Alpine Botany (2023) 133:149–161
https://doi.org/10.1007/s00035-023-00301-9

ORIGINAL ARTICLE

Plant diversity and composition vary with elevation on two equatorial high mountains in Uganda: baselines for assessing the influence of climate change

Fredrick Ssali[1] · **Badru Mugerwa**[1,2,3] · **Miriam van Heist**[4] · **Douglas Sheil**[5,6,7] · **Ben Kirunda**[8] · **Mariana Musicante**[9,10] · **Anton Seimon**[11] · **Stephan Halloy**[10,12]

Received: 1 April 2023 / Accepted: 23 August 2023 / Published online: 3 September 2023

Abstract

We describe the distribution and diversity of vascular plants at high elevations (3980–4570 m above sea level) in the Rwenzori Mountains and Mount Elgon National Parks in Uganda. These were the first target regions of the "Global Observation Research Initiative in Alpine Environments" ("GLORIA") on the African continent. In each target region, four summits spanning elevations from the treeline ecotone up to the limits of vascular plant life were selected and assessed in July and August 2011 using the standardised GLORIA protocol. Few vascular plant species were present on high elevation summits, particularly in Rwenzori, where many sub-plots had little or no vascular plant cover. Observations from Rwenzori include 26 vascular plant species, and from Mount Elgon 47, of which 10 and 15 species, respectively, were endemic. In contrast, non-vascular plant cover greatly increased with elevation. The lowest sites showed considerable diversity and were floristically dissimilar to the highest summits. Subsequent resurveys, repeating the GLORIA protocol, will be critical in the assessment of ongoing dynamics and change.

Keywords Afroalpine species · Climate change · Species richness · Endemism · Mount Elgon · Rwenzori Mountains · Climate warming · Biogeography

✉ Fredrick Ssali
ssalifb@yahoo.co.uk

1 Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, P.O. Box 44, Kabale, Uganda

2 Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Straße 17, 10315 Berlin, Germany

3 Department of Ecology, Technische Universität Berlin, Straße Des 17. Juni 135, 10623 Berlin, Germany

4 Graduate School Production Ecology and Resource Conservation, Wageningen University and Research, Droevendaalsesteeg 3-A, 6708 PB Wageningen, The Netherlands

5 Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

6 Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

7 Center for International Forestry Research (CIFOR), Kota Bogor, Jawa Barat 16115, Indonesia

8 Uganda Country Program, Wildlife Conservation Society, Kampala, Uganda

9 New Zealand BioSecure Entomology Laboratory, Southern Monitoring Services L., Lower Hutt, New Zealand

10 Universidad Nacional de Chilecito (UNdeC), Chilecito, Argentina

11 Center for Environmental Policy, Bard College, Annandale-On-Hudson, NY, USA

12 New Zealand Ministry for Primary Industries, Wellington, New Zealand

Introduction

Marked ecological impacts from a warming climate are expected in high-mountain regions (Pauli et al. 2012; Hantemirov et al. 2022). Endemic vascular plant species appear threatened, since their habitats could be drastically reduced. Studies conducted in Europe, Australia and South America suggest that the distribution of alpine plants will move upslope and that high elevation cryophilic species may decline because of limited dispersal opportunities and weak competitive abilities (Pickering et al. 2008; Gottfried et al. 2012; Carilla et al. 2018). Other studies have indicated that species restricted to narrow vegetation belts will also decline (Dirnböck et al. 2011; Chala et al. 2017; Valencia et al. 2020). The severity of such impacts, and their role among other potential drivers of ecological change—such as variations in moisture availability, cloud cover, disturbance, and alien plants—can best be detected through long-term observations designed to provide information directly applicable to conservation management and adaptation (Pauli and Halloy 2019).

With its network of long-term alpine biodiversity monitoring sites developed across six continents (Grabherr et al. 2001; Pauli et al. 2015), the "Global Observation Research Initiative in Alpine Environments (GLORIA)" aims to assess how alpine biota are changing across high mountain ecosystems (www.gloria.ac.at). High mountains are especially suited to studying effects of climate change because of their steep temperature gradients (Pauli et al. 2012; Dangles et al. 2017). GLORIA studies from Europe and South America have found that changes in species richness and composition are occurring across numerous summits on high mountains (Moret et al. 2016; Seimon et al. 2017; Carilla et al. 2018; Steinbauer et al. 2018; Cuesta et al. 2023). However, such assessments in Africa are few (see Gehrke and Linder 2014). Thus, in 2011, two GLORIA target regions were established in Tropical East Africa. The Rwenzori Mountains and Mount Elgon National Parks in Uganda are known hotspots of plant diversity and endemism and are highly vulnerable to climate change (Taylor et al. 2006; Gehrke and Linder 2014; Brochmann et al. 2022).

Here, we provide results of the initial baseline sampling in these first GLORIA target regions in Africa. We examined the distribution and abundance of vascular plant species on selected summits. Specifically, we asked: (1) how plant communities differ and (2) how the distributions vary with elevation and slope. We expected that the vascular plant communities would differ over the elevation gradient as well as between the mountain regions. This study offers a foundation for building the much-needed understanding of climate change and other potential impacts on vegetation in the mountains of Tropical East Africa.

Study area

The Rwenzori Mountains (hereafter "Rwenzori") are a 3000-km^2 metamorphic basement block within the Albertine Rift lying at the Uganda–Congo border just north of the equator. On the Ugandan side, the mountains lie within the Rwenzori Mountains National Park—a UNESCO World Heritage site located between 0°06–0°46' N and 29°47'–30°11' E and covering 996 km^2 (Butynski and Kalina 1993). The third highest massif in Africa (after Kilimanjaro and Mt Kenya), Rwenzori's topography ranges from about 1600 to 5109 m above sea level (asl; all elevations shown hereafter are asl) (Karner et al. 2000). The dominant bedrock is Precambrian comprising gneisses, schists and amphibolites belonging to the Toro-belt and the Archean basement of the Democratic Republic of Congo and Tanzania cratons (Eggermont et al. 2007). The mountains are steep, rugged and include the largest area of glaciers in Africa (Kaser and Noggler 1991). However, the glaciers are shrinking: from approximately 7.5 km^2 in 1906 to about 1 km^2 in 2003 (UNESCO and IUCN 2020). The Rwenzori range is associated with frequent cloud cover above 2500 m, where the mountains trap humid air from the Congo basin (Lentini et al. 2011; UNESCO and IUCN 2020). Annual precipitation is between 2000 and 3000 mm, with peaks in March–May and August–November (Osmaston 2006). Snowfall has been observed above 4300 m mainly during periods of heavy precipitation. Daily air temperature varies between – 5 and 20 °C in the alpine (~ 3800 to 4500 m) and nival zones (> 4500 m), with nocturnal freezing occurring 80–90% of nights (Eggermont et al. 2007).

Mount Elgon (hereafter "Elgon") is a Miocene volcanic mountain located at the border between Uganda and Kenya (0°54'–1°25' N and 34°14'–34°45' E). It is the oldest of the large (> 4000 m) East African volcanoes. The mountain is composed of tuff, rock, ash and coarse agglomerates (van Heist 1994; Lundberg and McFarlane 2006). Approximately 1120 km^2 of the Ugandan part comprises Mount Elgon National Park; a national park of similar size (1179 km^2) is contiguous on the Kenyan side of the border (Petursson et al. 2013). The mountain is capped by one of the world's largest calderas, measuring 8 km wide and bearing the highest peak, Wagagai, which reaches 4321 m and lies wholly within Uganda (Scoon 2017). On a larger scale the slopes are gentle, averaging about 4 degrees, though rocky cliffs and outcrops create a rugged terrain in many regions. Glaciers are believed to have covered the summit region during the Pleistocene, reaching as low as 3400 m, but the entire area is currently deglaciated (Lundberg and McFarlane 2006). The climate is dominated by seasonally alternating moist south-westerly and dry north-easterly winds. Annual precipitation on Elgon is between 1500 and 2000 mm, varying with elevation and slope aspect. The wettest months are April–May and September–November (Scott 1998). At high elevation (i.e., 3750 m and above), the mean minimum and maximum temperatures range between – 2.0 and 1.7 °C and between 11.2 and 20.4 °C, respectively (Wesche 2003).

