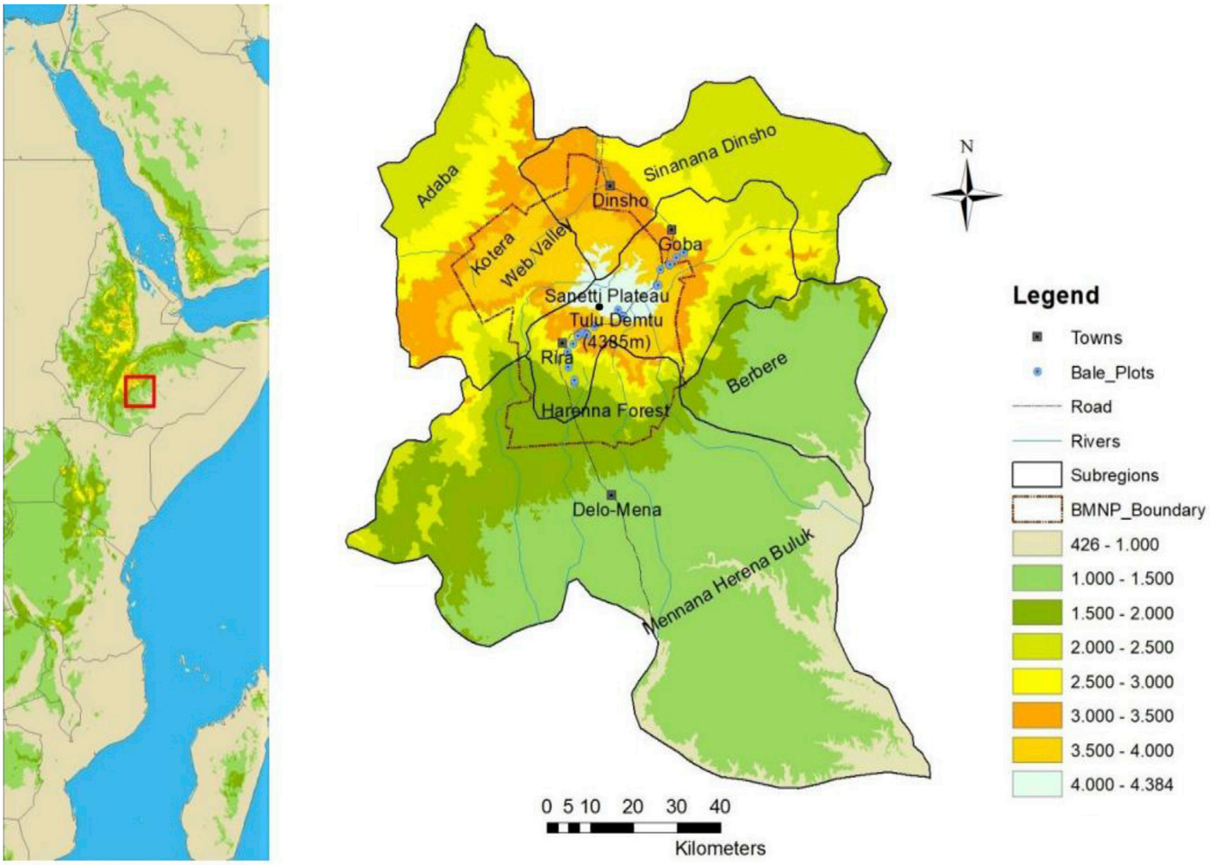

**Fig. 1.** The study area and the surrounding administrative sub-zones. The Ethiopian Bale mountains are located southeast of the Great East African Rift Valley. Sampled plots follow southwestern and north-eastern elevational gradients (light blue circles, total number of plots = 31). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

temperature fluctuation, labelled as “summer every day and winter every night” (Hedberg and Hillman, 1964). The unique climatic conditions supported the evolution of highly adapted plant species like the iconic specialized alpine giant rosette plants *Lobelia rhynchopetalum* and other Bale endemic plants such as *Alchemilla haumanii, Anthemis tigreensis, Agrostis gracilifolia* subsp. *parviflora, Droguetia iners* subsp. *Pedunculata, Helichrysum gofense, Sedum baleensis, Sedum mooney, Senecio unionis* and *Geranium arabicum.*

The Bale Mountains are fragmented by numerous volcanic plugs, peaks, alpine lakes, and rushing mountain streams that descend into deep rocky gorges on their way to the lowlands. The mountains geology is characterized by a vast high elevation volcanic plateau over much older volcanic material formed during the spreading of the Great East African Rift Valley system (Friis et al., 2005). The petrography is dominated by alkali basalt and tuffs, with occasional rhyolites (Uhlig and Uhlig, 1991). They have old geological formations, older than that of the Rift Valley (Mohr, 1971).

The uppermost part the Sanetti plateau is bordered by abrupt escarpments to the south, which fall from above 4000 m asl to below 2000m asl within a short aerial distance. The north and northeast are deeply dissected valleys descending to the northern slope, while to the west marks of ancient lava flows form spectacular bluffs (Osmaston et al., 2005). Soils in the area tend to be shallow, gravelly, and recently derived from stratigraphically youngest units derived mainly from the Miocene basalt and trachyte lavas that lay over Mesozoic sediments (Umer et al., 2007). They consist of a relatively silty loam, clay, sandy loam and silty loam of reddish brown to black colour.

### 2.2. Vegetation

Vegetation zonation of the Bale Mountains resembles that of other East African Mountains (Hedberg, 1951, Uhlig and Uhlig, 1991; Friis, 1992; Miehe and Miehe, 1994), and it lies within the Somali–Masai regional centre of endemism (White, 1983). The Mountains massif exhibits a steep gradient of ecological zones (Table 1) ranging from tropical rainforests to Afroalpine vegetation (Kidane et al., 2012). The historical climate dynamics, topography driven micro climate and the resulting habitat and resource diversity played a crucial role in shaping the contemporary vegetation. This habitat variation combined with the unique climate, large extent and the isolation of the Bale Mountains from other Ethiopian highlands, west of the Great Rift Valley, have resulted in high endemism (Friis et al., 2005). This plant biodiversity hot spot provides habitat for one of the largest concentrations of endemic plant and mammal species globally (Hillman, 1986). The BMNP harbours at least 111 or 18.8% of the national endemic flowering plant species (with 10 restricted to the park limits), 20 or 26.5% of the national

**Table 1**

Vegetation zones and major habitat types of the Bale Mountain. Overlaps in altitude are explained by differences in slope and aspect (based on Miehe and Miehe, 1994; Umer et al., 2007).

