


Varied plant species' responses to climate and environmental change on Mount Kenya after 40 years

Timothy A. Downing¹  | Daniel O. Olago¹ | Tobias O. Nyumba² | Mary M. Peacock³ | Truman P. Young⁴

¹Department of Earth and Climate Sciences, University of Nairobi, Nairobi, Kenya

²Department of Environment and Geography, University of York, York, UK

³Department of Biology, University of Nevada, Reno, Nevada, USA

⁴Department of Plant Sciences, University of California, Davis, California, USA

Correspondence

Timothy A. Downing, Department of Earth and Climate Sciences, University of Nairobi, Nairobi, Kenya.

Email: tarmdowning@gmail.com

Abstract

Tropical alpine areas are some of the most vulnerable areas in the world to climate change. Their plant communities have narrow thermal niches and have limited geographic areas to expand. Here we examine changes in plant species' abundance and distribution in the Teleki Valley (3900–4500 m asl) of Mount Kenya using a spatially explicit vegetation survey from 1980. Vascular plant species were re-sampled in 35 plots across the valley, and additional size and density data were collected for the two *Dendrosenecio* species. Overall species richness and diversity were lower in 2021 than in 1980, and the abundance of dominant species had declined. Changes in elevation suggested both upward and downward shifts had occurred. *Dendrosenecio keniodendron* exhibited a shift towards the valley bottom as well as a change in population structure towards younger individuals. The dominant environmental factors affecting plant composition were similar in both 1980 and 2021, namely elevation, vegetation cover and the presence of *D. keniodendron*. This keystone species plays a significant role in shaping communities but is undergoing rapid demographic changes, which may have cascading implications on the ecology of the system.

KEYWORDS

climate change, demography, species range shifts, temporal change, topographical niche, tropical alpine

Resume

Les zones alpines tropicales sont parmi les plus vulnérables du monde au changement climatique. Leurs communautés végétales ont des niches thermiques étroites et ont des zones géographiques limitées pour s'étendre. Nous examinons ici les changements dans l'abondance et la distribution des espèces végétales dans la vallée de Teleki (3900–4500 m asl) du Mont Kenya en utilisant une étude de la végétation spatialement explicite datant de 1980. Les espèces de plantes vasculaires ont été ré-échantillonnées dans 35 parcelles de la vallée, et des données supplémentaires sur la taille et la densité ont été recueillies pour les deux espèces de *Dendrosenecio*. La richesse et la diversité globales des espèces étaient plus faibles en 2021 qu'en 1980, et l'abondance des espèces dominantes avait diminué. Les changements d'altitude suggèrent que des déplacements vers le haut et vers le bas se sont produits. *Dendrosenecio keniodendron*

a montré un déplacement vers le fond de la vallée ainsi qu'un changement dans la structure de la population vers des individus plus jeunes. Les principaux facteurs environnementaux influençant la composition végétale étaient similaires en 1980 et en 2021, notamment l'altitude, la couverture végétale et la présence de *D. keniodendron*. Cette espèce clé joue un rôle important dans la formation des communautés, mais elle subit des changements démographiques rapides qui peuvent avoir des conséquences en cascade sur l'écologie du système.

1 | INTRODUCTION

Tropical alpine areas are home to a distinctive assemblage of plant species uniquely adapted to the climatic conditions of high elevation in the tropics. These areas are characterised by extreme diurnal temperature variations, but low seasonal temperature variations (Hedberg, 1964; Smith & Young, 1987). A variety of specialised plant growth forms have evolved across the globe, through convergent evolution, to deal with these unique conditions (Hedberg, 1964; Hedberg & Hedberg, 1979).

Climate change is of particular concern for species in these areas, given their specific thermal niches (Cuesta et al., 2020) and because the absolute level of warming in tropical alpine areas is expected to be greater than in surrounding lower elevation areas (Anthelme et al., 2014; Bradley et al., 2006; Nogués-Bravo et al., 2007). Because of their evolution under more seasonally constant air temperatures, these plants are likely to be sensitive to relatively small changes in mean air temperature, rainfall and radiation (Buytaert et al., 2011; Chala et al., 2016; Germino, 2014). Hypotheses for responses of alpine species worldwide to climate change include both upslope movement (in response to warming) (Lenoir et al., 2008; Walther et al., 2005) and downslope movement (in response to drying) (Crimmins et al., 2011; Lenoir et al., 2010), as well as adapting in-situ (Buytaert et al., 2011), local extirpation (Holt, 1990; Thuiller et al., 2005) and even tolerance/stability (Callaghan et al., 2022).

The rapid nature of the current global climate change is expected to lead to many instances of local extinction, as species may not have the genetic variation or mobility necessary for rapid evolution or responsive movement under climate change (Schierenbeck, 2017). Certain intrinsic factors may make a species more prone to extinction, including large body size, long life span, slow growth, few reproductive events, isolated or fragmented communities and narrow ecological niche (Isaac & Williams, 2007). Many plant species found in tropical alpine areas exhibit these life history and habitat characteristics. Some plant species may be able to shift geographic range within a few generations, though this will be limited by dispersal, edaphic and geological factors. Generation shifts, however, may require centuries for long-lived plants (Feeley et al., 2012; Lenoir & Svenning, 2015). Current temperature projections suggest a need for upward elevation shifts by 140–800m for many species over the next century in order to maintain similar climatic ranges

(Buytaert et al., 2011). On the other hand, the steep topographical gradients in these environments can create thermal refugia, allowing certain species to survive in situ (Ackerly et al., 2020; Buytaert et al., 2011). This topographic diversity can also create micro-refugia of genetic diversity, in a sense pre-adapting these populations to climate change (De Kort et al., 2020).

How plant species interact with each other further complicates the response to climate change. Responses to climate change will be muted if species ranges are determined by biotic, rather than climatic conditions. Facilitation can expand a species' realised niche but competition can reduce it (Hupp, 2016). Finally, climate changes go beyond temperature changes, to include changes in precipitation (Buytaert et al., 2006, 2011; Huss et al., 2017), soil nutrients (Buytaert et al., 2011; Körner, 2021), and even atmospheric carbon dioxide itself, which can stimulate plant growth (Körner, 2005; Shugart, 2005). Acting in concert, these can result in varying and often contradicting responses to climate change, or even little or no response (Callaghan et al., 2022).

There are few historical data sets with which to investigate climate change impacts on tropical alpine plant communities. Such studies that do exist are largely from the South American tropical alpine ecosystems and usually cover only a decade or so, durations that are not adequate to document climate-related changes in these environments (Carilla et al., 2018; Kuo et al., 2021; Sarmiento et al., 2003; Wahren et al., 2013). Other authors use time-for-space substitution to infer vegetation changes over time (Zimmer et al., 2018), but this method has limitations due to multiple confounding variables. In general, long-term ecological research in tropical alpine plant communities is needed in order to make realistic climate change predictions (Buytaert et al., 2011; Llambí & Rada, 2019). This has led to the development of the GLORIA (Global Observation Research Initiative in Alpine Environments) program, which is an attempt to formalise long-term monitoring in alpine regions globally (Pauli et al., 2005). However, this program still has a notable lack of coverage in Africa (see Figure 12 in Grabherr et al., 2010).

Fortunately, the Teleki Valley on Mount Kenya does offer an example of an afro-tropical alpine ecosystem that has valuable historical data. It has long been a base for explorers and researchers interested in exploring and documenting this magnificent World Heritage site (Arthur, 1921; Hedberg, 1964; Mackinder, 1900; Mahoney, 1980; Mizuno, 2005; Rehder et al., 1988; Young & Peacock, 1992). One such study, conducted in 1979–1980 (Young &

Peacock, 1992), quantitatively surveyed the plant communities in the valley, through a series of transects across elevation and landform. This survey included a focus on the characteristic giant rosettes—the *Dendrosenecios*. The Young & Peacock data set (originals in the possession of M. Peacock) provides a unique baseline data set for comparison with contemporary survey data to assess the impacts of climate change in these remote areas. The goal of the current study was to resurvey the original transect plots to document potential changes in abundance, distribution, diversity and elevation shifts of plant communities over the past 40 years (1980 vs. 2021).