Both these sites have high endemism but low floristic richness. Elgon supports a relatively richer flora due to being older and more centrally located within the tropical Afroalpine mountain region (Hedberg 1992; van Heist 1994; Gehrke and Linder 2014). Mountain-wide records show that 167 and 273 vascular plant species occur roughly above 3200 m in Rwenzori and Elgon, respectively (Gehrke and Linder 2014). The two mountains host a rich fauna, including buffalo *Syncerus caffer*, red-flanked duiker *Cephalophus rufilatus*, rock hyrax *Procavia capensis* and sunbirds *Nectarinia* spp. (Howard 1991; Mwaura and Oginah 2018). They both host and sustain the headwaters of rivers which drain into Lakes George, Edward and Albert (for Rwenzori) and Lakes Turkana, Kyoga and Victoria (for Elgon) and smaller lakes that provide water to a large number of people (Butynski and Kalina 1993; Scott 1998). The eight summits considered in this study are located in the alpine zone, above the climatic treeline. This alpine zone extends between about 3800 and 4500 m, while the nival zone, typified by sparse and discontinuous vegetation cover, occurs above 4500 m (Hedberg 1964; Wesche 2003; Linder and Gehrke 2006).

Methods

We established permanent vegetation plots in the Rwenzori and Elgon GLORIA target regions following standardised procedures in July and August 2011 (Ssali et al. 2011; Pauli et al. 2015; Fig. 1; S1 Appendix). In each region we selected four summits spanning elevations from the treeline ecotone up to the limits of vascular plant life. Each summit was divided into an upper summit area (5 m), down to five metres below the highest summit peak and a lower summit area (10 m), from the 5-m down to the 10 m contour line. Upper and lower summit areas were each subdivided into four summit area sections (SASs), oriented along the cardinal directions (N, E, S, W), i.e., a summit consisted of eight SASs. Vascular plants occurring in the SASs were inventoried using a line transect of 50 m length and pointing every 50 cm (100 points) in the case of the 5-m SASs and of 100 m length with 200 points in the larger 10-m SASs. Subsequently the entire area of each SAS was explored for additional species. Moreover, we established 3 × 3-m grids, comprising nine 1-m^2 quadrats, immediately upslope of each corner of the 5-m summit area, in each cardinal direction. The four corner quadrats were then established as permanent plots, with short aluminium tubes positioned at the corners of the quadrats as permanent marks. With each of the 16 quadrats per summit, the top cover of surface types (i.e., vascular plant cover, solid rock, lichens on soil, bryophytes on soil, bare ground and litter) as well as the vascular plant species were recorded (see Pauli et al. 2015). Plant species were inventoried using a wooden frame of 1-m^2 inner width at 100 crossthread points. Plant species that occurred at the summits which were not detected under the 100 points were recorded and their respective percent cover values visually estimated. Voucher specimens were collected and deposited in the herbarium at the Institute for Tropical Forest Conservation (ITFC) research station for identification by an experienced botanist. Photographs of each of the 16 quadrats were taken perpendicular to the slope, both with and without the sampling grid in place, and the position of every plot marked using a handheld GPS. The full setup and the standardised recording required approximately 86 person-days in Rwenzori and approximately 94 person-days in Elgon (Ssali et al. 2011).

After completing the field expeditions, taxonomic identities were verified with the help of botanical specialists at the Institute for Tropical Forest Conservation (ITFC) research station, Makerere University herbarium and the GLORIA coordination office. Species and family names follow CJB African plant Database (https://www.africanplantdatabase.ch). We determined whether each of the identified species was endemic to the high East African mountains using the Global Biodiversity Information Facility (GBIF) (www.gbif.org) and assigned a life form category to each species following Hedberg (1964) and other authorities on Afroalpine vegetation (e.g.,Gehrke and Linder 2014; Kipkoech et al. 2020; Kidane 2022; Rono et al. 2023).

To examine patterns in the diversity and distribution of vascular plant species and to determine whether the observed patterns vary with topographic factors data were managed, summarised, plotted and analysed using R (R Core Team 2020). We tested associations between variables using bivariate Kendall's rank correlations and summarised species diversity patterns using Shannon and Fisher's diversity indices. We performed non-metric multidimensional scaling (NMDS) to assess compositional dissimilarity between neighbouring summits and between the lowest and highest elevation summits using the community ecology package "vegan" (Oksanen et al. 2020).

Results

We established permanent vegetation plots on eight summits in the two target regions in Rwenzori and Elgon under difficult field conditions, including dense fog and snow cover at higher elevations. The summits were typically steep with slopes along the four cardinal directions ranging between 10 and 45° for Rwenzori and between 1 and 45° for Elgon. The summits' elevations spanned 590 m (from 3980 to 4570 m

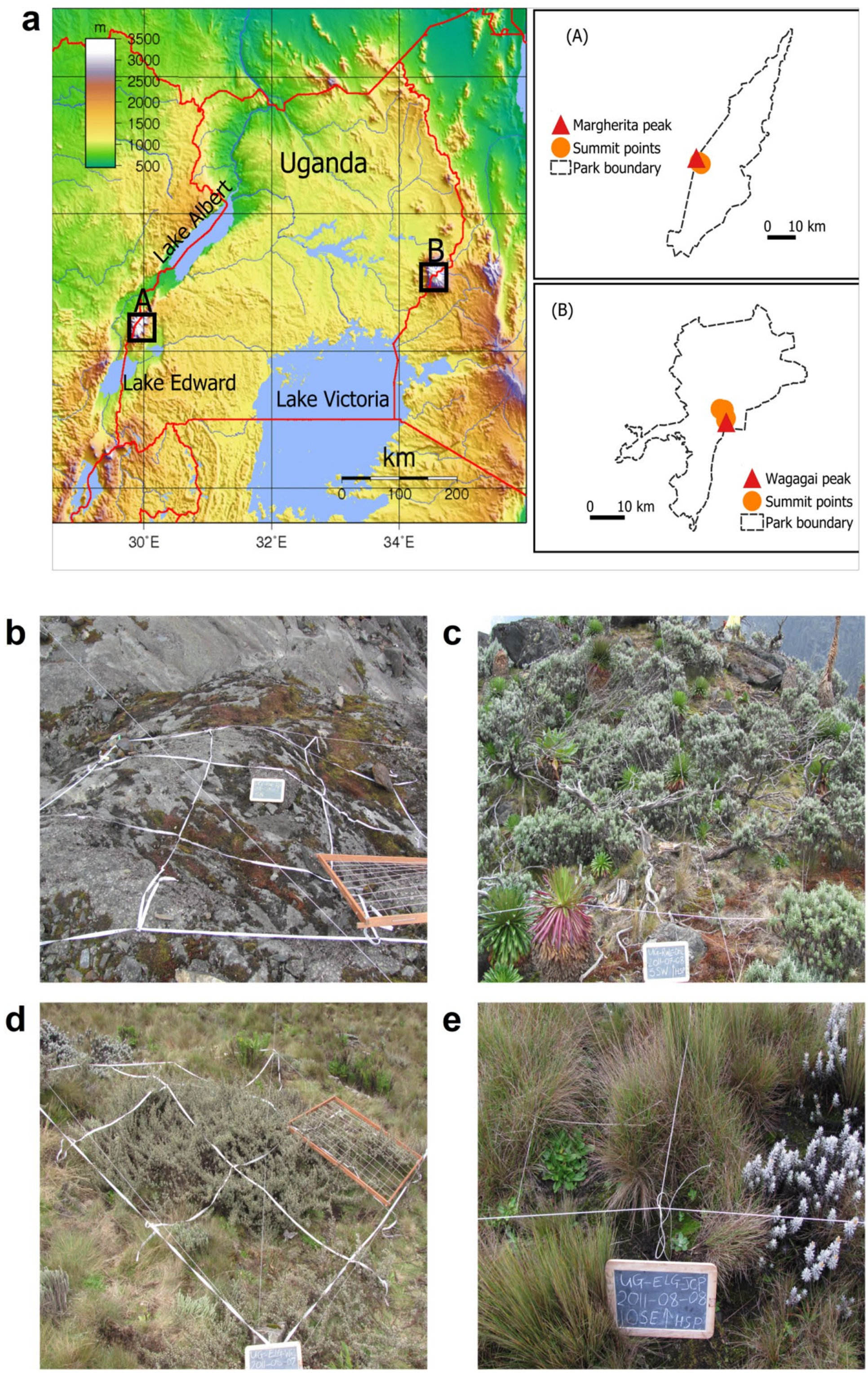

Fig. 1 **a** GLORIA summits established in **A** Rwenzori Mountains National Park and **B** Mount Elgon National Park, Uganda; **b**–**e** overview of selected summits: RWE1, RWE3, ELG2 and ELG4 located at 4570 m, 4115 m, 4201 m and 3948 m asl, respectively. The country map was adapted from www.mapsland.com