| N° | Cover Classes | Aspect | Altitude | Description |
|---|---|---|---|---|
| 1 | **Afroalpine dwarf shrubs and herbs formation** | **S, SW and SE** | **3800–4385m** | Afroalpine vegetation: including the dwarf shrubs *Helichrysum splendidum*, *Alchemilla haumanii*, the Giant Lobelia (*Lobelia rhynchopetalum*), isolated groves of dwarf *Erica trimera up to 4100m asl.* |
| 2 | **Tussock grasslands** | **N and NW** | **3800–4050m** | Extensive grasslands: dominated by grasses (*Festuca richardii*) with large number of herbaceous species. Bogs vegetated by *Eriocaulon schimperi* and *Carex monostachya.* |
| 3 | **Isolated Erica shrubs** | **S, SW, SE and NW** | **3600–4000m** | *Erica* groves within Afroalpine *Helichrysum* heathland. Frequent bush fires keeping Erica in low (up to 3 m), shrubby regeneration phases. *Erica trimera* is restricted to distinct patches or solitary individual shrubs. |
| 4 | **Ericaceous Belt** | **S, SW and NW** | **3200–3600m** | Forest, thickets and scrublands of *Erica trimera* and E. *arborea* communities. *E. trimera* forms tall trees up to 15 m height with abundant epiphytes, especially the moss *Antitrichia curtipendula* and the lichen *Usnea articulata*. Above 3,400 m a.s.l., which is the well-marked limit of *Hagenia emergents*, *Erica trimera* canopy height diminishes further and grasses and mosses predominate in the ground layer. |
| 5 | **Upper Montane forests** | **N and NW** | **3000–3400m** | Dominated by trees such as *Pittosporum viridiflorum, Myrsine melanophloeos, Discopodium eremanthum,* and prominent bushes such as *Rosa abyssinica and Solanum garae*. Dispersed individuals of large trees such as *Hagenia abyssinica, Hypericum revolutum,* and *Juniperus procera*. |
| 6 | **Bamboo forest** | **S and SW** | **2800–3100m** | Dominated by bamboo *Sinarundinaria alpine* or *Arundinaria alpine.* |
| 7 | **Juniperus, Hypericum and Hygenia Woodland** | **N, and NE** | **2500–3400m** | Mainly dominated by a mixed *Juniperus* forest. *Hagenia* and *Hypericum* zone. It is dominated by 12–18 m tall *Hypericum revolutum* and *Rapanea melanophloeos*, accompanied by *Schefflera* and bamboo (*Sinarundinaria alpina*), with *Hagenia abyssinica* up to 25 m tall. |
| 8 | **Afromontane rainforest** | **S and SW** | **1450–3250m** | The rainforest is located mainly at the southern slopes and receives rainfall during more than eight months of a year. It is dominated by *Podocarpus* associated with *Syzygium guineense* and *Aningeria adolfi-friederici*. |
| 9 | **Farmland, Settlements and Fragmented Landscape** | **E, NE and N** | **2000–3400** | Highly fragmented landscape characterized by expanding agricultural land, infrastructure and settlements. |

endemic mammal species and 9 or 53.3% of the national endemic birds. In addition, on the Bale Mountain endemic plants density is 2.5 taxa per 100 km$^2$ (Friis et al., 2005).

Vegetation structure and composition differ between the southwestern and northeastern gradients. On the southwestern transect the vegetation changes from moist tropical rainforest at 2000 m asl (altitude of our lowest sampled plot) to broadleaf evergreen forest at around 2800 m, to ericaceous forest around 3200 m asl, ericaceous shrubland between 3600 m and 4100 m asl and finally to the Afroalpine shrub and grassland habitat at the Sanetti plateau. On the northeastern transect, the area south of Goba around 2700 m asl is dominated by small rainfed agriculture, heavy livestock grazing and browsing grassland and shrublands, and vast plantation of exotic tree species such as Eucalyptus and Cypresses. From 2800 m asl first isolated remnant of *Juniperus procera*, *Hagenia abyssinica* and *Hypericum revolutum* and Hypericum woodlands with bushy understories of *Rosa abyssinica* and different species of *Solanum (S. anguivi and S. nigrum)* can be observed. Those fade over into Ericaceous belt around 3700masl and isolated Erica shrubs at around 4100 m asl. The main high elevation plateau is characterised by Afroalpine Dwarf Shrubs and various herbaceous formations. Agricultural land encrauches up to around 3500 m asl, small scale Garlic plantation may reach to even higher altitude.

### 2.3. Sampling design

Two floristic inventory transects were established across the elevational gradient along the Goba-Rira-Dolo Mena road. The southwestern transect reached from the humid tropical rain forest to the summit at mount Tullu Demtus 4385 m asl, with the northeaster transect approach the summit on the other slope. Starting at 2000 m asl, nested circular plots of 20 m (1256 m$^2$) and 40 m (5024 m$^2$) radii were established along the Southwestern (19 plots) and Northeaster (13 plots) transect of Massif, and all the way up to the summit at every 250—300 m altitude difference. Presence absence data of all vascular plants in each plot were collected. In addition, plot dominant cover type was visually estimated.

Three replicated plots were established per elevation level following guidelines for optimal sampling along environmental gradients (Schweiger et al., 2016). We used the same approach (same size of sampling plots, at least 500 m apart and same duration of surveys) across elevations, zonal habitats and mountain ranges. Prior to vegetation sampling, a reconnaissance survey was carried out along the sampling transect to decide on potential plot locations. Plots location selection and establishment were carried out randomly after visually judging the environmental. Areas of less disturbance, accessible, slope less than 25° were selected. All plots avoided settlements, roads, plantations, farmland, and logging site.

The field data collection was carried out in April 2011. Altogether, 448 different plant species of 89 families of 6 functional groups were collected. Most species were identified on the spot, with few critical species being pressed and taken to the National Herbarium of Ethiopia located at Addis Ababa University for further identification. The nomenclature and functional group classification follow published flora of Ethiopia and Eritrea (Hedberg and Edwards, 1989, 1995; Edwards et al., 1995, 1997; 2000; Hedberg et al., 2003, 2004; Puff and Nemomissa, 2005). All the recorded flowering plant species were classified as non-endemics (plants that are common all-over east Africa and the rest of the world), Ethiopian endemics, and Bale endemic (i.e. of course these are Ethiopian endemics but are exclusively found only in the Mountains area).

Altitude, ground position and geographic location of each plot were recorded using Garmin Global Positioning System (GPS) 3.1. Slope and aspect information was derived from Digital Elevation Models (DEMs) (Jarvis et al., 2018). Along altitudinal gradient temperature is the most determinant factor (Beierkuhnlein, 2007; Körner, 2007; Nagy and Grabherr, 2009). Therefore, for this analysis we focus primarily on temperature and less so on the effects of other environmental variables.

For the estimation of climate change impacts, we assumed 2 °C, 3 °C and 4 °C change, which fall within the Intergovernmental panel on Climate Change (IPCC) optimistic to pessimistic scenarios of the 21$^{st}$ century The IPCC has stated that "warming of the climate system is unequivocal, it will result in above average warming of waterbodies (sea, ocean and snow), air and land surface warming." More specifically, the 21$^{st}$ century climate change induced warming is likely to exceed 1.5 °C relative to the 1850—1900 period in all scenarios and exceeds 2 °C in many scenarios (IPCC et al., 2014).

### 2.4. Statistical analysis

Overall richness as well as number of Ethiopian (national) and Bale mountain (local) endemics were calculated for each plot. Generalized Linear Models (GLMs) were used to analyse the relationship between these richness indices as well as percentages of endemic species with elevation. To allow non-linear relationships, the full models included elevation and elevation$^2$ as explanatory variables.