2 | MATERIALS AND METHODS

2.1 | Study area

Mount Kenya is the tallest mountain in Kenya and the second tallest in Africa, with a peak elevation of 5199 m.asl. It is located in central Kenya astride the equator and provides vital ecosystem services for much of Kenya. These services include precipitation capture, water regulation, biodiversity retention and carbon storage (Buytaert et al., 2011), causing it to be designated a World Heritage natural site in 1997 (van den Akker, 2016). Mt. Kenya is an extinct volcano that last erupted 2–3 million years ago (Bhatt, 1991), and its geology comprises basalts and pyroclastics (Baker, 1967). The soils are volcanic derivatives, largely andosols, as well as peat soils in the upper valley bottoms formed under cold temperatures (Speck, 1982).

The Teleki Valley, on the west side of Mount Kenya, is the headwaters of the Naro Moru River, a tributary of the Ewaso Ngiro. It is oriented East–West, and the upper U-shaped (glacial) part of the valley extends from around 3900 m to 4500 m above sea level. The climate is typical of tropical alpine climates, characterised by ‘winter every night, summer every day’ (Hedberg, 1964). A freeze–thaw cycle occurs on a daily basis; air temperatures drop below freezing virtually every night at elevations above 4000 m, but then warm up rapidly to 15°C or more during the day (Beck et al., 1981; Coe, 1967; Young & Robe, 1986). Vegetation is characterised by tussock grasses, rosette plants and shrubs, similar to tropical alpine areas around the world, although most species found here are endemic to Mount Kenya and the neighbouring East African mountains (Hedberg, 1964).

2.2 | Climate data

Climate trends from 1980 to 2021 were investigated using the TerraClimate reanalysis data set (Abatzoglou et al., 2018). This data set has a temporal and spatial coverage and resolution that is informative for this study (1958 to present at a monthly time-step and a spatial footprint of ~18 km²). Monthly precipitation and mean temperatures were obtained for the Teleki Valley (10 km²) and plotted as a time series. Trends were assessed with the Mann–Kendall trend test (Kendall, 1975).

2.3 | Vegetation and study species

The vegetation of Mount Kenya was mapped in 1979–1986 by Rehder et al. (1988), who distinguished several plant community types. The dominant species used to characterise vegetation types for the upper alpine zone were *Dendrosenecio keniensis* (formerly *D. brassica*), *Dendrosenecio keniodendron*, *Lobelia deckenii* subsp. *keniensis* (formerly *L. keniensis*, *Lobelia telekii*, *Erica trimera* (formerly *Philippia keniensis*) and *Alchemilla argyrophylla* (Rehder et al., 1988). Of these, the two most distinct species are *D. keniensis* and *D. keniodendron* (Beck, 1986; Smith & Young, 1994). The two species are closely related, yet in growth form very distinct: *D. keniensis* has a low stature, growing along the ground with largely buried stems, and a rosette like a cabbage plant, hence the original name (*brassica*). *Dendrosenecio keniodendron* also has stems terminating in large rosettes but can grow up to 5 m tall with up to several dichotomous branches. *Dendrosenecio keniensis* dominates in the valley bottoms and lower elevations, whereas *D. keniodendron* dominates in the upper slopes and ridges (Beck, 1986; Smith & Young, 1994; Tusiime et al., 2020). While the exact ecological niches of these two species are imperfectly understood, the valley bottom-dwelling *D. keniensis* community is associated with poorly drained soils, higher atmospheric humidity and lower temperature fluctuations compared to *D. keniodendron* inhabiting the ridges and slopes (Beck et al., 1981).

Dendrosenecio keniodendron is the dominant arborescent species in the area and occurs in dense stands, many of which appear to be even-aged (Smith & Young, 1982). These stands enable *D. keniodendron* to act as a habitat modifier, facilitating other species to grow underneath while sometimes excluding others. The understory of *D. keniodendron* stands can be dominated by shrubs (*Alchemilla* spp.) or grasses (*Festuca* spp.) and there may be a cyclical pattern of succession between these two, driven perhaps by fire at the lower elevations and by senescence of single-aged stands at the higher elevations (Rehder et al., 1988; Young & Peacock, 1992). Germination, growth and survival of *D. keniodendron* itself depend highly on the adequate cover—either rock talus or other species (Smith & Young, 1994).

2.4 | 1980 study

The 1980 vegetation survey (Young & Peacock, 1992) consisted of 45 plots located along six cross-valley transects (Figure 1). Each cross-valley transect was separated by 1 km, and within the first five, there were seven sampling plots based on topographic position (north ridge, north mid-slope, north valley bottom, streamside, south valley bottom, south mid-slope and south ridge). The last transect (furthest upslope) had 10 sampling plots because the river forks at the top, creating a different valley configuration. Each sampling plot was 30 m long and 20 m wide, running parallel to the ridge crest. Ten 1 m × 1 m quadrats were laid down at three-meter intervals along the centerline of the plot, in which the presence of each vascular

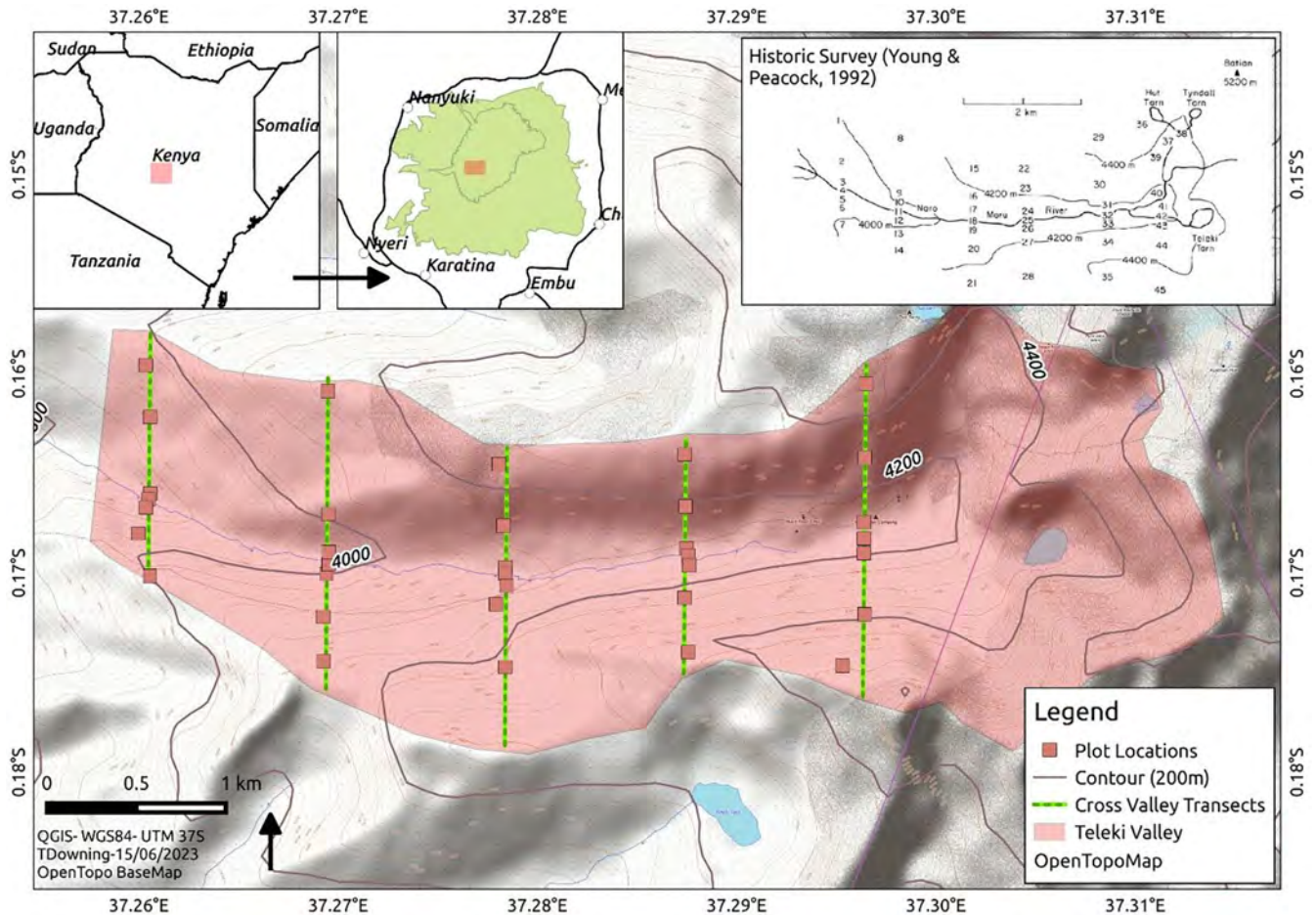


FIGURE 1 Study design in the Teleki Valley of Mount Kenya: locations of the cross valley transects and the plots (The 1980 survey layout is also included with permission from Young & Peacock, 1992).