asl) for Rwenzori and 351 m (from 3948 to 4299 m asl) for Elgon (Table 1; Fig. 1). Faeces of wild animals (mainly duikers and rodents) and charred vegetation were noted in plots on the two lowest elevation summits in Rwenzori and within all four summits in Elgon. While both national parks are occasionally visited by mountain climbers, there were no obvious signs of human trampling within any of the plots or the vicinity.

Vegetation varied considerably among the plots (Table 1). Across the four Rwenzori GLORIA summits we recorded 26

Table 1 Characteristics of each GLORIA summit in Rwenzori and Elgon

Summits	Elevation (m asl)	Average slope	*N* species in 1-m^2 quadrats	*N* species in 5-m SASs	*N* species in 10-m SASs	Total *N* species	*N* endemic species (%)	Plant cover (%)	Shannon index	Fisher's alpha
Rwenzori Mountains										
RWE1	4570	21.0°								
North			1	1	2	3	2 (66.7)	2.0	0	N/A
East			0	1	1	1	1 (100)	0	0	N/A
South			0	0	2	2	2 (100)	0	0	N/A
West			0	0	2	2	1 (50)	0	0	N/A
All aspects combined			1	2	3	3	2 (66.7)	2.0	0	N/A
RWE2	4306	24.5°								
North			1	4	5	5	2 (40)	25.5	0	N/A
East			2	2	2	2	2 (100)	5.3	0.49	0.54
South			2	4	3	4	2 (50)	15.0	0.36	0.4
West			2	3	3	3	2 (66.7)	17.3	0.65	0.4
All aspects combined			2	5	5	6	2 (33.3)	15.8	0.55	N/A
RWE3	4115	16.0°								
North			8	15	20	21	8 (38.1)	79.8	1.03	1.32
East			4	7	13	15	7 (46.7)	37.3	1.08	0.76
South			8	8	12	12	6 (50)	45.5	1.13	0.95
West			8	15	13	17	7 (41.2)	74.0	1.18	1.05
All aspects combined			13	19	23	25	10 (40)	59.1	1.40	1.76
RWE4	3980	19.5°								
North			7	7	9	10	7 (70)	80.5	1.50	1.05
East			5	7	11	11	8 (72.7)	40.3	1.52	0.98
South			3	4	8	9	6 (33.3)	23.3	0.87	0.67
West			5	8	8	10	7 (70)	86.3	1.07	0.83
All aspects combined			8	11	14	15	9 (60)	59.9	1.66	1.22
Mount Elgon										
ELG1	4299	14.5°								
North			11	15	13	19	9 (47.4)	29.8	1.53	2.68
East			5	11	19	19	9 (47.4)	22.5	0.66	1.29
South			5	17	18	20	10 (50)	36.3	0.74	1.05
West			4	15	19	20	8 (40)	40.0	1.12	0.78
All aspects combined			13	21	25	27	11 (40.7)	32.7	1.80	2.31
ELG2	4201	17.0°								
North			13	24	23	26	10 (38.5)	75.8	1.07	1.99
East			9	20	24	29	11 (37.9)	25.0	1.93	2.83
South			10	20	24	27	9 (33.3)	84.0	1.52	1.98
West			14	20	21	25	9 (36.0)	87.0	1.64	2.68
All aspects combined			20	29	31	35	13 (37.1)	70.8	1.80	3.11

Table 1 (continued)

Summits	Elevation (m asl)	Average slope	*N* species in 1-m^2 quadrats	*N* species in 5-m SASs	*N* species in 10-m SASs	Total *N* species	*N* endemic species (%)	Plant cover (%)	Shannon index	Fisher's alpha
ELG3	4143	10.3°								
North			12	23	20	27	9 (33.3)	23.6	1.84	3.65
East			10	24	24	30	11 (36.7)	52.3	1.77	2.18
South			4	14	19	23	9 (39.1)	97.5	0.10	0.44
West			11	18	17	24	8 (33.3)	45.9	0.99	1.71
All aspects combined			21	32	32	39	15 (38.4)	54.8	1.83	3.64
ELG4	3948	19.0°								
North			14	22	24	27	6 (22.2)	19.7	2.07	3.55
East			7	22	24	30	7 (23.3)	46.5	0.42	0.86
South			12	27	28	33	12 (36.4)	92.5	1.70	2.36
West			17	26	27	36	11 (30.6)	42.6	1.92	4.33
All aspects combined			27	36	37	42	14 (33.3)	50.9	2.39	5.04
Total for Rwenzori Mountains			17	25	24	26	10 (38.5)	43.7	1.77	2.20
Total for Mount Elgon			38	45	43	47	15 (31.9)	52.4	2.42	6.13

The summits in Rwenzori are RWE1 = the summit near Elena Hut, RWE2 = the summit near Scott Elliot Pass, RWE3 = the summit dominated by *Dendrosenecio*, *Helichrysum* and *Lobelia* and RWE4 = the summit dominated by *Erica* spp. In Elgon, the summits are ELG1 = summit within the immediate vicinity of Wagagai peak, ELG2 = the second highest summit near Wagagai peak, ELG3 = summit located on the upper side of Jackson's Pool and ELG4 = summit within the immediate vicinity of Jackson's Pool

vascular species, belonging to 21 genera and 15 families. Of these species 10 (39%) are endemic. Across the four Elgon GLORIA summits we recorded 47 vascular plant species, belonging to 33 genera and 19 families. Of these species 15 (32%) are endemic. In Rwenzori, only two species *Dendrosenecio adnivalis* and *Helichrysum stuhlmannii* occurred on all four summits, while 16 species, mainly shrubs and forbs, such as *Hypericum bequaertii*, *Lobelia wollastonii* and *Galium ruwenzoriense*, were restricted to the two lowest elevation summits (Table 2). In Elgon, 24 species including *Dendrosenecio elgonensis*, *Deschampsia cespitosa* and *Agrostis quinqueseta* occurred on all four summits, while 11 species that included *Erica arborea*, *Galium ossirwaense* and *Kniphofia thomsonii* were restricted to the two lowest elevation summits. Both mountain regions shared five species, including *Afrosciadium kerstenii*, *Arabis pterosperma* and *Deschampsia cespitosa* (Table 2). Lower elevation summits on both mountains had higher species richness, Shannon and Fisher's diversity indices and vascular plant cover values compared to higher elevation summits (Table 1). In contrast, non-vascular vegetation cover (bryophyte and lichen) increased from the lower to the higher sites. We confirmed negative and highly significant correlations between vascular plant species richness and elevation in Rwenzori ($\tau = -0.56$, $n = 16$, $P = 0.006$) and Elgon (Kendall's rank correlation, $\tau = -0.67$, $n = 16$, $P = 0.001$) and between vascular plant cover and elevation in Rwenzori ($\tau = -0.75$, $n = 16$, $P < 0.001$). Other relationships, including Fisher's alpha versus elevation, species richness versus slope and vascular plant cover versus slope on each mountain, were not significant (Fig. 2).