**model formula: y ~ elevation + elevation$^2$ + transect + transect: elevation**

Stepwise model selection based on Akaike information criterion (AIC) was used to remove non-relevant variables from the model (R-function *step* in the *stats* package). Poisson error distribution (log-link function) was implemented for all richness-based indices, while binomial error distribution (logit-link function) was used to assess changes in percentage values. The binomial error distribution for percentage values has the advantage that it accounts for the number of observations (i.e. species) that underlies a specific percentage value.

Prior to data analysis the full natural elevational ranges of each species (upper and lower limits of occurrence range) and endemism of all the species were derived from all eight volumes of Flora of Ethiopia and Eritrea books (Hedberg and Edwards, 1989, 1995; Edwards et al., 1995, 1997; 2000; Hedberg et al., 2003, 2004; Puff and Nemomissa, 2005). In addition, plot occurrence data was used to extract local occurrence range of each species. Both information on species range distributions were used to estimate potential consequences of warming induced shifts under different climate change scenarios. We calculated the potential endemic species altitudinal range shift for each species applying a laps rate of 0.6 °C per 100 m of elevation. All statistical analyses and visualisations were performed in R version 3.3.3 (R Development Core Team, 2016).

## 3. Results

### 3.1. Gradients of plant species richness

Out of the overall 448 identified vascular plant species, 114 species are endemic to Ethiopia, of which 27 species are Bale mountain area endemic. Species richness showed a significant ($p < 0.001$) mid elevation richness peak at around 2800 m asl on the southwestern and at 3500 m asl on the northerneastern transect (Fig. 2a). After reaching a peak at mid altitude, overall richness decreases slowly towards the summit. Endemic richness per plot showed significant differences between transects, slightly lower on the northeaster transect and increased on the more humid southwestern transect ($p < 0.01$). However, it has shown significant increase with altitude. Endemics richness peaked at higher elevations for both transect (Fig. 2b and c; $p < 0.001$, Table 2).

The percentage of endemic species increased with elevation for Ethiopian endemics ($p < 0.001$; Fig. 2d) as well as for Bale mountain area endemics on the northerneaster transect ($p < 0.001$, Fig. 2e) but showed a tendency of reaching a maximum around 3500 m asl (towards hump shaped relationship) for the southwestern transect (Fig. 2e). The south-western transect showed on average higher percentage values than the northeaster transect ($p < 0.001$, Fig. 2). The percentage of national endemics showed significant increase with elevation for both transects. However, the percentage of Bale endemics shows increase for the Northeaster transect, while it peaked at around 3500 m asl for the southwestern transect.

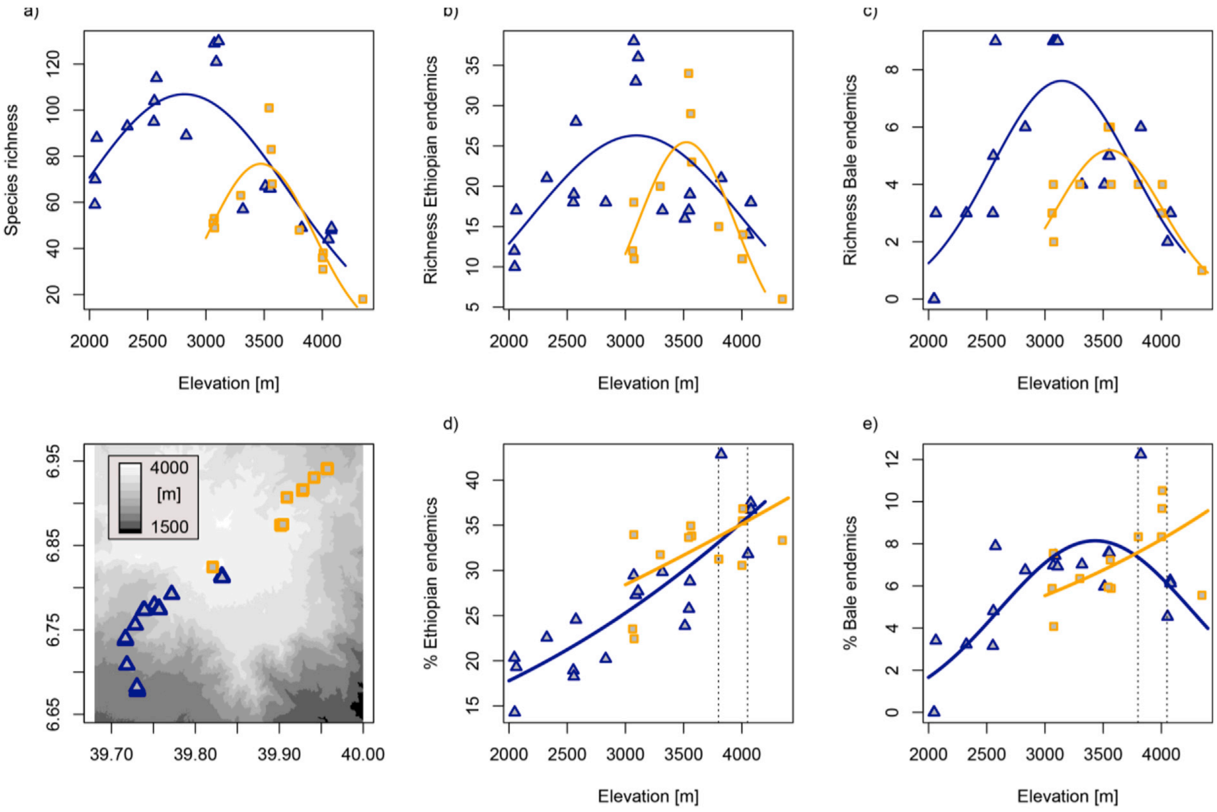

**Figure 2.** Species diversity and percent endemic species richness along altitudinal gradient: (a) Overall species richness for both Southwester (blue) and Notheastern (orange) transects. (b) richness of Ethiopian endemics (c) richness of Bale area endemic (d) percent Ethiopian endemics and (e) percent Bale area endemics. The map shows the distribution of sampling plots along elevational gradient on both transects of the study area. Note that the models shown in the figures were fitted independently after separating the southern and the northern transect data while the main text reports results of the overall richness model (Table 2 below), except the percentage of Bale area endemics (e) where the northern transect shows only a linear fit, results don't differ qualitatively.