species was recorded. The frequency for each species was calculated as the total proportion of quadrats containing that species. Environmental factors were also recorded for each plot, including average slope, aspect and per cent live vegetation cover. In addition, all *Dendrosenecio* individuals within 10m of the centerline of the plot were tallied. Within this 600 m² plot, each *D. keniensis* was tallied, and each *D. keniodendron* was tallied according to height class (in 0.5m intervals) and number of forks (Young & Peacock, 1992).

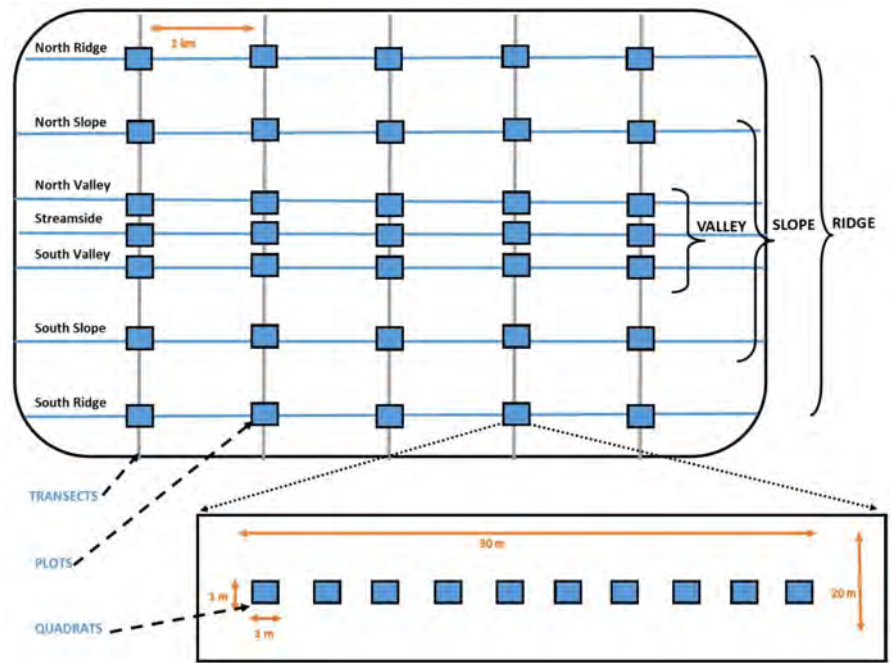
2.5 | 2021 data collection

The procedures from the 1980 study were repeated as closely as possible for the present study, with a few variations. The original survey was conducted before the days of GPS, and no permanent markers had been left in place, so it was not possible to revisit the exact locations. However, the locations were marked on a topographic map obtained from the authors, and using this map it was possible to roughly locate the original cross-valley transects (estimated to be within a 100 m). Ten plots were not resurveyed, being on the upper extremes of the valley where it forked, and had little to no vegetation. This left 35 (30m×20m) plots: 5 cross-valley transects × 7 topographic positions (Figures 1 and 2). The original data

set was similarly truncated for comparison. Consistently to the 1980 study, in each plot, the 1m x 1m quadrats were laid down at 3 m intervals, parallel to the ridge, in which the presence of each vascular species was recorded.

Slope, aspect, and elevation were recorded in the field, and then again in the office using a 90m Digital Elevation Model (DEM). Ground cover classifications recorded in the field were simplified to % rock/bare ground/detritus and % live vegetation. The giant senecios—*D. keniensis* and *D. keniodendron*—were tallied within the 600 m² plot counting each individual within 10m on either side of the centerline. An additional tally of standing dead *D. keniodendron* individuals was also recorded, to document mortality. Vascular species were tallied by quadrat as in the original study, but unfortunately, the grasses could not be confidently identified to species level in their mostly non-reproductive status at the time of the resurvey. Therefore, graminoids were excluded from both data sets. In addition, certain species could only be identified at the genus level both in 1980 and 2021. These included the genera of *Sedum*, *Wahlenbergia*, *Cerastium*, *Anemone* and *Erica*. There were several species that did not appear in the quadrats but were noted within the plots. As in the original study, these were given a 'presence' value of 0.5 (Nuzzo, 1996; Young & Peacock, 1992; Zorio et al., 2016). Taxonomic classification was done with the aid of the

FIGURE 2 Schematic layout of the sample design in the Teleki Valley of Mount Kenya.



Field Guide to Wild Plants of Africa: Mt. Kenya (Zhou et al., 2018) and with the assistance of the vegetative key put together from the original study (Young & Peacock, 1985).

2.6 | Data analysis

Resurvey of historical vegetation data can be challenging due to the difficulty in precisely locating the original study sites. However, stratification according to an underlying environmental gradient can provide an unbiased representation of vegetation that can be replicated (Kapfer et al., 2017; Lenoir et al., 2008). This study design was only stratified by elevation and topographic position, but carried out in close proximity to previous transects, making it possible to make generalised comparisons between the two time periods. Species richness—the total number of species—and diversity—assessed by Shannon's diversity index (Shannon & Weaver, 1948) and Simpson's diversity index (Simpson, 1949)—were calculated for the whole valley. Differences between time periods were assessed at the 95% confidence level by the Wilcoxon-signed rank test (Woolson, 2007). Changes in species dominance between the two periods were assessed by comparing the frequency (% of quadrats occupied out of 350) and constancy (% of plots occupied out of 35) of the main species. Following Zorio et al. (2016), only species with >15% constancy in the original study were compared in this way. Mean elevation for these species (weighted according to frequency) was calculated for both time periods, and the direction and magnitude of shifts in mean elevation were recorded.

The distribution of the most dominant species from both time periods (>30% constancy in each period) was also compared according to topographic position and elevation. Topographic positions were simplified to ridge (10 plots), mid-slope (10 plots) and valley bottom (15 plots—combining riverside with valley bottom plots). Elevations were similarly grouped in 200 m elevational increments:

3850–4050 m, 4050–4250 m and 4250–4450 m. Due to the incline of the valley, the lower elevation ridges were of a similar elevation as the higher elevation valley bottom. Differences between the two time periods were assessed at the 95% confidence level using the Wilcoxon-signed rank test. The additional density and population structure data collected for the two *Dendrosenecio* species allowed for a more detailed examination of these two species. Counts of individuals within the 600 m² plot were converted to standardised densities (counts/100m²) and compared by elevation and topographic position with the Wilcoxon signed rank test. Finally, a histogram of *D. keniodendron* height was compared for both periods using the Kolmogorov–Smirnov test (Massey, 1951).

Community composition and associated environmental factors were assessed with a Canonical Correspondence Analysis (CCA) and compared between the two data sets. Eight environmental variables were examined: altitude, mean slope, mean north–south aspect, mean east–west aspect, *D. keniodendron* density, *D. keniensis* density, mean *D. keniodendron* height and % live vegetation cover. The aspect was broken into a north–south component and an east–west component, scaled from 0 to 1, to make a linear scale more appropriate for ordination, as was done in the original study (Young & Peacock, 1992). Changes in community structure in multidimensional space were assessed using Bray–Curtis dissimilarity for paired plots, visualised in a Non-Metric Multidimensional Scaling (NMDS) plot of the data from both surveys (Zorio et al., 2016). Permutational Anova (PERMANOVA) was used to test if the two periods were distinct in multi-dimensional space (Anderson, 2005). The ecological importance of *D. keniodendron* was further assessed by testing the association between this species and the other most dominant species (>30% constancy in both time periods) using a chi-square test in both periods. Correlation between mean *D. keniodendron* height and the frequency of this species was also compared between the two periods. All graphics and statistical analysis were done using R software (R Core Team, 2021).