The vast majority of vascular plants encountered in the two mountains were identified to family (66 of 67), genus (66 of 67) and species (63 of 67); the family of just one voucher specimen remained unknown (Table 2). Of the 15 families recorded in Rwenzori, Asteraceae dominated with about a quarter (6 of 26) of the species, followed by Poaceae (5 of 26), Rosaceae (2 of 26) and Brassicaceae (2 of the 26 species recorded, see S2 Appendix). Asteraceae also dominated in Elgon, representing about two fifths (19 of 47) of the species recorded (S2 Appendix). Poaceae, Apiaceae and Rosaceae (each represented by 3 of 47 species) were the other well-represented families in Elgon. Just under three quarters of the families recorded in Rwenzori (11 of 15) and just under two-thirds of the families in Elgon (12 of 19) were represented by a single species (S2 Appendix).

In Rwenzori the highest summit had a high proportion of bare soil and rock (average of all samples was 36%), and this was much lower on the next highest summit (17%) and on the two lower summits (9% and 13% for RWE3 and RWE4, respectively) (S3 Appendix). On the other hand, the higher elevation sites had the greatest non-vascular plant cover (bryophytes and lichens) of 58% and 65% for RWE1 and

RWE2, respectively, compared to the lower sites (13% and 29% for RWE3 and RWE4, respectively). Graminoids and forbs were the two most dominant vascular plant life forms in terms of number of species recorded in Rwenzori, while forbs and shrubs formed the two most dominant groups in Elgon (S4 Appendix). Caulescent rosettes of *Dendrosenecio adnivalis* in Rwenzori and *Dendrosenecio elgonensis* and *Lobelia gregoriana* in Elgon reached larger sizes and occurred at lower and higher elevations (Table 2). Out of 26 species, 21 genera and 15 families recorded in Rwenzori, only two species, two genera and two families were shared across all four summits. In Elgon, 23 of 47 species, 15 of 32 genera and 10 of 19 families were shared across all four summits (Table 2; S5 Appendix). The two lower elevation summits in Rwenzori and Elgon (RWE3 versus RWE4 and ELG3 versus ELG4) shared 14 and 36 species, respectively, while the two higher elevation summits (RWE1 versus RWE2 and ELG1 versus ELG2) shared three species: *Dendrosenecio adnivalis*, *Deschampsia flexuosa* and *Helichrysum stuhlmannii* and 25 species, respectively. The lowest and highest elevation summits in Rwenzori (RWE1 versus RWE4) spanned 590 m and shared two species, i.e., *Dendrosenecio adnivalis* and *Helichrysum stuhlmannii,* while the equivalent pair of summits in Elgon (ELG1 versus ELG4) spanned 351 m but shared 25 species (Table 2; S5 Appendix).

Non-metric multidimensional scaling (NMDS) indicated that Elgon summits were more similar to each other in ordination space compared to Rwenzori summits, suggesting again that the observed floristic dissimilarity may be explained by elevation (Fig. 3). Unsurprisingly given the high levels of endemism, when we compared summits that are most similar in elevation, we found that few species were shared (maximum was 7% of the combined total between RWE3 and ELG3), though greater similarity emerged at the genus and family levels (S6 Appendix). The summits in Elgon consistently displayed a higher number of vascular plant species and endemics compared to the summits in Rwenzori (for all vascular species: ELG1 versus RWE2; Mann Whitney test, $W=16$, $P=0.028$; ELG3 versus RWE3; $W=16$, $P=0.029$; ELG4 versus RWE4; $W=16$, $P=0.029$; for endemics: ELG1 versus RWE2; $W=16$, $P=0.020$; ELG3 versus RWE3; $W=15.5$, $P=0.040$; ELG4 versus RWE4; $W=10.56$, $P=0.552$; see Table 1).

Discussion

This study provides baseline data for monitoring the distribution of vascular plant species in the first GLORIA target regions in Africa. As climate warming continues to accelerate and glaciers recede rapidly (Taylor et al. 2009; Chala et al. 2016; Brochmann et al. 2022), plant species are likely to shift their ranges.

Species richness and vascular plant cover were negatively correlated with elevation (Table 1; Fig. 2), indicating the effects of decreasing temperature, dispersal capabilities and areal extent of the mountains on establishment and persistence of plants (Cuesta et al. 2017; Körner and Hiltbrunner 2021). High elevation summits, particularly the two summits above 4300 m in Rwenzori, typically contained few vascular plant species ($n \leq 6$ species, see Table 1). This suggests that with a few exceptions, including *Dendrosenecio adnivalis* (Asteraceae), *Deschampsia flexuosa* (Poaceae) and *Helichrysum stuhlmannii* (Asteraceae), most vascular plants on the two high summits probably reach their limits at or close to these elevations, where plants have to cope with lower air and soil temperatures and heavier night frosts (Hedberg 1964; Wesche 2003). On Rwenzori, in addition, steepness and the limited availability of substrate at higher elevations could be important. Range-restricted taxa, such as *Anthoxanthum nivale* and giant rosette plants, including *Dendrosenecio* and *Lobelia* spp. recorded here, could be at a high risk of extinction following the ongoing climate change which is increasingly becoming evident in East Africa's high mountain regions as indicated by glaciers which continue to recede rapidly (Taylor et al. 2009; Chala et al. 2016; Brochmann et al. 2022). Continued monitoring is needed to determine how the expected changes in climate will impact high elevation taxa, many of which are range restricted and vulnerable.

Our data show that graminoids and forbs were the dominant vascular plant life forms in terms of number of species recorded in Rwenzori, while forbs and shrubs were dominant in Elgon (Table 2 and S4 Appendix). The tall caulescent rosettes of *Dendrosenecio* spp., were a remarkable and dominant feature of the landscape in the two mountains occurring at lower and higher elevations (Table 2). Giant rosette plants such as *Dendrosenecio* and *Lobelia* spp. tend to maintain a layer of insulating old leaves that acts as a defence against frost (as the ground freezes nightly) and fire and herbivory (noted at the lowest summits in Rwenzori and across the summits in Elgon), while graminoids such as *Carex runssoroensis*, *Carpha eminii* and *Festuca abyssinica* grow as dense tussocks, which insulate the youngest leaves in the central part of the tussock (Hedberg 1964; Beck et al. 1982; Smith and Young 1987; Wesche 2000; Struhsaker 2020). In addition, graminoids may employ supercooling, a mechanism by which plants slow cooling and thus limit ice growth, to withstand recurrent night frosts (Sakai and Larcher 1987).

Total vascular plant species richness in the Elgon target region (47 species) was nearly twice that in Rwenzori (26 species) but much lower than those recorded at GLORIA summits in Europe, Australia and South America. A total

Table 2 Mean percentage cover of species recorded in 1-m^2 quadrats on each GLORIA summit in Rwenzori and Elgon