**Table 2**
Best models after stepwise model selection (based on AIC). E: elevation, T: transect (souths).

| *Dependent variable* | *Best model formula after stepwise model selection* | *Error distribution* |
|---|---|---|
| Richness | $-3.3 \pm 0.9$ ($p < 0.001$) + $4.6x10^{-3}\pm0.5x10^{-3}$ *E ($p < 0.001$) - $7.1x10^{-7}\pm0.7x10^{-7}$ *E$^2$ ($p < 0.001$) + $2.3 \pm 0.5$ * T ($p < 0.001$) - $5.7\ x10^{-4}\pm1.4x10^{-4}$ *E:T ($p < 0.001$) | Poisson (log-link) |
| Number of Ethiopian endemics | $-5.3 \pm 1.8$ ($p < 0.01$) + $4.9x10^{-3}\pm1.0x10^{-3}$ *E ($p < 0.001$) - $7.3x10^{-7}\pm1.3x10^{-7}$ *E$^2$ ($p < 0.001$) + $1.6 \pm 8.6$ * T (non sig.) - $4.0\ x10^{-4}\pm2.4x10^{-4}$ *E:T (non sig.) | Poisson (log-link) |
| Number of Bale Mountains area endemics | $-16.7 \pm 4.3$ ($p < 0.001$) + $1.0x10^{-2}\pm0.2x10^{-2}$ *E ($p < 0.001$) - $1.5x10^{-6}\pm0.3x10^{-6}$ *E$^2$ ($p < 0.001$) + $4.3 \pm 2.0$ * T ($p < 0.05$) - $1.1\ x10^{-3}\pm0.6x10^{-3}$ *E:T ($p < 0.05$) | Poisson (log-link) |
| % Ethiopian endemics | $-2.4 \pm 0.3$ ($p < 0.001$) + $4.7x10^{-4}\pm0.8x10^{-4}$ *E ($p < 0.001$) | Binomial (logit-link) |
| % Bale Mountains area endemics | $-9.9 \pm 2.7$ ($p < 0.001$) + $4.1x10^{-3}\pm1.7x10^{-3}$ *E ($p < 0.05$) − $5.7x10^{-7}\pm2.7x10^{-7}$ *E$^2$ ($p < 0.05$) | Binomial (logit-link) |

### 3.2. Estimated future altitudinal range shift

When analysing plot species occurrence data (Figure 3a) estimated altitudinal range shifts following temperature increase cause the potential local extinction of 8.7%of all endemic species at 2 °C increase. Plants that are threatened with extinction include *Sedium mooney, Anthemis tigreensis, Helichrysum harennensis, Lobelia rhynchopetalum, Minuaritia filitolia, Senecio schimperi, Geranium arabicum Subsp. Pedunculata, Carex simensis, Helichrysum horridium*, and *Senecio inarnatus* of which 3 or one in five are exclusively Bale mountains area endemic. The temperature increases by 3 °C or 4 °C predicted the same rate of endemic extinction, about 36% (of 41 endemic species) local extinction of species.

When estimating the effect of temperature induced altitudinal range shifts based on the species natural elevational occurrence range reported in the literature (Figure 3b) analyses predict the local extinction of four species (3.5%: *Senecio schimperi, Festuca richardii, Veronica gunae*, and *Agrostis gracilifollia*). Temperature increase by 3 °C–4 °C, however model predicted approximately similar larger rate of extinction i.e. up to 60 species (52.6%) and 65 species (57%) respectively.

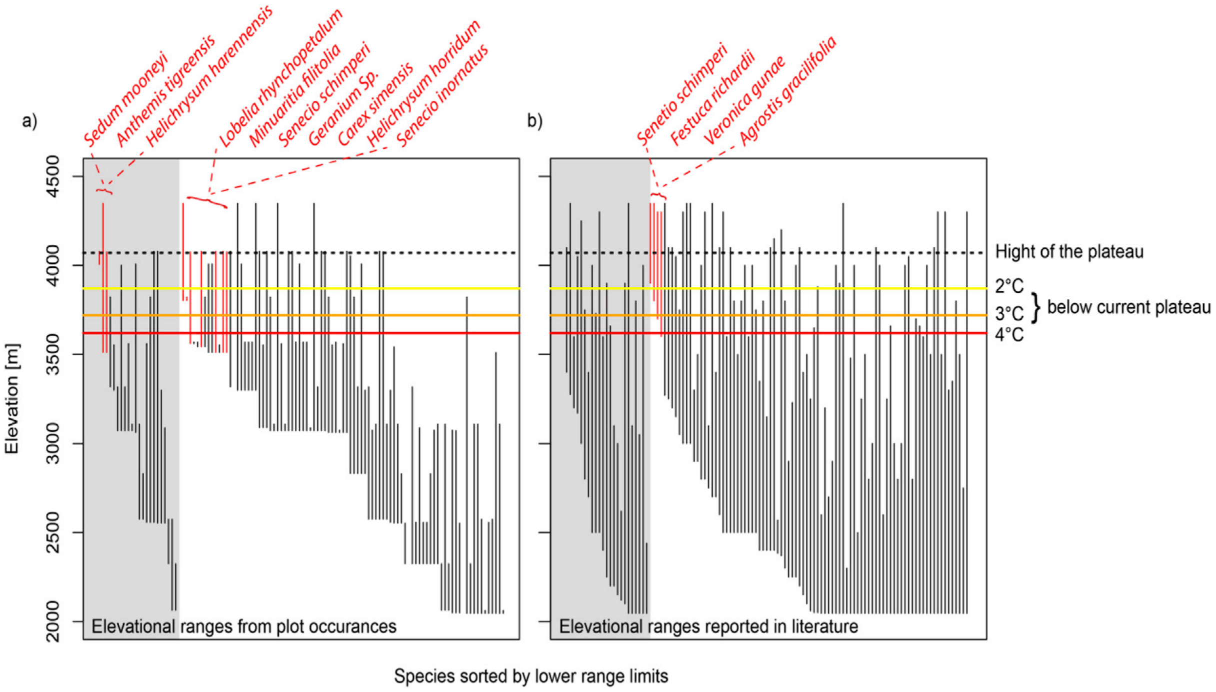

**Fig. 3.** All identified Bale area and national endemic species sorted by lower and upper range limits acquired from plot occurrence data (a) and endemic species documented natural lower and upper range acquired from literature (b). The dashed line indicates maximum elevation of the plateau, beyond which are three emerging small peaks. Those peaks are small in area and are unlikely to sustain independent populations of species. Hence, here marks the elevation of the plateau as a hard boundary for long term species survival. The yellow (2 °C), orange (3 °C) and red (4 °C) lines indicate a shift in elevation caused by temperature. Red species ranges loose at least 90% of their current range by the expected temperature increase (4 °C). The gray shaded indicates Bale mountains area endemic species, while the none shaded area indicate national endemic species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

## 4. Discussion

### 4.1. Vegetation zonation and plant species diversity and distribution

Our field data revealed a hump shaped pattern (i.e. diversity peaks at intermediate elevations) for overall species and endemic richness in the Bale mountains as well as increasing numbers of endemic towards the Afroalpine plateau. These result mirror similar patterns observed in other Ethiopian mountain (Wana and Beierkuhnlein, 2010) and are also common in mountains globally (Bruun et al., 2006; Lomolino, 2001; Steinbauer et al. 2016a, 2018). Simulations have shown that a hump-shaped pattern of species richness could result from a random placement of species' geographical ranges along a gradient with hard boundaries (such as elevation, temperature etc; Grytnes, 2003). Mid elevation peaks in species density or diversity may also be caused by reoccurring elevation altitudinal range shifts, when the uppermost and lowermost species face higher extinction risks during environmental fluctuations (Lomolino, 2001).