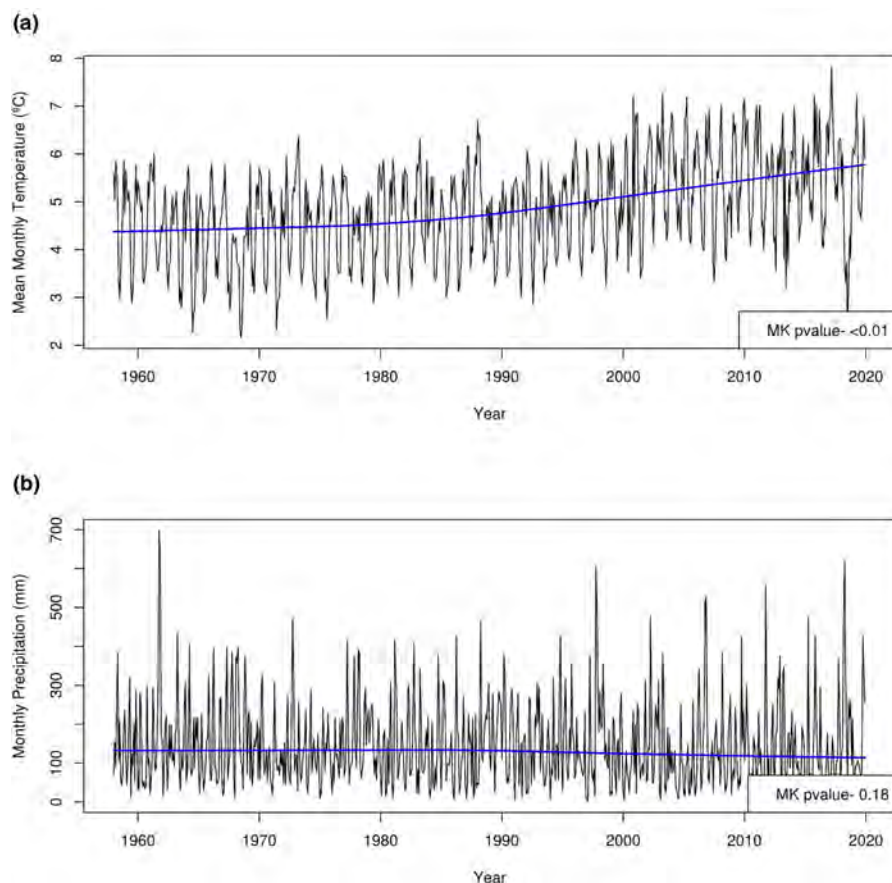


FIGURE 3 TerraClimate monthly data for (a) temperature and (b) precipitation data for Teleki Valley 1958–2020, with Lowess line showing trend pattern and Mann–Kendall p value.

3 | RESULTS

3.1 | Climate changes

Mean monthly temperature in the Teleki Valley (3900 m asl – 4500 m asl) varied from -3.3°C to 14.7°C , with a geographic mean of 4.8°C over the entire time series from 1958 to 2021. TerraClimate is known to have a positive elevation bias in the tropics (Abatzoglou et al., 2018; Hijmans et al., 2005), so the actual mean temperature is likely a little higher. The temperature increased across the whole valley since 1958 ($Z=10.74$, $p<0.01$) at a rate of roughly $0.24^{\circ}\text{C}/$ decade. Between the study surveys of 1980 and 2021, this increase amounts to $\sim 1.0^{\circ}\text{C}$. Monthly precipitation, on the other hand, did not show any trend since 1958 ($Z=-1.33$, $p=0.18$) (Figure 3). Mean monthly precipitation across the valley was 145 mm, with peak rainfall peaks in April and October. For temperature, on the other hand, there was little seasonal variation.

3.2 | Changes in species richness and diversity

A total of 33 vascular plant taxa were recorded in Teleki Valley in the 2021 survey, not including graminoids. By comparison, the 1980 study identified 45 species in the valley (56 including graminoids (Young & Peacock, 1992). There were no new species identified in 2021, but several species recorded in 1980 were not observed in 2021.

TABLE 1 Comparison of richness and diversity measures for the Teleki Valley between 1980 and 2021.

Parameter	Mean 1980	Mean 2021	Wilcoxon p value
Richness (species/site)	12.43	7.43	<0.01
Shannon diversity index	2.04	1.60	<0.01
Simpson diversity index	0.82	0.74	<0.01

These were *Cerastium* spp., *Subularia monticola*, *Cardamine obliqua*, *Oreophyton falcatum*, *Alchemilla cyclophylla* and *Geranium arabicum*. *Cerastium* spp. is notable as this taxon was identified in 73.5 quadrats (21%) in 1980, but not identified in any quadrat in 2021. There was a significant decrease in species richness and diversity across the whole valley from 1980 to 2021. Richness decreased from 12.4 species per plot to 7.4 ($W=1043$, $p<0.01$), Shannon's diversity index decreased from 2.04 to 1.60 ($W=983$, $p<0.01$), and Simpson's diversity index decreased from 0.82 to 0.74 ($W=963$, $p<0.01$) (Table 1).

3.3 | Changes in dominance

There was a decline in frequency (% of quadrats occupied out of 350) for most species from 1980 to 2021. Of the most constant species ($>15\%$ constancy in 1980), 18 declined in frequency, 3 had the same frequency and 5 increased in frequency (Table 2). More common

TABLE 2 Comparison of most abundant species in 1980 and 2021 (listed are species with >15% constancy in 1980 ordered by frequency in 1980).

Species	Life form ^a	Constancy (%) 1980	Mean frequency (%) 1980	Rank 1980	Mean elevation (m asl) 1980	Constancy (%) 2021	Mean frequency (%) 2021	Rank 2021	Mean elevation (m asl) 2021	Shift in elevation (m)	Change in frequency (%)
<i>Alchemilla johnstonii</i> Oliv.	Sclerophyllous shrub	86	71	1	4068	83	67	1	4079	11	-6
<i>Ranunculus oreophytus</i> Delle.	Acaulescent rosette	60	44	2	4061	46	14	6	4051	-10	-68
<i>Haplosciadium abyssinicum</i> Hochst.	Acaulescent rosette	51	26	3	4115	26	3	12	4111	-4	-88
<i>Haplocarpha rueppellii</i> K. Lewin	Acaulescent rosette	49	25	4	4029	51	31	2	4066	37	24
<i>Cerastium</i> spp. (<i>C. octandrum</i> Hochst.; <i>C. afromontanum</i> T.C.E.Fr.)	Cushion plant	69	21	4	4156	0	0	12	n/a	n/a	-100
<i>Luzula abyssinica</i> Parl.	Cushion plant	57	18	4	4052	11	1	12	4200	148	-94
<i>Alchemilla argyrophylla</i> Oliv.	Sclerophyllous shrub	51	18	4	4124	46	25	3	4198	74	39
<i>Dendrosenecio keniensis</i> (Baker f.) Mabb.	Giant rosette	57	17	4	4001	46	16	3	4004	3	-6
<i>Lobelia deckenii</i> subsp. <i>keniensis</i> (R.E.Fr. & T.C.E.Fr.) Mabb.	Giant rosette	66	16	4	4039	71	21	3	4084	45	31
<i>Lobelia telekii</i> Schweinf.	Giant rosette	69	14	10	4172	46	11	6	4216	44	-21
<i>Sagina afroalpina</i> Hedberg	Cushion plant	46	14	10	4122	17	3	12	4135	13	-79
<i>Dendrosenecio keniodendron</i> (R.E.Fr. & T.C.E.Fr.) B.Nord.	Giant rosette	94	12	10	4174	37	8	6	4203	29	-33
<i>Swertia</i> spp. (<i>S. volkensis</i> Gilg./ <i>crassiuscula</i> Gilg.)	Cushion plant	40	10	10	3991	17	4	12	3958	-33	-60
<i>Senecio keniophytum</i> R.E.Fr.	Sclerophyllous shrub	43	11	10	4261	3	<1	12	4500	239	-100