Species	Family	Life form	Rwenzori Mountains				Mount Elgon			
			RWE1	RWE2	RWE3	RWE4	ELG1	ELG2	ELG3	ELG4
**Afrosciadium kerstenii* (Engl.) P.J.D.Winter	Apiaceae	Forb[2,4]	0	0	0†	0	0	0†	0†	0.1
Haplosciadium abyssinicum Hochst	Apiaceae	Forb[1,2,3,4]	0	0	0	0	0	0	0†	0
Heracleum elgonense (H. Wolff) Bullock	Apiaceae	Forb[2,3,4]	0	0	0	0	0.4	0†	1.2	0.2
Asplenium aethiopicum (Burm. f.) Becher	Aspleniaceae	Fern[2,3,4]	0	0	0	0	0	0†	0†	0.1
Asplenium sp. in UG-RWE	Aspleniaceae	Fern	0	0	0	0†	0	0	0	0
Artemisia afra Jacq. ex Willd	Asteraceae	Shrub[2,4]	0	0	0	0	0	0	0	0†
Carduus chamaecephalus (Vatke) Oliv. and Hiern	Asteraceae	Forb[3]	0	0	0	0	0†	0.2	0	0†
**Carduus keniensis* R.E. Fries	Asteraceae	Forb[2,4]	0	0	0	0	0†	0†	0†	0†
Cineraria deltoidea Sond	Asteraceae	Forb[2,3,4]	0	0	0	0	0.5	0†	0.4	0.3
Conyza subscaposa O. Hoffm	Asteraceae	Forb[1,2]	0	0	0	0	0	4.7	1.8	0.7
***Dendrosenecio adnivalis* (Stapf) E.B.Knox**	Asteraceae	Shrub/caulescent rosette[1]	0†	3.0	0.2	0†	0	0	0	0
***Dendrosenecio elgonensis* (T.C.E.Fr.) E.B.Knox**	Asteraceae	Shrub/caulescent rosette[4]	0	0	0	0	3.2	0†	0†	0†
Haplocarpha rueppellii (Sch. Bip.) K. Lewin	Asteraceae	Forb[1,2,3,4]	0	0	0	0	0	0†	0†	0.1
***Helichrysum amblyphyllum* Mattf**	Asteraceae	Shrub[1,4]	0	0	0	0	0.7	0.1	0.5	2.3
Helichrysum citrispinum Delile	Asteraceae	Shrub[1,2,3,4]	0	0	0	0	0†	0.1	3.2	1.6
Helichrysum cymosum (L.) D. Don ex G. Don	Asteraceae	Shrub[1]	0	0	0	0	0†	5.9	2.4	0.5
Helichrysum formosissimum Sch.Bip	Asteraceae	Shrub[2,4]	0	0	0	0	0.4	0†	0†	0.4
Helichrysum forskahlii (J.F.Gmel.) Hilliard and B.L.Burtt	Asteraceae	Shrub[2,4]	0	0	0	0	0†	0†	0†	2.3
**Helichrysum newii* Oliv. and Hiern	Asteraceae	Shrub[1,2,4]	0	0	0	0	0.1	0†	0.6	0.8
Helichrysum odoratissimum (L.) Sweet	Asteraceae	Shrub[2]	0	0	0	0	0	0	0†	0†
**Helichrysum stuhlmannii* O.Hoffm	Asteraceae	Shrub[1]	0†	9.6	29.3	15.2	0	0	0	0
**Senecio jacksonii* S. Moore	Asteraceae	Forb[2,4]	0	0	0	0	2.8	0†	0.1	1.0
***Senecio mattirolii* Chiov**	Asteraceae	Forb	0	0	0.5	0†	0	0	0	0
***Senecio rhammatophyllus* Mattf**	Asteraceae	Shrub[4]	0	0	0	0	0	0.1	0†	0
***Senecio snowdenii* J. Hutch**	Asteraceae	Forb[4]	0	0	0	0	0†	1.3	0†	0.1
Senecio sp. in UG-RWE	Asteraceae	Unknown	0	0	0†	0†	0	0	0	0
**Stoebe kilimandscharica* O. Hoffm	Asteraceae	Shrub/Tree[1]	0	0	0	0	0	0	0†	0†
Arabis pterosperma Edgew	Brassicaceae	Forb	0	0	0†	0	0†	0	0†	0
Cardamine africana L	Brassicaceae	Forb[2,4]	0	0	0.1	0	0	0	0	0
***Lobelia gregoriana* Baker f**	Campanulaceae	Shrub/caulescent rosette[1,2,4]	0	0	0	0	0.1	0†	0†	0†
***Lobelia lindblomii* Mildbr**	Campanulaceae	Forb [1,2,4]	0	0	0	0	0†	0†	0.1	0†
**Lobelia wollastonii* Baker.f	Campanulaceae	Shrub/caulescent rosette[1]	0	0	10.7	4.1	0	0	0	0
Cerastium afromontanum T.C.E. Fries and Weimarck	Caryophyllaceae	Forb[2,3,4]	0	0	0	0	0	0.3	0.3	0†
Cerastium octandrum Hochst. ex A. Rich	Caryophyllaceae	Forb[3,4]	0	0	0†	0	0	0	0	0
Sagina abyssinica Hochst. ex A.Rich	Caryophyllaceae	Forb[2,3,4]	0	0	0	0	0	0†	1.2	0.3
Tillaea schimperi (Fisch. and C.A. Mey.) M.G. Gilbert, H. Ohba and K.T. Fu	Crassulaceae	Forb[2]	0	0	0	0	0†	0.1	0.3	0.8

Table 2 (continued)

Species	Family	Life form	Rwenzori Mountains				Mount Elgon			
			RWE1	RWE2	RWE3	RWE4	ELG1	ELG2	ELG3	ELG4
**Carex runssoroensis* K. Schum	Cyperaceae	Graminoid[1,4]	0	0	5.2	7.8	0	0	0†	0†
Polystichum sinense (Christ) Christ	Dryopteridaceae	Fern[4]	0	0	0†	0	0	0	0	0
Erica arborea L	Ericaceae	Shrub/Tree[2,3,4]	0	0	0	0	0	0	0†	5.1
**Erica kingaensis* Engl	Ericaceae	Shrub/Tree	0	0	0†	19.4	0	0	0	0
Erica trimera (Engl.) Beentje	Ericaceae	Shrub/Tree[3,4]	0	0	0	0	0	0	0	0†
Trifolium acaule Steud. ex A.Rich	Fabaceae	Forb[3,4]	0	0	0	0	0	2.0	0	0
**Swertia subnivalis* T.C.E.Fr	Gentianaceae	Forb[1,4]	0	0	0	0	0.3	0.4	0†	0.1
**Hypericum bequaertii* De Wild	Hypericaceae	Shrub/Tree[1]	0	0	0†	0.4	0	0	0	0
Luzula abyssinica Parl	Juncaceae	Graminoid[1,2,4]	0	0	0	0	0†	1.1	0.8	1.8
Phlegmariurus saururus (Lam.) B. Øllg	Lycopodiaceae	Fern[1,2]	0	0†	0†	0	0	0	0	0
Bartsia decurva Hochst. ex Benth	Orobanchaceae	Shrub[1,3]	0	0	0	0	0†	0†	0.2	0†
Agrostis quinqueseta (Steud.) C.E. Hubb	Poaceae	Graminoid[3,4]	0	0	0	0	0†	0†	0†	0†
Agrostis sp. in UG-RWE	Poaceae	Graminoid[2]	0	0	0†	0	0	0	0	0
Anthoxanthum nivale K. Schum	Poaceae	Graminoid[1,2,4]	0	0	0.1	0	0	0	0	0
Deschampsia cespitosa (L.) P. Beauv	Poaceae	Graminoid[1,2,3,4]	0	0	0†	1.4	10.6	27.3	12.1	9.8
Deschampsia flexuosa (L.) Trin	Poaceae	Graminoid[1,2,3]	0.1	0†	0.1	0	2.4	6.9	0	0
Koeleria capensis (Steud.) Nees	Poaceae	Graminoid[1,2,3,4]	0	0	0	0	0†	0†	5.4	10.7
Pentameris borussica (K. Schum.) Galley and H.P. Linder	Poaceae	Graminoid[2,3,4]	0	0	3.3	2.7	0	0	0	0
Pentameris pictigluma (Steud.) Galley and H.P. Linder	Poaceae	Graminoid[2,3,4]	0	0	8.1	0	0	0	0	0
Melpomene flabelliformis (Poir) A.R.Sm. and R.C. Moran	Polypodiaceae	Fern[2,4]	0	0†	0†	0	0	0	0	0
Alchemilla abyssinica Fresen	Rosaceae	Forb[2,3,4]	0	0†	0†	0†	0	0	0	0
**Alchemilla argyrophylla* Oliv	Rosaceae	Shrub[2,4]	0	0	0†	3.8	0	0	0	0
**Alchemilla elgonensis* Mildbr	Rosaceae	Shrub[2,4]	0	0	0	0	4.6	11.6	24.1	0.1
Alchemilla ellenbeckii Engl	Rosaceae	Forb[2,4]	0	0	0	0	0	0	0	3.8
Alchemilla volkensii Engl	Rosaceae	Forb[4]	0	0	0	0	0	0.6	0.1	0†
Galium ossirwaense K. Krause	Rubiaceae	Climber[2,4]	0	0	0	0	0	0	0.3	0.1
**Galium ruwenzoriense* (Cortesi) Chiov	Rubiaceae	Climber[1,2,4]	0	0	0.1	0†	0	0	0	0
Hebenstretia dentata L	Scrophulariaceae	Shrub[1,3,4]	0	0	0	0	0	0	0	0.6
Unknown sp. in UG-ELG	Unknown	Unknown	0	0	0	0	0†	0.3	0†	0†
**Valeriana kilimandscharica* Engl	Valerianaceae	Shrub[4]	0	0	0	0	0†	0.3	0†	0†
Kniphofia thomsonii Baker	Xanthorrhoeaceae	Forb[2,4]	0	0	0	0	0	0	0	1.3