One of the most important factors defining species richness is area (species-area relationship; Würtz and Annila, 2008). The decline in are with elevation found on conical mountains supports a steady decline in species richness. In contrast, the presence of the high elevation plateau in the Bale mountains would favour a richness peak at high elevations. Such area effects are unlikely to directly affect the observed mid elevation richness peak in our analyses as the area of the elevational belts with highest diversity is not particularly large. It is more likely that vegetation dynamics following historic climate changes may have contributed to shape current diversity patterns.

Our finding is in line with a recent diversity analysis across ecosystems in Ethiopia explaining the exceptional diversity with the presence of high diversity of trees, shrubs and herbs across all ecosystems of the country as compared to more specialised succulents, grasses, climbers, lianas, epiphytes and geophytes (Lemessa and Teka, 2017). We further speculate that orography related precipitation effects and resources diversity may influence the current diversity pattern. Precipitation is higher in mid-elevations when compared to the flat alpine plateau (Hillman, 1986). In addition, the topography of the steeper slopes may cause small-scale climatic heterogeneity allowing the coexistence of species with differing environmental tolerances in smaller areas when compared to the relatively flat plateau (Diamond, 1988; Winkler et al., 2016). The steep slopes may also shelter plant species from the large density of natural and domestic herbivores which particularly are affecting the flat plateau area (Irl et al., 2014).

Endemic richness was found to reach its maximum in higher elevations than overall richness likely reflecting the in-situ evolution of novel species in isolated high-elevation habitats of afroalpine mountains (Steinbauer et al., 2013). The resulting increase - or high elevated peak - in the percentage of endemic species is consistent with similar patterns on other tropical mountains (Mallet-Rodrigues et al., 2010; Jump et al., 2012; Nogué et al., 2013) and reported from mountains on oceanic islands (Steinbauer et al., 2012). Therefore, the term “sky islands” has been coined to reflect the island-like character of tropical alpine mountains (Irl and Beierkuhnlein, 2011). An increase in ecological isolation with elevation promotes isolation driven speciation and thus higher rates of evolutionary activity (Steinbauer et al., 2016a). In line with this phylogenetic evidence across the globe indicate that many high-elevation endemics are phylogenetically young taxa resulting from fast diversification (Hutter et al., 2013; Salerno et al., 2012; Merckx et al., 2015). The Bale Mountains afroalpine ecosystems are geographically isolated patches among the mountains along the Great Rift Valley. The high elevation and unique topography of these mountains disconnects them from the rest of east African mountains causing considerable geographically isolation from neighbouring mountains and landscapes. High altitude related strong environmental filters enable unique and specialized species to survive under such harsh conditions, which favours endemism over long evolutionary times.

Adding to the effect of largescale isolation, orography causes considerable small-scale differences in environmental conditions promoting environmental heterogeneity and thus the coexistence of a high diversity of species. The mountains receive high amount of rainfall differing considerably between the south-western and the north-eastern transects. Hence, over time different pools of species adapted to different microclimatic condition have evolved. We found considerable differences in species richness, but also in the spatial patterns of diversity along elevation on alternating sites of the mountain's slopes.

While Bale Mountains have always been inhabited by humans, the recent population growth and intensification of activities influence the distribution of species (i.e. domestic animal grazing, fire, expansion of agricultural land, deforestation, overgrazing, and unmanaged settlement). Burgess et al. (2007), found strong positive correlation between human density and local species richness, the number of endemic species and the density of threatened species across the three tropical African mountain ranges, and all sub-Saharan Africa. While a positive relationship between human density and species richness may partly be explained by a biased species sampling (Barbosa et al. 2010, 2013), this may also mirror the focus of human activities on productive, often diverse sites as well as the ecosystem services which highly diverse ecosystems provide for human livelihood. Particularly the increase in the percentage of threatened species with human settlement density is of major concern for future development in the Bale mountains where human settlement activity has increased considerable in recent years. While across most high mountain ranges anthropogenic disturbance usually declines with increasing elevation and isolation, recent development suggests intensifying human disturbance in high elevation sites of the Bale mountains. Raising temperatures are expected to make the high elevation plateau of the Bale Mountains even more suitable for human land use. The increasing and more frequent domestic stock grazing on the Afroalpine zone may be a first sign of this climate driven land use change. While the Afroalpine plateau has traditionally been used only for pastoral activities, year-round grazing is becoming increasingly common. These challenges are not restricted to the Bale mountains but threat on unique diversity in all

African tropical mountains, which are increasingly populated by dense and poor rural population with livelihood strategies largely relying on farming (Burgess et al., 2007).

Fire is another important factor affecting plant species composition across the massive. The entire Bale Mountains massif, the high-altitude belt but to a lesser extent also Harenna Forest, is affected by recurrent fires which often significantly threaten local biodiversity and key habitats (Wesche et al., 2000; Johansson et al., 2012).

### 4.2. *Ppotential altitudinal range shift and local extinction*

Our climate projections indicate that climate change induced warming may have far reaching impact on the afroalpine plants. Many of the afroalpine species are facing their uppermost range boundaries above the limit of the plateau and are expected to suffer from range losses and potential extinction. Our estimates predicted potential species extinction even under the uninventable warming scenario of 2 °C temperature increase. Mountain top extinction is a strong concern for endemic species lacking disjunct populations elsewhere on higher mountains or at cooler latitudes (Lenoir et al., 2010). In the Bale mountain, particularly the national and Bale area endemic species are highly endangered than others. Our results mirror similar studies on the impacts of climate change on the natural systems of Guhe mountains of Ethiopia (Kreyling et al., 2010). The results also reflect in more advanced modelling approaches for single species, like the endemic *Lobelia rhynchopetalum*, for which extinction in Bale mountains and Semen Mountains is predicted based on large number single species observations covering a large area (Chala et al., 2016).

Accelerated climate change effects observed in better studied mountain regions (Steinbauer et al., 2018) would particularly affect plants that are unable to adapt to the rapidly changing climate or with limited potential to move their occurrence range. This likely includes many of the Afroalpine specialist that are adapted to the intense daily cycles including freezing night temperatures. With climate changing, these adaptations are less relevant making the native flora susceptible to completion by newly established species.

Besides range contraction and habitat loss climate change induced warming may also result in increased susceptibility of vascular plants to pests and diseases, effect on carbon sequestration, and other far reaching genetic and evolutionary implications (Jump et al., 2009). Even species persisting in fragmented localities due to high phenotypic plasticity and present microclimatic refugia may face a decline in their genetic diversity endangering the long-term viability of their populations (Struebig et al., 2011).

Climate change may even result in fundamental ecosystems transformations or collapse, hence a change or loss in species functionality. With climate change induced thermal isotherms shift, dominant thermophilus plant species such as Erica will be able to establish and transform ecosystems on the plateau. Historical records indicate that Erica may have been dominating the alpine plateau during warm phases just after the start of the Holocene, around 11,200 cal BP (Kuzmicheval et al., 2013). Erica is currently distributed all over the massive between 3200 and 4200 m asl with growth form ranging from tall tree of up to 12 m to small dwarf shrubs. The potential effects of a new dominant species establishing on the plateau demand further investigations.