(Continues)

TABLE 2 (Continued)

Species	Life form ^a	Constancy (%) 1980	Mean frequency (%) 1980	Rank 1980	Mean elevation (m asl) 1980	Constancy (%) 2021	Mean frequency (%) 2021	Rank 2021	Mean elevation (m asl) 2021	Shift in elevation (m)	Change in frequency (%)
<i>Helichrysum brownnei</i> S. Moore	Sclerophyllous shrub	40	11	10	4045	43	11	6	4012	-33	0
<i>Galium glaciale</i> K. Krause	Cushion plant	46	9	10	4122	9	2	12	4000	-122	-78
<i>Carduus platyphyllus</i> R. E. Fr.	Acaulescent rosette	37	7	10	4235	31	4	12	4272	37	-43
<i>Romulea keniensis</i> Hedberg	Cushion plant	37	6	10	4114	20	5	12	4106	-8	-17
<i>Crepis dianthoseris</i> N. Kilian, Enke, Sileshi & Gemeinholzer	Acaulescent rosette	20	6	10	4191	9	1	12	4300	109	-83
<i>Valeriana kilimandscharica</i> Engl.	Cushion plant	17	6	10	4302	6	<1	12	4133	-169	-100
<i>Erica</i> spp. (<i>E. arborea</i> L./ <i>E. timera</i> (Engl.) Beentje)	Sclerophyllous shrub	20	5	10	3995	23	9	6	3975	-20	80
<i>Arabis alpina</i> Krock.	Cushion plant	23	5	23	4372	14	2	12	4313	-59	-60
<i>Senecio purtschelleri</i> Engl.	Sclerophyllous shrub	23	4	23	4288	26	4	12	4265	-23	0
<i>Helichrysum cymosum</i> D. Don	Sclerophyllous shrub	26	2	23	4100	17	5	6	4334	234	150
<i>Lycopodium saururus</i> Lam.	Sclerophyllous shrub	17	1	23	3986	20	1	12	4022	36	0
<i>Crassula granvikii</i> Mildbr.	Cushion plant	17	0	23	4107	0	0	12	n/a	n/a	-100

^aLife form as described by Hedberg (1964). Hedberg did not classify all species into one of these life forms, so some are just the closest approximation.

species that showed notable declines in frequency (decreasing by over 75% from 1985 to 2021) were *Haplosciadium abyssinicum*, *Luzula abyssinica*, *Sagina afroalpina*, *Galium glaciale*, *Senecio keniophytum*, *Crepis dianthoseris*, *Valeriana kilimandscharica* and *Crassula granvikii*. These species have similar morphologies, most of them being flat rosette or low-lying cushion plants (Hedberg, 1964). Species that showed notable increases in frequency (by >75%) were *Erica* spp. and *Helichrysum cymosum* (Table 2). In both surveys, *Alchemilla johnstonii* was the most abundant species, but the next two most frequent species in 1980—*Ranunculus oreophytus* and *H. abyssinicum*—ranked 6th and 12th, respectively, in frequency in 2021. The most frequent species in 2021 after *A. johnstonii* were *A. argyrophylla* and *Haplocarpha rueppellii*. *Dendrosenecio keniodendron* declined substantially in constancy (% of transects out of 35), but not overall frequency: constancy declined from 94% to 37%, but only a 12% to 8% decline in frequency (Table 2).

3.4 | Elevation and topographic position changes

Both upward and downward shifts were observed for plant species in Teleki Valley from 1980 to 2021. Of the 33 species recorded in 2021, 13 exhibited downward shifts (mean shift of -49m) and 17 upward shifts (mean of 77m). Three species were only incidentally observed at transect plots, but not found in any of the quadrats (*Limosella africana*, *Myostis keniensis*, *Montia fontana*). Of the most constant species in 1980 (>15% constancy), there were 10 species with downward shifts (mean of -48m) and 14 with upward shifts (mean of 76m). The species with the biggest change in mean elevation (> ±50m elevation change) were *Galium glaciale*, *Valeriana kilimandscharica* and *Arabis alpina* (downward); *Luzula abyssinica*, *Senecio keniophytum*, *Crepis dianthoseris*, *Helichrysum cymosum* and *A. argyrophylla* (upward) (Table 2).

TABLE 3 Comparison of most abundant species (>30% constancy) by elevation and topographic position in 1980 and 2021 (presented frequency % plots occupied out of 350).

Species	Year*	Ridge	Slope	Valley	3850–4050 m asl.	4050–4250 m asl.	4250–4450 m asl.
<i>Alchemilla johnstonii</i> Oliv.	1980	45	74	87	92	80	29
	2021	48	60	84	96	66	23
	<i>p</i> -value	1.00	0.41	0.58	0.31	0.12	0.56
<i>Alchemilla argyrophylla</i> Oliv.	1980	9	50	3	21	10	26
	2021	23	58	3	14	25	40
	<i>p</i> -value	0.54	0.79	1.00	0.30	0.38	0.24
<i>Carduus platyphyllus</i> R.E.Fr.	1980	15	5	4	1	7	18
	2021	9	4	1	0	5	9
	<i>p</i> -value	0.56	0.96	0.65	0.40	0.68	0.21
<i>Lobelia telekii</i> Schweinf.	1980	21	17	9	8	13	26
	2021	16	19	3	2	15	19
	<i>p</i> -value	0.35	0.91	0.29	0.05	0.98	0.36
<i>Lobelia deckenii</i> subsp. <i>keniensis</i> (R.E.Fr. & T.C.E.Fr.) Mabb.	1980	13	13	19	23	20	0
	2021	20	15	27	22	29	3
	<i>p</i> -value	0.18	0.97	0.35	0.93	0.46	0.12
<i>Dendrosenecio keniodendron</i> (R.E.Fr. & T.C.E.Fr.) B.Nord.	1980	13	13	10	7	11	19
	2021	5	9	10	1	12	11
	<i>p</i> -value	0.01	0.23	0.47	<0.01	0.71	0.26
<i>Dendrosenecio keniensis</i> (Baker f.) Mabb.	1980	5	4	33	31	13	0
	2021	9	5	28	40	7	0
	<i>p</i> -value	0.54	0.51	0.74	0.48	0.52	NA
<i>Haplocarpha rueppellii</i> K. Lewin	1980	11	8	46	40	26	0
	2021	13	8	59	48	33	0
	<i>p</i> -value	1.00	1.00	0.34	0.58	0.90	NA
<i>Helichrysum brownei</i> S. Moore	1980	5	4	19	13	15	1
	2021	10	5	15	27	3	3
	<i>p</i> -value	0.65	0.67	0.76	0.14	0.22	0.16
<i>Ranunculus oreophytus</i> Delile.	1980	40	11	69	54	58	9
	2021	1	5	28	22	14	0
	<i>p</i> -value	0.02	1.00	0.01	0.08	0.02	0.23

**p* value represents the Wilcoxon test for significant difference between the 2 years. Bold values show significance at the 95% confidence level.

Within the dominant species (species with >30% constancy in both periods), there were few major changes by elevation or topographic position over the 40 years. *Ranunculus oreophytus* declined everywhere, but more so at the mid-elevations ($W=164$, $p=0.02$), valleys ($W=179$, $p=0.01$) and ridges ($W=78$, $p=0.02$). *Dendrosenecio keniodendron* declined at the lower elevations ($W=132$, $p<0.01$) and ridges ($W=83$, $p=0.01$), and *L. telekii* declined at the lower elevations ($W=103$, $p=0.05$) from 1980 to 2021 (Table 3).

3.5 | *Dendrosenecio* densities by elevation and topographic position

The density counts of *Dendrosenecios* provided more detailed information than the quadrat data (frequency) alone could provide. Overall, the densities of the two *Dendrosenecio* species were not significantly different between 1980 and 2021 by either topographic position or elevation (Table 4; Figure 4). For *D. keniodendron*, however, there were indications of substantial changes, even if some were not statistically significant. There was a marked change in densities at the high elevations: in 1980, *D. keniodendron* density peaked

at 4400m and then declined to zero at 4500m. In 2021, however, densities reached a smaller peak at 4200m, with a gentler decline to zero after 4500m (Figure 4). Although the differences in *D. keniodendron* densities were not individually significant by topographic position, there was an overall shift from ridge to valley bottom that was highly significant ($\chi^2=64.86$, $p<0.001$) (Table 4).