Percentage cover was calculated from the pointing hits tallied in each of the 16 1-m^2 quadrats surveyed per summit. Species and family names follow the CJB African plant Database (www.africanplantdatabase.ch). Species that are endemic to the high East African mountains are denoted with asterisks (*) and narrowly range restricted endemics highlighted in bold (see also S7 Appendix). "0" indicates that the species was not found on a summit, while "0†" indicates that the species was not hit by pointing within 1-m^2 quadrats but was found by subsequent exploration and pointing within the SASs (see Pauli et al. 2015). The species are ordered by family followed by genus and species. The superscripts indicate references used: 1 = Hedberg (1964), 2 = Kipkoech et al. (2020), 3 = Kidane (2022) and 4 = Rono et al. (2023)

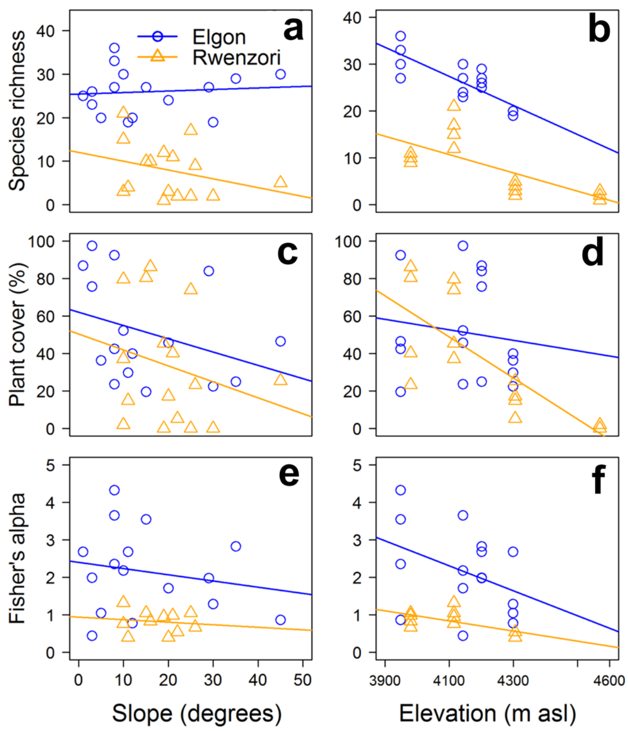

Fig. 2 Vascular plant species richness (**a**, **b**), cover (**c**, **d**) and Fisher's alpha (**e**, **f**) versus topographic variables across four GLORIA summits in each mountain. The data points represent values calculated for each aspect at the summit scale. Tested relationships are as follows: species richness versus elevation; in Rwenzori, Kendall's rank correlation, $\tau = -0.56$, $n = 16$, $P = 0.006$; in Elgon, $\tau = -0.67$, $n = 16$, $P = 0.001$; species richness versus slope; in Rwenzori, $\tau = -0.23$, $n = 16$, $P = 0.236$; in Elgon, $\tau = 0.07$, $n = 16$, $P = 0.716$; vascular plant cover versus elevation; in Rwenzori, $\tau = -0.75$, $n = 16$, $P < 0.001$; in Elgon, $\tau = -0.14$, $n = 16$, $P = 0.455$; vascular plant cover versus slope; in Rwenzori, $\tau = -0.19$, $n = 16$, $P = 0.317$; in Elgon, $\tau = -0.31$, $n = 16$, $P = 0.103$; Fisher's alpha versus elevation; in Rwenzori, $\tau = -0.41$, $n = 16$, $P = 0.112$; in Elgon, $\tau = -0.27$, $n = 16$, $P = 0.175$; Fisher's alpha versus slope; in Rwenzori, $\tau = -0.07$, $n = 16$, $P = 0.753$; in Elgon, $\tau = -0.09$, $n = 16$, $P = 0.618$

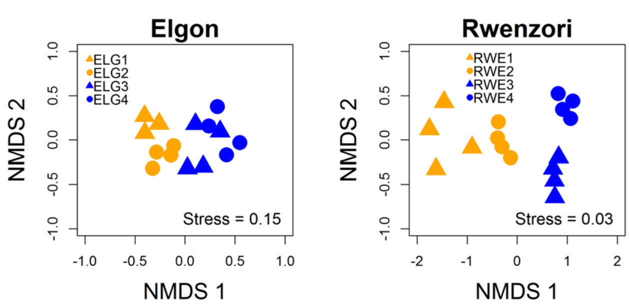

Fig. 3 Ordination plots for the vascular plants recorded at each set of GLORIA summits in Rwenzori and Elgon along two non-metric multidimensional scaling axes based on Bray–Curtis dissimilarities (Bray and Curtis 1957). Species abundance data for summit area sections in each of the four aspects were $\log_{10}(x+1)$ transformed to minimise the influence of the most abundant species. Summit area sections located closer to each other in the figure indicate higher levels of floristic similarity

of 140 species were recorded in the Central Alps (Erschbamer et al. 2010), 116 species in the Central Caucasus (Erschbamer et al. 2010), 91 species on Mount Clarke in the Australian Alps (Verrall et al. 2021), 139 species in Cumbres Calchaquíes, Tucumán, Argentina (Carilla et al. 2018) and 175 species in Sierra de Famatina, Argentina (Muscicante et al. 2015). The lower species richness at our summits likely reflects the small areas above the climatic treeline involved in this "archipelago of isolated mountain tops" that comprises the Afroalpine flora with about 370 species in 140 genera (Hedberg 1969). The relatively richer flora in Elgon may be explained by the greater geological age of this mountain, and thus more time for plants to accumulate and differentiate, as well as its more central location and presence of hot springs which likely provided refugia during past glaciations, and by the more extensive glacial advances over the higher Rwenzori range (Hedberg 1992; Taylor et al. 2009; Gehrke and Linder 2014). Finally, Elgon's gentle slope and lower elevations (e.g., the highest summit on Elgon is 270 m lower and thus not as close to the limits of plant life as the one on Rwenzori, see Table 1) likely enabled the establishment of a richer vascular plant community.

Similar to observations in high elevation sites in the Andes and western Himalayas (Cuesta et al. 2017; Carilla et al. 2018; Chandra et al. 2018), just a few plant families dominate the summits in Rwenzori and Elgon (S2 Appendix). In our study, Asteraceae and Poaceae accounted for more than two fifths of the vascular plant species in Rwenzori and Elgon (S2 Appendix).

The marked floristic dissimilarity observed between the lowest and highest summits in Rwenzori and Elgon (Table 1; Fig. 3) reflects the limited elevational ranges of many species. Many authors have observed that plant species which colonise tropical alpine habitats are predominantly bird- and wind-dispersed species that can cross topographic barriers (e.g.,Hedberg 1964; Chala et al. 2017; Tovar et al. 2020). After arriving on high summits (effectively insular areas), some species subsequently tend to evolve towards a loss of such dispersal capability, as a means to ensure seeds are retained within the adapted ecological area (Carlquist 1974; Tovar et al. 2020). The upper limits of these species tend to be determined by physical factors (such as temperature, frost or period of freezing) and their lower limits by interspecific competition (Sheil 2016). As climate warms, plant species are expected to move upslope to zones with a colder bioclimate. Especially cold-adapted species and endemic species may experience range contractions. However, our understanding of which species are moving upslope and what they require for dispersal is limited. Subsequent resurveys will determine if range shifts, which have been observed elsewhere (Gigauri et al. 2016; Carilla et al. 2018), are occurring in the Afroalpine region.