## 5. Conclusions

Our analysis indicates that the plant species diversity around the Bale Afroalpine ecosystem is rich and the area harbours exceptional concentrations of endemic species. The Mountains ecosystem and adjacent tropical mountain rainforest forests harbours exceptional high numbers of endemic plants and animals. Despite, the wide recognition of the area as the world's greatest biodiversity hotspots, the commitment to give the area international recognition, conservation management support and protection seems to be delayed.

Currently, the natural habitat is under threat from climate change and immediate human activities. Warming induced thermal isotherm shift will compel plants to either move, adapt or face extinction. Our finding provide evidence that climate change endangers a significant part of the unique Afroalpine flora. Intensified land use activities may further exacerbate the situation.

Conservation management strategies need to address these novel challenges not only within the areas of the national park but also include the buffer zone around the boundaries and subzones surrounding the national park. Effective strategies need to acknowledge local people and their socio-economic situation. Particularly the intensified grazing driven by a larger number of domestic animals, large-scale land grabbing and agricultural expansion are realities that needs to be studied and addressed in efficient conservation planning.

To date, climate change impacts on the biodiversity, the afroalpine endemics and the ecosystems services of the Bale mountains are not well studied. Scientific investigation and predictions on the complex interactions between biota (i.e. competition, priority effects etc.) and climate change are urgently needed for this sky island system along with ecological studies that consider human population and socioeconomic growth, and its impacts on ecosystem in the face of climate change.

## Acknowledgements

We express gratitude to the UK based Rufford Small Grants Foundation for financially supporting the field work, travel and material purchases. Furthermore, this study has received funding from the European Union's Horizon 2020 research and innovation programme through the project ECOPOTENTIAL under grant agreement No 641762.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00670.

## Biosketches

Yohannes Kidane Ogubamichael is interested in the characterization and protection of biodiversity in tropical landscapes and mountain ecosystems, global change issues and the response of ecosystems to climate change; research of Manuel Steinbauer focusses on the processes that generate and maintain diversity of life on earth. Carl Beierkuhnlein focuses among other topics on the role of biodiversity for ecosystem functioning, on the explanation of spatial patterns of biodiversity and on biogeography in the face of Global Change.

## Author contributions

Y.K. and C.B. conceived the ideas; Y.K. collected the data; Y.K. and M.S. analysed the data; and Y.K. led the writing.

## References

Barbosa, A.M., Real, R., Vargas, J.M., 2010. Use of coarse-resolution models of species' distributions to guide local conservation inferences. Conserv. Biol. 24 (5), 1378–1387. https://doi.org/10.1111/j.1523-1739.2010.01517.x.

Barbosa, A.M., Real, R., Roman Munoz, A., Brown, J.A., 2013. New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers. Distrib. 19, 1333–1338. https://doi.org/10.1111/ddi.12100.

Beierkuhnlein, C., 2007. Biogeografie. Die räumliche Organisation des Lebens in einer sich verändernden Welt. Eugen Ulmer Verlag, Stuttgart, Germany.

Bhattarai, K.R., Vetaas, O.R., 2003. Variation in plant species richness of different life forms along a subtropical elevation gradient in the Himalayas, east Nepal. Glob. Ecol. Biogeogr. 12, 327–340.

Bonnefille, R., 1983. Evidence for a cooler and drier climate in the Ethiopian uplands towards 2.5 Mys ago. Nature 303, 487–491. https://doi.org/10.1038/303487a0.

Bruun, H.H., Moen, J., Virtanen, R., Grytnes, J.A., Oksanen, L., Angerbjorn, A., 2006. Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. J. Veg. Sci. 17, 37–46. https://doi.org/10.1111/j.1654-1103.2006.tb02421.x.

Burgess, N.D., Balmford, A., Cordeiro, N.J., Fjeldsa, J., Kuper, W., Rahbek, C., Sanderson, E.W., Scharlemann, J.P.W., Sommer, J.H., Williams, P.H., 2007. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. Biol. Conserv. 134, 164–177. https://doi.org/10.1016/j.biocon.2006.08.024.

Buytaert, W., Cuesta-camacho, F., Tobon, C., 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. Glob. Ecol. Biogeogr. 20, 19–33. https://doi.org/10.1111/j.1466-8238.2010.00585.x.

Chala, D., Brochmann, C., Psomas, A., Dorothee Ehrich, D., Gizaw, A., Masao, C.A., Bakkestuen, V., Zimmermann, N.E., 2016. Good- bye to tropical alpine plant giants under warmer climates? Loss of range and genetic diversity in Lobelia rhynchopetalum. Ecol. Evol 6, 8931–8941. https://doi.org/10.1002/ece3.2603.

Davis, M.B., Shaw, R.G., Etterson, J.R., 2005. Evolutionary responses to changing climate. Ecology 86 (7), 1704–1714. https://doi.org/10.1890/03-0788.

Development Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL. http://www.R-project.org.

Diamond, J., 1988. Factors controlling species diversity: overview and synthesis. Ann. Mo. Bot. Gard. 75 (1), 117–129. https://doi.org/10.2307/2399469.

Dullo, B.W., Grootjans, A.P., Roelofs, J.G.M., Senbeta, A.F., Fritz, C., 2015. Fen mires with cushion plants in Bale mountains, Ethiopia. Mires Peat 15, 1–10 [UNSP 07].

Edwards, S., Mesfin, T., Hedberg, I. (Eds.), 1995. Flora of Ethiopia and Eritrea, vol. 2. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala, Sweden. No. 2.

Edwards, S., Sebsebe, D., Hedberg, I. (Eds.), 1997. Flora of Ethiopia and Eritrea, vol. 6. The National Herbarium, Addis Ababa and Department of Systematic Botany, Sweden.

Edwards, S., Mesfin, T., Sebsebe, D. (Eds.), 2000. Flora of Ethiopia and Eritrea, vol. 2. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala, Sweden. No. 1.

Enquist, C.A.F., 2002. Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. J. Biogeogr. 29, 519–553.

Friis, I., 1992. Forests and Forest Trees of Northeast Tropical Africa. Their Natural Habitats and Distribution Patterns in Ethiopia, Djibouti and Somalia. Kew Bull Additional Series, vol. 15. HMSO, London.

Friis, I., Thulin, M., Adsersen, H., Burger, A.M., 2005. Patterns of plant diversity and endemism in the Horn of Africa. Biol. Skr. 55, 289–314, 0366-3612. ISBN 87-7304-304-4.

Gehrke, B., Linder, H.P., 2014. Species richness, endemism and species composition in the tropical Afroalpine flora. Alpine Bot. 124, 165–177. https://doi.org/10.1007/s00035-014-0132-0.

Grytnes, J.A., 2003. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. Ecography 26, 291–300.

Hedberg, O., 1951. Vegetation belts of the East african mountains. Sven. Bot. Tidskr. 45, 140–202.

Hedberg, I., Edwards, S. (Eds.), 1989. Flora of Ethiopia: Pittosporaceae to Araliaceae, vol. 3. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala. Sweden.

Hedberg, I., Edwards, S. (Eds.), 1995. Flora of Ethiopia and Eritrea, vol. 7. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala, Sweden.

Hedberg, O., 1964. Features of Afroalpine Plant Ecology. Acta Phytogeographica Suecica, vol. 49, pp. 1–144.