3.6 | *Dendrosenecio keniodendron* age/size distributions

While densities of *D. keniodendron* changed only moderately, the overall size class distribution of stands across the valley was significantly different between the two periods ($D=0.45$, $p<0.01$) (Figure 5). Stands in 2021 were composed of much smaller (younger) individuals than in 1980. The frequency-size curves in 2021 reflect the classic inverse J-shaped curve (negative exponential) of an uneven age stand much more than in 1980, and this difference is most pronounced in the valley bottom (Figure 5). In 1980, 21% of individuals were of the smallest size class (<0.5m) in the valley, but by 2021, this was 88%. On the ridgetops, the change was much smaller:

TABLE 4 *Dendrosenecio keniensis* and *D. keniodendron* counts/density by topographic position and elevation groups in 1980 and 2021.

Topographic position	<i>D. keniensis</i> count (density #/100 m ²)			<i>D. keniodendron</i> (density #/100 m ²)		
	1980	2021	Wilcoxon p-value*	1980	2021	Wilcoxon p-value
Ridge	502 (8.37)	508 (8.47)	0.79	169 (2.82)	68 (1.13)	0.31
Slope	187 (3.12)	331 (5.52)	0.96	190 (3.17)	118 (1.97)	0.21
Valley	2007 (22.30)	1795 (19.94)	1	128 (1.42)	200 (2.22)	0.55
Elevation (m asl)						
3850–4050	1656 (27.60)	1991 (33.18)	0.52	56 (0.93)	28 (0.47)	0.36
4050–4250	1040 (9.63)	643 (5.95)	0.99	281 (2.60)	316(2.93)	0.85
4250–4450	0 (0)	0 (0)	n/a	150 (3.57)	42 (1.00)	0.25

*p-value is the Wilcoxon test for significant difference between the 2 years.

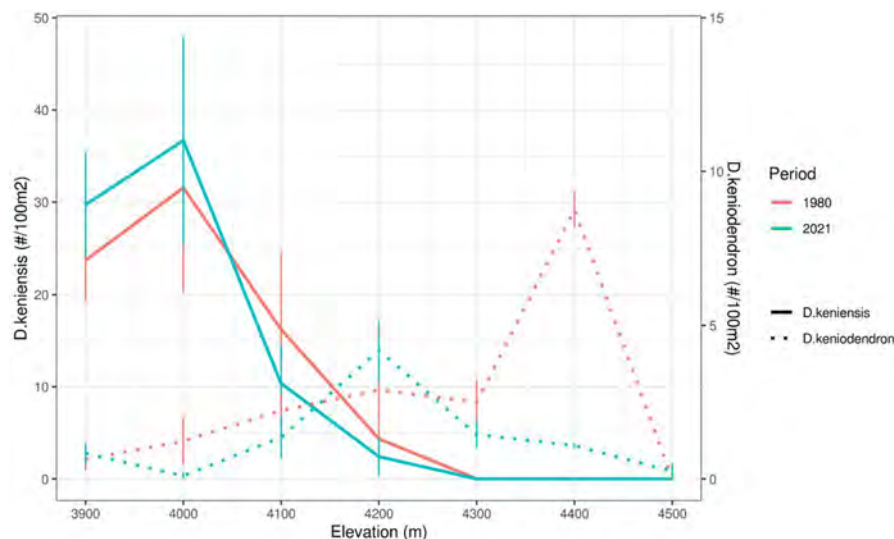


FIGURE 4 Densities of *Dendrosenecio keniensis* and *Dendrosenecio keniodendron* by elevation 1980 vs. 2021.

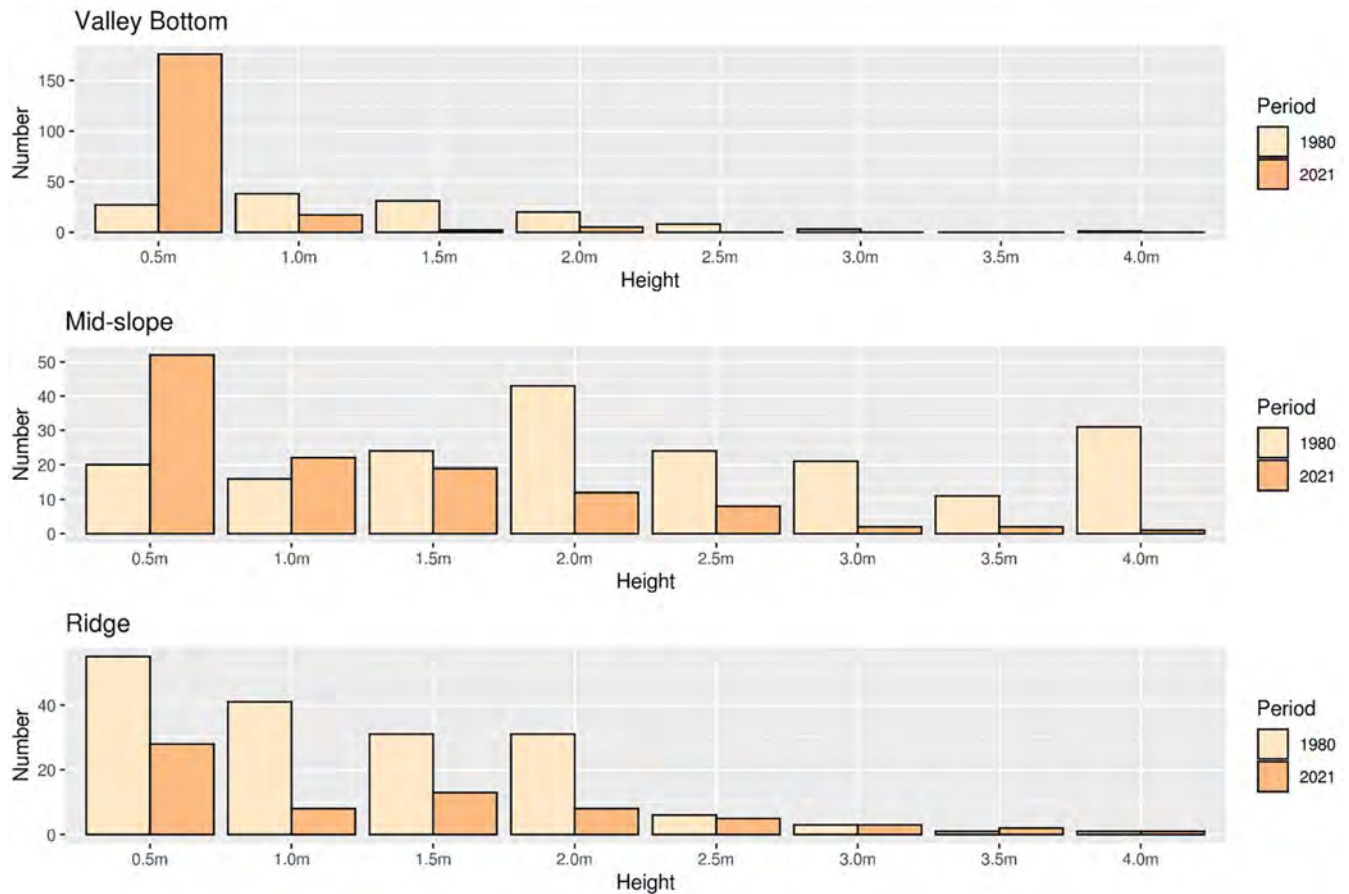


FIGURE 5 Number of *Dendrosenecio keniodendron* individuals by height class 1980 vs. 2021.

TABLE 5 Tally of live and dead *D. keniodendron* by height class-2021.