Conclusion

We have described the patterns of diversity and distribution of vascular plants from the baseline survey conducted in the first GLORIA target regions on the African continent. We hope to revisit these summits once per decade and evaluate changes over time, which may involve losses or additions of certain species (see Klanderud and Birks 2003; Wipf et al. 2013). Additional studies directly related to GLORIA target regions, particularly in regard to arthropods, amphibians, and land use changes, should also be conducted if the necessary funds and support become available.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00035-023-00301-9.

Acknowledgements This project was the result of close collaboration among researchers and managers at the Institute of Tropical Forest Conservation (ITFC), Uganda Wildlife Authority (UWA), Wildlife Conservation Society (WCS), The Nature Conservancy (TNC), Universidad Nacional de Chilecito (UNdeC), Universidad Nacional de Córdoba (UNC) and local community representatives and elders. We wish to thank the John D. and Catherine T. MacArthur foundation (grant number 93424 to WCS) for funding a two-phase project during which local researchers were trained in survey methods and subsequently tasked with conducting fieldwork. The field team are all greatly thanked for their enthusiasm and dedication: Robert Barigyira, Badru Mugerwa, Fredrick Ssali, Ben Kirunda, Abel Basikania, Erick Mulewa, Alfred Masereka, Joseph Wasike, James Matanda, Patrick Muzaale, Alex B. Salim, Francis Musobo, Mike Mazune, Stephan Halloy, Anton Seimon and Mariana Musicante. Douglas Sheil and Miriam van Heist supervised the study. We thank the editors and reviewers for improving the quality of the manuscript.

Author contributions FS, BM, MvH, DS, BK, MM, AS and SH planned and developed the study. FS wrote the first draft; BM, MvH, DS, MM, AS, SH reviewed and edited the manuscript. All authors read and approved the final manuscript.

Funding The authors would like to thank the John D. and Catherine T. MacArthur foundation for funding this work.

Availability of data and materials Data available from a central GLORIA database (www.gloria.ac.at).

Declarations

Conflict of interest The authors declare no potential conflict of interest with respect to the research, authorship and/or publication of this article.

References

Beck E, Senser M, Scheibe R, Steiger H, Pongratz P (1982) Frost avoidance and freezing tolerance in Afroalpine “giant rosette” plants. Plant, Cell Environ 5:215–222

Bray J, Curtis J (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol Monogr 27:325–349

Brochmann C, Gizaw A, Chala D, Kandziora M, Eilu G, Popp M, Pirie MD, Gehrke B (2022) History and evolution of the afroalpine flora: in the footsteps of Olov Hedberg. Alp Bot 132:65–87

Butynski TM, Kalina J (1993) Three new mountain national parks for Uganda. Oryx 27(4):214–224

Carilla J, Halloy S, Cuello S, Grau A, Malizia A, Cuesta F (2018) Vegetation trends over eleven years on mountain summits in NW Argentina. Ecol Evol 8(23):11554–11567

Carlquist S (1974) Island biology. Columbia University Press, New York

Chala D, Brochmann C, Psomas A, Ehrich D, Gizaw A, Masao CA, Bakkestuen V, Zimmermann NE (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

Chala D, Zimmermann NE, Brochmann C, Bakkestuen V (2017) Migration corridors for alpine plants among the ‘sky islands’ of eastern Africa: do they, or did they exist? Alp Bot 127:133–144

Chandra S, Singh A, Singh CP, Nautiyal MC, Rawat LS (2018) Vascular plants distribution in relation to topography and environmental variables in alpine zone of Kedarnath Wild Life Sanctuary, West Himalaya, India. J Mt Sci 15(9):1936–1949

Cuesta F, Muriel P, Llambi LD, Halloy SRP, Aguirre N, Beck S, Carilla J, Meneses RI, Cuello S, Grau A, Gamez LE, Irazabal J, Jacome J, Jaramillo R, Ramirez L, Samaniego N, Suarez-Duque D, Thompson N, Tupayachi A, Vinas P, Yager K, Becerra MT, Pauli H, Gosling WD (2017) Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. Ecography 40(12):1381–1394

Cuesta F, Carilla J, Lambí LD, Muriel P, Lencinas MV, Meneses RI, Feeley KJ, Pauli H, Aguirre N, Beck S, Bernardi A, Cuello S, Duchicela SA, Eguiguren P, Gamez LE, Halloy S, Hudson L, Jaramillo R, Peri PL, Tovar C (2023) Compositional shifts of alpine plant communities across the high Andes. Glob Ecol Biogeogr 00:1–16. https://doi.org/10.1111/geb.13721

Dangles O, Rabatel A, Kraemer M, Zeballos G, Soruco A, Jacobsen D, Anthelme F (2017) Ecosystem sentinels for climate change? Evidence of wetland cover changes over the last 30 years in the tropical Andes. PLoS ONE 12:e0175814

Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Change Biol 17:990–996

Eggermont H, Russell JM, Schettler G, van Damme K, Bessems I, Verschuren D (2007) Physical and chemical limnology of alpine lakes and pools in the Rwenzori Mountains (Uganda–DR Congo). Hydrobiologia 592:151–173

Erschbamer B, Mallaun M, Unterluggauer P, Abdaladze O, Akhalkatsi M, Nakhutsrishvili G (2010) Plant diversity along altitudinal gradients in the Central Alps (South Tyrol, Italy) and in the Central Greater Caucasus (Kazbegi region, Georgia). Tuexenia 30:11–29

Gehrke B, Linder HP (2014) Species richness, endemism and species composition in the tropical Afroalpine flora. Alp Bot 124:165–177

Gigauri K, Akhalkatsi M, Abdaladze O, Nakhutsrishvili G (2016) Alpine plant distribution and thermic vegetation indicator on Gloria summits in the Central Greater Caucasus. Pak J Bot 48:1893–1902

Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barancok P, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, Kazakis G, Krajci J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A, Theurillat, J.- P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. and Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. Nat Clim Chang 2:111–115

Grabherr G, Gottfried M, Pauli H (2001) Long-term monitoring of mountain peaks in the Alps. In: Burga CA, Kratochwil A (eds) Biomonitoring: General and applied aspects on regional and global scales. Tasks for vegetation science, vol 35. Kluwer, pp 153–177

Hantemirov RM, Corona C, Guillet S, Shiyatov SG, Stoffel M, Osborn TJ, Melvin TM, Gorlanova LA, Kukarskih VV, Surkov AY, von Arx G, Fonti P (2022) Current Siberian heating is unprecedented during the past seven millennia. Nat Commun 13:4968

Hedberg O (1964) Features of afroalpine plant ecology. Acta Phytogeographica Suecica 49:1–144

Hedberg O (1969) Evolution and speciation in a tropical mountain flora. Biol J Linn Soc 1:135–148

Hedberg O (1992) Afroalpine vegetation compared to páramo: convergent adaptations and divergent differentiation. Páramo: an Andean ecosystem under human influence. Academic Press, London, UK, pp 15–29

Howard PC (1991) Nature conservation in Uganda's tropical forest reserves. IUCN, Gland, Switzerland

Karner GD, Byamungu BR, Ebinger CJ, Kampunzu AB, Mukasa RK, Nyakaana J, Rubondo ENT, Upcott NM (2000) Distribution of crustal extension and regional basin architecture of the Albertine rift systems, East Africa. Mar Pet Geol 17:1131–1150

Kaser G, Noggler B (1991) Observations of Speke glacier, Ruwenzori range, Uganda. J Glaciol 37:313–318

Kidane YO (2022) Vegetation diversity and distribution along the Bale mountains Afroalpine hotspot of biodiversity in the face of a fast-changing world. PhD. thesis, University of Bayreuth, Bayreuth (Germany)

Kipkoech S, Melly DK, Muema BW, Wei N, Kamau P, Kirika PM, Wang QF, Hu GW (2020) An annotated checklist of the vascular plants of Aberdare Ranges Forest, a part of Eastern Afromontane Biodiversity Hotspot. PhytoKeys 149:1–88

Klanderud K, Birks HJB (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. The Holocene 13:1–6