Hedberg, I., Edwards, S., Sileshi, N. (Eds.), 2003. Flora of Ethiopia and Eritrea, vol. 4. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala, Sweden, 1.

Hedberg, I., Friis, I., Edwards, S. (Eds.), 2004. Flora of Ethiopia and Eritrea, vol. 4. The National Herbarium, Addis Ababa and Department of Systematic Botany, Uppsala, Sweden, 2.

Hillman, J.C., 1986. Conservation in Ethiopia's Bale mountains. Endangered Species 3, 1–4.

Hillman, J.C., 1988. The Bale Mountains National Park Area, Southeast Ethiopia and its Management, vol. 8. Mountain Research and Development, pp. 253–258.

Hutter, C.R., Guayasamin, J.M., Wiens, J.J., 2013. Explaining Andean megadiversity: the evolutionary and ecological causes of glassfrog elevational richness patterns. Ecol. Lett. 16, 1135–1144. https://doi.org/10.1111/ele.12148.

IPCC, 2014. In: Pachauri, R.K., Meyer, L.A. (Eds.), Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team. IPCC, Geneva, Switzerland, p. 151.

Irl, S.D.H., Beierkuhnlein, C., 2011. Distribution of endemic plant species on an oceanic island – a geospatial analysis of La Palma (Canary Islands). Proc. Environ. Sci. 7, 170–175. https://doi.org/10.1016/j.proenv.2011.07.030.

Irl, S., Steinbauer, M., Epperlein, L., Harter, D., Jentsch, A., Pätz, S., Wohlfahrt, C., Beierkuhnlein, C., 2014. The hitchhiker's guide to island endemism - biodiversity and endemic perennial plant species in roadside and surrounding vegetation. Biodivers. Conserv. 23, 2273–2287. https://doi.org/10.1007/s10531-014-0722-6.

Itescu, Y., 2018. Are island-like systems biologically similar to islands? A review of the evidence. Ecography 42, 1–17. https://doi.org/10.1111/ecog.03951.

Jacob, M., Annys, S., Frankl, A., De Ridder, M., Beeckman, H., Guyassa, E., Nyssen, J., 2014. Tree line dynamics in the tropical African highlands identifying drivers and dynamics. J. Veg. Sci. 26, 9–20. https://doi.org/10.1111/jvs.12215.

Jarvis, A., Reuter, H.I., Nelson, A., Guevara, E., 2018. Hole-filled SRTM for the globe version 4, available from the CGIAR-CSI SRTM 90m database. Available online. http://srtm.csi.cgiar.org. accessed on.

Jentsch, A., Beierkuhnlein, C., 2003. Global climate change and local disturbance regimes as interacting drivers for shifting altitudinal vegetation patterns. Erdkunde 57, 216–231.

Johansson, M.U., Fetene, M., Malmer, A., Granström, A., 2012. Tending for cattle: traditional fire management in Ethiopian montane heathlands. Ecol. Soc. 17 (3), 19. https://doi.org/10.5751/ES-04881-170319.

Jump, A.S., Matyas, C., Penuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24, 694–701. https://doi.org/10.1016/j.tree.2009.06.007.

Jump, A.S., Huang, T.J., Chou, C.H., 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. Ecography 35, 204–210. https://doi.org/10.1111/j.1600-0587.2011.06984.x.

Kidane, Y., Stahlman, R., Beierkuhnlein, C., 2012. Vegetation dynamics, and land use and land cover change in the Bale Mountains, Ethiopia. Environ. Monit. Assess. 184 (12), 7473–7489. https://doi.org/10.1007/s10661-011-2514-8.

Körner, C., 2007. The use of ‘altitude’ for ecological research. Trends Ecol. Evol. 22 (11), 569–574. https://doi.org/10.1016/j.tree.2007.09.006.

Körner, C., Jetz, W., Paulsen, J., Payne, D., Rudmann-Maurer, K., Spehn, E.M., 2017. A global inventory of mountains for bio-geographical applications. Alpine Bot. 127, 1–15. https://doi.org/10.1007/s00035-016-0182-6.

Kreyling, J., Wana, D., Beierkuhnlein, C., 2010. Climate warming and tropical plant species - consequences of potential upslope shift of isotherms in southern Ethiopia. Divers. Distrib. 16, 593–605. https://doi.org/10.1111/j.1472-4642.2010.00675.x.

Kuzmicheval, E.A., Debella, H., Khasanov, B., Krylovich, O., Babenko, A., Savinetsky, A., Severova, E., Yirga, S., 2013. Holocene hyrax dung deposits in the Afroalpine belt of the Bale Mountains (Ethiopia) and their palaeoclimatic implication. J. Environ. Archaeol. 18 (1), 72–81. https://doi.org/10.1179/1461410313Z.00000000018.

Kuzmicheval, E.A., Khasanov, B.F., Krylovich, O.A., Savinetsky, A.B., 2014. Vegetation and climate reconstruction for the Bale mountains (Ethiopia) in the Holocene according to the pollen analysis and radiocarbon dating of zoogenic deposits, 458 (1), 116–121. https://doi.org/10.1134/S0012496614050019.

Lemessa, D., Teka, Y., 2017. Patterns of the diversity of characteristic species across vegetation ecosystems of Ethiopia. Ecol. Evol. Biol. 2 (3), 34–44. https://doi.org/10.11648/j.eeb.20170203.11.

Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Svenning, J.C., 2010. Going against the flow: potential mechanisms for unexpected downslope altitudinal range shifts in a warming climate. Ecography 33, 295–303. https://doi.org/10.1111/j.1600-0587.2010.06279.x.

Lomolino, M.V., 2001. Elevation gradients in species density: historical and prospective views. Glob. Ecol. Biogeogr. 10, 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x.

Lovejoy, T., 2008. Climate change and biodiversity. Rev. sci. tech. Off. int. Epiz. 27 (2), 331–338.

Malcolm, J.R., Liu, C., Neilson, R.O., Hansen, A., Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conserv. Biol. 20 (2), 538–548. https://doi.org/10.1111/j.1523-1739.2006.00364.x.

Mallet-Rodrigues, F., Parrini, R., Pimentel, L.M.S., Bessa, R., 2010. Altitudinal distribution of birds in a mountainous region in southeastern Brazil. Zool. 27, 503–522. https://doi.org/10.1590/S1984-46702010000400003.

Merckx, V.S.F.T., Hendriks, K.P., Beentjes, K.K., Mennes, C.B., Becking, L.E., Peijnenburg, K.T.C.A., Afendy, A., Arumugam, N., de Boer, H., Biun, A., Buang, M.M., Chen, P.-P., Chung, A.Y.C., Dow, R., Feijen, F.A.A., Feijen, H., Soest, C.F., Geml, J., Geurts, R., Gravendeel, B., Hovenkamp, P., Imbun, P., Ipor, I., Janssens, S.B., Jocque, M., Kappes, H., Khoo, E., Koomen, P., Lens, F., Majapun, R.J., Morgado, L.N., Neupane, S., Nieser, N., Pereira, J.T., Rahman, H., Sabran, S., Sawang, A., Schwallier, R.M., Shim, P.-S., Smit, H., Sol, N., Spait, M., Stech, M., Stokvis, F., Sugau, J.B., Suleiman, M., Sumail, S., Thomas, D.C., van Tol, J., Tuh, F.Y.Y., Yahya, B.E., Nais, J., Repin, R., Lakim, M., Schilthuizen, M., 2015. Evolution of endemism on a young tropical mountain. Nature 524, 347–350. https://doi.org/10.1038/nature14949.