Height class (m)	Dead count	Live count
0.5	6	256
1	6	47
1.5	2	34
2	5	25
2.5	0	13
3	2	5
3.5	1	4
4	1	2
Total	23	386

32% were of the smallest size class in 1980 vs. 41% in 2021. Despite the decline in the frequency of large *D. keniodendron* individuals, relatively few standing dead were tallied in any of the size classes. Only 23 dead individuals were tallied out of a total of 409 individuals (5.6%), and most were in the younger size classes (Table 5).

Dendrosenecio keniodendron species grow in height continuously with age, and they fork after each reproductive episode (Beck et al., 1984; Smith & Young, 1982). Therefore, height can be used as a rough proxy for age, and number of forks corresponds to the number of reproduction events an individual has undergone. Over 80% of

the individuals tallied in 2021 had only one branch (no forks) compared to 60% in 1980, whereas just 10% had three or more branches compared to 24% in 1980.

3.7 | Environmental correlates of plant communities

A canonical correspondence analysis of the two data sets (comparing the 35 repeat plots) showed that in both years the first axis—explaining 40–45% of the variance—was equally correlated with elevation and live vegetation cover, a proxy for soil moisture (Table 6). The second axis most strongly correlated with slope in 1980, but *D. keniodendron* density in 2021. For the third axis, these results were flipped, being correlated with *D. keniodendron* density in 1980 and live vegetation cover (with slope a close second) in 2021 (Table 6). The NMDS of the combined data set showed the community structures of the two sampling periods were distinct (PERMANOVA $F = 5.3, p < 0.01$), but there was not a uniform shift across the valley: different plots shifted along different axes and in different directions. However, low-altitude ridges and high-altitude valleys did show a more or less consistent shift towards increasing live vegetation cover (soil moisture) and towards increasing *D. keniodendron* density/height (Figure 6).

Environmental factor	1980			2021		
	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3
Elevation	0.832*	0.450	0.255	0.791	0.324	0.198
Slope	0.261	-0.779	0.486	0.476	-0.206	-0.429
<i>D. keniensis</i> density	-0.579	-0.093	-0.140	-0.676	-0.337	0.129
EW Aspect	-0.003	-0.109	0.044	0.134	-0.411	0.126
NS Aspect	-0.058	0.140	0.128	-0.302	-0.096	-0.020
<i>D. keniodendron</i> density	0.298	0.169	0.609	0.198	0.812	-0.053
<i>D. keniodendron</i> height	0.141	-0.362	0.586	0.751	-0.012	-0.324
Live vegetation cover	-0.849	-0.260	0.369	-0.791	0.205	-0.548
Cumulative variance	39.6%	59.2%	73.3%	44.5%	61.7%	72.4%

*Bold values show the most correlated environmental factor for each axis of the CCA.

TABLE 6 Biplot scores for constraining variables in Canonical Correspondence Analysis for 1980 and 2021 (repeat plots only for 1980).

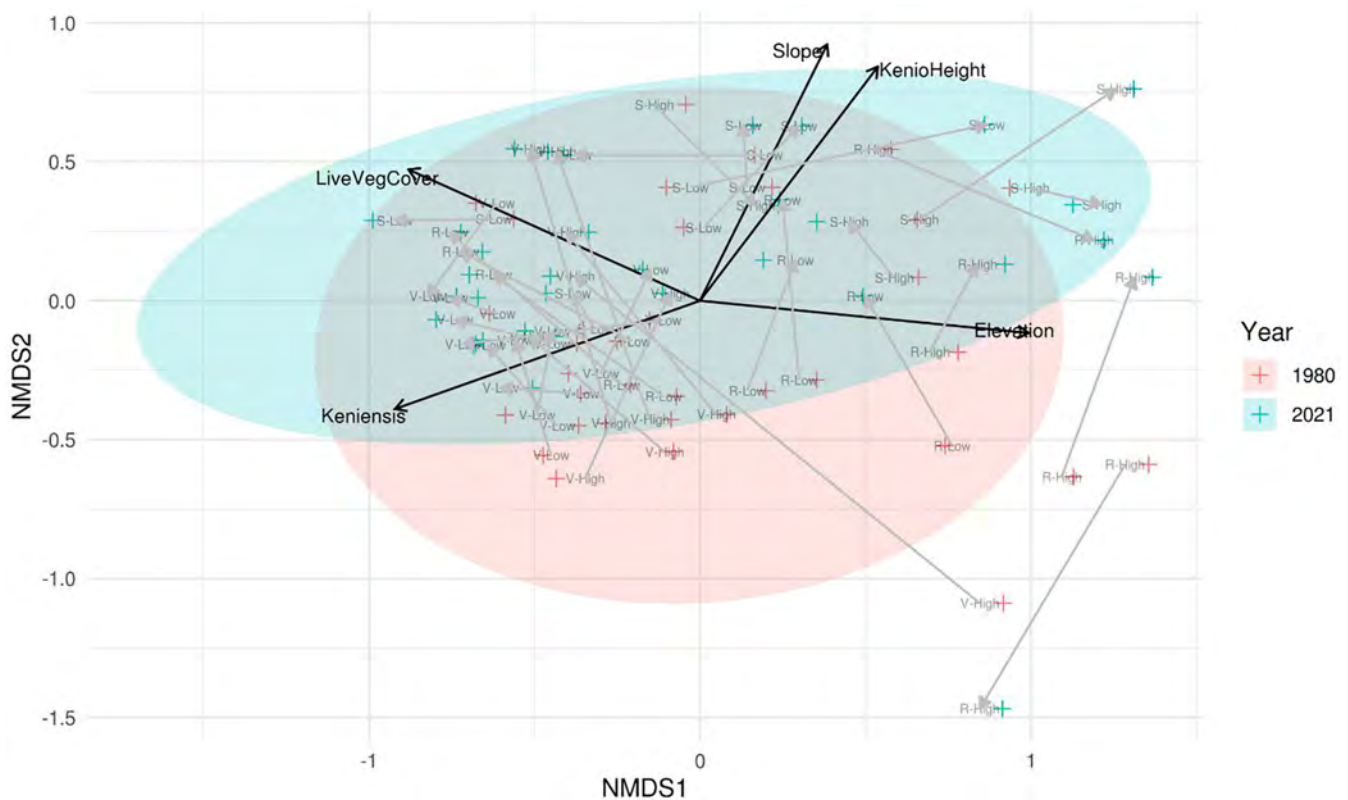


FIGURE 6 Non-metric multidimensional scaling (NMDS) plot of Bray-Curtis dissimilarity for paired plots for 1980 and 2021. Arrows show a shift for each site from 1980 to 2021 (V = valley, S = slope, R = ridge, low = low altitude, high = high altitude).

3.8 | Influence of *Dendrosenecio keniodendron* on plant communities

In 1980, *D. keniodendron*, most common on slopes, exhibited a clear niche differentiation (negative association) from the valley bottom species of *D. keniensis* ($\chi^2 = 5.55$, $p = 0.02$), and *L. deckenii* subsp. *keniensis* ($\chi^2 = 10.19$, $p < 0.01$) (Table 7). This differentiation was no longer significant in 2021 (*D. keniensis*, $\chi^2 = 1.86$, $p = 0.17$; *L. deckenii* subsp. *keniensis*, $\chi^2 = 0.05$, $p = 0.82$). Conversely, *Helichrysum browneii* was independent of *D. keniodendron* in 1980 ($\chi^2 = 1.79$, $p = 0.18$) but had a strong negative association in 2021 ($\chi^2 = 7.68$; $p = 0.01$) (Table 7). The 1980 study also documented an

interesting relationship between frequencies of *Alchemilla* spp. and *Helichrysum* spp. and mean *D. keniodendron* height. *Alchemilla* spp. frequency increased with stand height (age), whereas *Helichrysum* spp. decreased. In 2021, the same pattern was seen, although there were fewer taller (older) stands (Figure 7). In fact, most of the dominant species had a negative (or near zero) correlation with mean *D. keniodendron* height, except for *A. argyrophylla* and *L. teltekii* ($r = 0.45$ and $r = 0.26$, respectively) (Table 7). These correlations increased to $r = 0.60$ and $r = 0.53$, respectively, in 2021. Overall, there were stronger correlations—both positive and negative—in 2021 compared to 1980. Interestingly, *A. johnstonii* changed from a positive ($r = 0.23$) to a negative ($r = -0.42$) correlation from 1980

TABLE 7 Relationship of most abundant species with *D. keniodendron* in 1980 and 2021 (species with >50% constancy in 1980).