Körner C, Hiltbrunner E (2021) Why is the alpine flora comparatively robust against climatic warming? Diversity 13:383

Lentini G, Cristofanelli P, Duchi R, Marinoni A, Verza G, Vuillermoz E, Toffolon R, Bonasoni P (2011) Mount Rwenzori (4750 m a.s.l., Uganda): meteorological characterization and air-mass transport analysis. Geogr Fis Din Quat 34:183–193

Linder HP, Gehrke B (2006) Common plants of the Rwenzori, particularly the upper zones. Institute for Systematic Botany, University of Zurich, Zurich

Lundberg J, McFarlane DA (2006) Speleogenesis of the Mount Elgon elephant caves, Kenya. Geol Soc America 404:51–63

Moret P, Aráuz MDLÁ, Gobbi M, Barragán Á (2016) Climate warming effects in the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. Insect Conserv Divers 9(4):342–350

Musicante M, Jausoro M, Cantón N, Rivera P, Montero L, Juri D, Videla M, Jaime G, Jayat P, Luna Toledo ES, Lobo R, Varela O, Halloy S (2015) Biological altitudinal transect in the Famatina Range, Argentina. Perth III: Mountains of our future earth, Perth, Scotland

Mwaura A, Oginah S (2018) Large mammals of Mount Elgon forest ecosystem. Biodiversity status report of Mount Elgon forest ecosystem, Kenya Forestry Research Institute (KEFRI)

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) Vegan: Community Ecology Package. R package version 2.5–7. https://CRAN.R-project.org/package=vegan

Osmaston HA (2006) Guide to the Rwenzori. The Rwenzori Trust (Ulverston)

Pauli H, Halloy S (2019) High mountain ecosystems under climate change. Oxford research encyclopedia of climate science. Oxford University Press, Oxford, pp 1–56

Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Benito Alonso JL, Coldea G, Dick J, Erschbamer B, Fernández Calzado R, Ghosn D, Holten JI, Kanka R, Kazakis G, Kollár J, Larsson P, Moiseev P, Moiseev D, Molau U, Molero Mesa J, Nagy L, Pelino G, Puşcaş M, Rossi G, Stanisci A, Syverhuset AO, Theurillat J-P, Tomaselli M, Unterluggauer P, Villar L, Vittoz P, Grabherr G (2012) Recent plant diversity changes on Europe's mountain summits. Science 336:353–355

Pauli H, Gottfried M, Lamprecht A, Niessner S, Rumpf S, Winkler M, Steinbauer K, Grabherr G (2015) The GLORIA field manual – standard multi-summit approach, supplementary methods and extra approaches, 5th edn. GLORIA-Coordination, Austrian Academy of Sciences and University of Natural Resources and Life Sciences, Vienna

Petursson JG, Vedeld P, Sassen M (2013) An institutional analysis of deforestation processes in protected areas: the case of the transboundary Mt. Elgon, Uganda and Kenya. Forest Policy Econ 26:22–33

Pickering CM, Hill W, Green K (2008) Vascular plant diversity and climate change in the alpine zone of the Snowy Mountains, Australia. Biodivers Conserv 17:1627–1644

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rono PC, Mutie FM, Kathambi V, Wei N, Watuma BM, Nanjala C, Wagutu GK, Kirika PM, Malombe I, Hu GW, Wang QF (2023) An annotated plant checklist of the transboundary volcanic Mt Elgon, East Africa. PhytoKeys 223:1–174

Sakai A, Larcher W (1987) Frost survival of plants. Responses and adaptation to freezing stress. In: Billings WD, Golley F, Lange OL, Olson JS, Remmert H (eds) Ecological studies, vol 62. Springer, Berlin

Scoon RN (2017) Geotraveller 30: geology of Mount Elgon, Uganda and Kenya. Geobulletin 60:47–53

Scott P (1998) From conflict to collaboration: people and forests at Mount Elgon, Uganda. IUCN, Gland, Switzerland and Cambridge UK

Seimon TA, Seimon A, Yager K, Reider K, Delgado A, Sowell P, Tupayachi A, Konecky B, McAloose D, Halloy S (2017) Long-term monitoring of tropical alpine habitat change, Andean anurans, and chytrid fungus in the Cordillera Vilcanota, Peru: results from a decade of study. Ecol Evol 7(5):1527–1540

Sheil D (2016) Disturbance and distributions. Ecol Soc 21(1):10

Smith AP, Young TP (1987) Tropical alpine plant ecology. Annu Rev Ecol Syst 18:137–158

Ssali F, Halloy S, Seimon A, Musicante M (2011) Monitoring climate change impacts on biodiversity: training and establishment of the first GLORIA sites in Africa on Rwenzori mountains and Mount Elgon, Uganda. ITFC report, Kabale, Uganda

Steinbauer MJ, Grytnes J-A, Jurasinski G, Kulonen A, Lenoir J, Pauli H, Rixen C, Winkler M, Bardy-Durchhalter M, Barni E, Bjorkman AD, Breiner FT, Burg S, Czortek P, Dawes MA, Delimat A, Dullinger S, Erschbamer B, Felde VA, Fernandez-Arberas O, Fossheim KF, Gomez-Garcia D, Georges D, Grindrud ET, Haider S, Haugum SV, Henriksen H, Herreros MJ, Jaroszewicz B, Jaroszynska F, Kanka R, Kapfer J, Klanderud K, Kuhn I, Lamprecht A, Matteodo M, di Cella UM, Normand S, Odland A, Olsen SL, Palacio S, Petey M, Piscova V, Sedlakova B, Steinbauer K, Stöckli V, Svenning J-C, Teppa G, Theurillat J-P, Vittoz P, Woodin SJ, Zimmermann NE, Wipf S (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. Nature 556(7700):231–234. https://doi.org/10.1038/s41586-018-0005-6

Struhsaker TT (2020) Growth rates in the giant rosette plants *Dendrosenecio adnivalis* and *Lobelia wollastonii* on the Ruwenzori mountains, Uganda. J East Afr Nat Hist 109(2):59–68

Taylor RG, Mileham LJ, Tindimugaya C, Majugu A, Muwanga A, Nakileza N (2006) Recent recession in the Rwenzori Mountains of East Africa due to rising air temperature. Geophys Res Lett 33:L10402

Taylor RG, Mileham L, Tindimugaya C, Mwebembezi L (2009) Recent glacial recession and its impact on alpine riverflow in the Rwenzori Mountains of Uganda. J Afr Earth Sc 55:205–213

Tovar C, Melcher I, Kusumoto B, Cuesta F, Cleef A, Meneses RI, Halloy S, Llambi LD, Beck S, Muriel P, Jaramillo R, Jacome J, Carilla J (2020) Plant dispersal strategies of high tropical alpine communities across the Andes. J Ecol 108:1910–1922

UNESCO and IUCN (2020) Reactive monitoring mission report to Rwenzori Mountains National Park World Heritage property, Uganda. Paris, France and Gland, Switzerland: UNESCO World Heritage Centre and IUCN

Valencia JB, Mesa J, León JG, Madriñán S, Cortés AJ (2020) Climate vulnerability assessment of the *Espeletia* complex on Páramo sky islands in the northern Andes. Front Ecol Evol 8:565708

van Heist M (1994) Land unit map of Mount Elgon National Park. Mount Elgon Conservation and Development Project, Mbale, Uganda

Verrall B, Green K, Pickering CM (2021) Dynamics in plant diversity and composition on Australian alpine summits over time. Biodivers Conserv 30:1855–1880

Wesche K (2000) The high-altitude environment of Mt. Elgon (Uganda, Kenya): climate, vegetation, and the impact of fire. Ecotropical monographs 2. Society of Tropical Ecology, Bonn, Germany, p 253

Wesche K (2003) The importance of occasional droughts for afroalpine landscape ecology. J Trop Ecol 19:197–208

Wipf S, Stöckli V, Herz K, Rixen C (2013) The oldest monitoring site of the Alps revisited: accelerated increase in plant species richness on Piz Linard summit since 1835. Plant Ecolog Divers 6:447–455