Miehe, G., Miehe, S., 1994. Ericaceous Forests and Heathlands in the Bale Mountains of South Ethiopia: Ecology and Man's Impact. Stiftung Waldurhaulting in Afrika (Humburg. Germany).

Mittermeier, R.A., Robles Gil, P., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., da Fonseca, G.A.B., 2004. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. CEMEX, Mexico City. Mexico.

Mohr, P.A., 1971. In: The Geology of Ethiopia, second ed. Haile Sellassie I University Press, Addis Ababa. Ethiopia.

Mutke, J., Kier, G., Braun, G., Schultz, Chr, Barthlott, W., 2001. Patterns of African vascular plant diversity: a GIS based analysis. Syst. Geogr. Plants 71 (2), 1125–1136. https://doi.org/10.2307/3668744.

Nagy, L., Grabherr, G., 2009. The Biology of Alpine Habitats. Oxford University Press, Oxford.

Nogué, S., Rull, V., Vegas-Vilarrúbia, T., 2013. Elevational gradients in the neotropical table mountains: patterns of endemism and implications for conservation. Divers. Distrib. 19, 676–687. https://doi.org/10.1111/ddi.12017.

Osmaston, H.A., Mitchell, W.A., Osmaston, J.A.N., 2005. Quaternary glaciation of the Bale mountains, Ethiopia. J. Quat. Sci. 20, 593–606. https://doi.org/10.1002/jqs.931.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys. 37.091305.110100.

Peyron, O., Jolly, D., Bonnefille, R., Vincens, A., Guiot, J., 2000. Climate of east Africa 6000 14 C yr B.P. As inferred from pollen data. Quat. Res. 54, 90–101. https://doi.org/10.1006/qres.2000.213.

Puff, C., Nemomissa, S., 2005. Plants of the Simien: A Flora of the Simien Mountains and Surroundings, Northern Ethiopia. Scripta Botanica Belgica, vol. 37. National Botanical Garden, Belgium.

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x.R.

Salerno, P.E., Ron, S.R., Señaris, C., Rojas-Runjaic, F.J.M., Noonan, B.P., Cannatella, D.C., 2012. Ancient Tepui summits harbour young rather than old lineages of endemic frogs. Evolution 66, 3000–3013. https://doi.org/10.1111/j.1558-5646.2012.01666.x.

Sanchez-Gonzalez, A., Lopez-Mata, L., 2005. Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. Divers. Distrib. 11, 567–575.

Schweiger, A.H., Irl, S.D.H., Steinbauer, M.J., Dengler, J., Beierkuhnlein, C., 2016. Optimizing sampling approaches along ecological gradients. Methods. Ecol. Evol. 7, 463–471.

Stattersfield, A.J., Crosby, M.J., Long, A.J., Wege, D.C., 1998. Endemic Bird Areas of the World. Priorities for Biodiversity Conservation. BirdLife Conservation Series No. 7. BirdLife International, Cambridge, UK.

Steinbauer, M., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., Fernández-Palacios, J.M., 2012. Increase of island endemism with altitude - speciation processes on oceanic islands in. Ecography 35, 23–32. https://doi.org/10.1111/j.1600-0587.2011.07064.x.

Steinbauer, M., Irl, S., Beierkuhnlein, C., 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands in. Acta Oecologica-International Journal of Ecology 47, 52–56. https://doi.org/10.1016/j.actao.2012.11.004.

Steinbauer, M.J., Field, R., Grytnes, J.A., Trigas, P., Ah-Peng, C., Attorre, F., et al., 2016a. Topography-driven isolation, speciation and a global increase of endemism with elevation. Glob. Ecol. Biogeogr. 25 (9), 1097–1107. https://doi.org/10.1111/geb.12469.

Steinbauer, M.J., Irl, S.D.H., González-Mancebo, J.M., Breiner, F.T., Hernández-Hernández, R., Hopfenmüller, S., Kidane, Y., Jentsch, A., Beierkuhnlein, C., 2016b. Plant invasion and speciation along elevational gradients on the oceanic island La Palma, Canary Islands. Ecol. Evol 7 (2), 771–779. https://doi.org/10.1002/ece3.2640.

Steinbauer, M.J., et al., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. Nature. https://doi.org/10.1038/s41586-018-0005-6.

Struebig, M.J., Kingston, T., Petit, E.J., Le Comber, S.C., Zubaid, A., Mohd-Adnan, A., Rossiter, S.J., 2011. Parallel declines in species and genetic diversity in tropical forest fragments. Ecol. Lett. 14, 582–590. https://doi.org/10.1111/j.1461-0248.2011.01623.x.

Uhlig, S.K., 1990. In: Messerli, B., Hurni, H. (Eds.), Mountain Forests and the Upper Tree Limit on the Southeastern Plateau of Ethiopia. African Mountains and Highlands: Problems and Perspectives. Walsworth Press Co., Inc., Missouri, pp. 237–248. The African Mountain Association (AMA).

Uhlig, S., Uhlig, K., 1991. Mountain Chronicles. Studies on the Altitudinal Zonation of Forests and Alpine Plants in the Central Bale Mountains, Ethiopia, vol. 11. Mountain Research and Development, pp. 153–256.

Umer, M., Lamb, H.F., Bonnefille, R., Lezine, A.M., Tiercelin, J.J., Gibert, E., Cazet, J.P., Watrin, J., 2007. Late Pleistocene and Holocene vegetation history of the Bale mountains, Ethiopia. Quat. Sci. Rev. 26, 2229–2246. https://doi.org/10.1016/j.quascirev.2007.05.004.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesank, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395. https://doi.org/10.1038/416389a.

Wana, D., Beierkuhnlein, C., 2010. Plant species and growth form richness along altitudinal gradients in the southwest Ethiopian highlands. J. Veg. Sci. 21, 617–626.

Wesche, K., Miehe, G., Kaeppeli, M., 2000. The significance of fire for Afroalpine ericaceous vegetation. Mt. Res. Dev. 20, 340–347. https://doi.org/10.1659/0276-4741(2000)020[0340:TSOFFA]2.0.CO;2.

White, F., 1983. The Vegetation of Africa: a Descriptive Memoir to Accompany the UNESCO/AETFAT Vegetation of Africa. UNESCO, Paris, FR.

Winkler, M., Lamprecht, A., Steinbauer, K., Hülber, K., Theurillat, J.P., et al., 2016. The rich sides of mountain summits—a pan-European view on aspect preferences of alpine plants. J. Biogeogr. 43 (11), 2261–2273. https://doi.org/10.1111/jbi.12835.

Würtz, P., Annila, A., 2008. Roots of diversity relations. J. Biophysics 2008, 1–8. https://doi.org/10.1155/2008/654672.