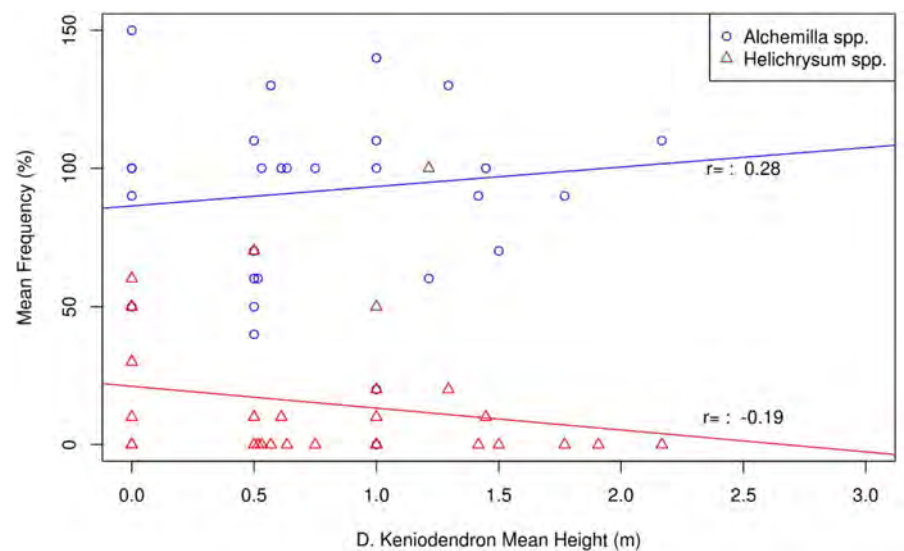
Species	Chi-squared test 1980 ^a	Chi-squared test 2021	Mean height correlation 1980 ^b	Mean height correlation 2021
<i>Alchemilla johnstonii</i>	0.08 ($p=0.78$)	1.30 ($p=0.25$)	0.23	-0.42
<i>Alchemilla argyrophylla</i>	0.57 ($p=0.45$)	1.86 ($p=0.17$)	0.45	0.6
<i>Carduus platyphyllus</i>	1.15 ($p=0.28$)	0.31 ($p=0.58$)	0.03	0.52
<i>Lobelia telekii</i>	2.45 ($p=0.11$)	0.33 ($p=0.57$)	0.26	0.53
<i>Lobelia deckenii</i> subsp. <i>keniensis</i>	10.19 ($p < 0.01$)	0.05 ($p=0.82$)	-0.09	-0.38
<i>Dendrosenecio keniensis</i>	5.55 ($p=0.02$)	1.86 ($p=0.17$)	-0.22	-0.59
<i>Haplocarpha rueppellii</i>	0.94 ($p=0.33$)	0.05 ($p=0.83$)	-0.15	-0.48
<i>Helichrysum brownei</i>	1.79 ($p=0.18$)	7.68 ($p=0.01$)	0.01	-0.34
<i>Ranunculus oreophytus</i>	0.01 ($p=0.92$)	0.02 ($p=0.89$)	-0.13	-0.29

Note: Bold values show significance at the 95% confidence level.

^aChi-square test of association between each species and *D. keniodendron* (presence/absence matrix).

^bCorrelation coefficient of frequency of each species with mean *D. keniodendron* height.

FIGURE 7 Mean frequencies of *Helichrysum* spp. and *Alchemilla* spp. by *Dendrosenecio keniodendron* height-2021. Frequencies sometimes exceed 100% as there are two species for each genus which often overlap.



to 2021, and *Helichrysum brownei* changed from no correlation ($r=0.01$) to a negative correlation ($r=-0.34$) (Table 7).

4 | DISCUSSION

4.1 | Climate changes in the Teleki Valley

Climate has changed in the Teleki Valley over the last 40 years. The two biggest changes expected from global climate change are temperature warming and changes in precipitation patterns (IPCC, 2018). While there is evidence from the Teleki Valley for the first—temperatures have increased by 0.24°C /decade—mean precipitation has been more or less stable over the past half century (Figure 3). The resolution of the TerraClimate reanalysis data set is too coarse (~18 km²) to reveal how these trends vary across the valley, but some inferences can be made based on geomorphology. Temperature varies by cover and aspect, but the biggest driver of

spatial variability is the lapse rate of temperature by elevation (Lute & Abatzoglou, 2021). Moisture, on the other hand, varies more according to topographic position: the valley bottom has the greatest soil moisture, and the upper slopes and ridges have the lowest (Young, 1994; Young & Peacock, 1992). Even if mean precipitation has not changed significantly, soil moisture will likely decrease due to increased evaporation and surface drying from warmer temperatures (Trenberth, 2011). As temperatures warm in the valley, therefore, higher elevations can be assumed to remain cooler than lower elevations, while valley bottoms will remain wetter.

4.2 | Plant community changes in the Teleki Valley 1980–2021

Species richness and diversity decreased significantly across the whole valley (Table 1), and certain species have disappeared altogether in our sample (see Table 2), suggesting these species may

have become locally extinct or at least too rare to catch with our sampling. A more thorough inventory would be needed to determine if local extinction is indeed the case. Many of these species have low-lying growth forms and a preference for boggy areas, which may have been under-sampled in this resurvey. Nonetheless, the decline in frequency of even the most dominant species suggests that these reductions are real (Table 2). Climate change in alpine regions has generally been associated with increases in species diversity (alpha diversity) (Grabherr et al., 1994; Jurasinski & Kreyling, 2007; Salick et al., 2019; Walther et al., 2005), as species shift upward in elevation in response to warming temperatures. The decline in diversity in this study is therefore somewhat unusual and may reflect the lack of a consistent upward shift for many plant species.

The two stresses associated with climate change (increased temperature and increased drought stress) should result in opposing predictions for range shifts in alpine plants. Species can be expected to shift up in elevation in response to increased temperatures (Bässler et al., 2013; Buytaert et al., 2011; Konvicka et al., 2003; Lenoir et al., 2008; Moritz et al., 2008; Walther et al., 2005), but also to shift downslope in response to increased aridity or other ecological factors such as disturbance and competition (Bodin et al., 2013; Crimmins et al., 2011; Hemp, 2009; O'Sullivan et al., 2021; Zu et al., 2021). The sampling in this study across both elevation and topographic gradients allows unique insights into these two possibilities. Both upward and downward shifts in mean elevations were observed, whereas some species did not shift appreciably (Table 2). Meanwhile, among the most dominant (and long-lived) species, there was little change with respect to topographic position or elevation, and the few changes that were apparent were variable. *Lobelia telekii* declined in the lower elevations, while *R. oreophytus* declined everywhere, but most significantly in the middle elevations, ridges, and valley bottoms (Table 3). *Lobelia telekii*, a giant rosette, may be responding more to temperature, while *R. oreophytus*, an acaulescent rosette, may be responding more to aridity. *Dendrosenecio keniodendron* declined on both the lower elevations and the ridges, but taken along with the demographic data, the overall pattern appears to be a shift towards the valley bottom (Figure 5; Table 4). Indeed, the opposing stressors of temperature and aridity may even be expected to often offset each other, resulting in cryptic patterns of species responses to climate change.

Dendrosenecio keniodendron declined in constancy but not frequency from 1980 to 2021. This may be explained by the apparent shift of the species towards the valley bottoms. Although there were no significant differences in density for topographic position individually, there was an overall significant shift from ridge to valley bottom (Table 4) and, more importantly, there was a large increase in younger stands in the valley (Figure 5). Another piece of evidence is the lack of niche separation in 2021 between *D. keniodendron* and the main valley bottom species: *D. keniensis* and *L. deckenii* subsp. *keniensis* (Table 7). The two *Dendrosenecio* species were noted in the 1980 study for their clear (and visually striking) niche separation by elevation and landform, with *D. keniensis* dominating in the lower

elevations and valleys and *D. keniodendron* in the higher elevations and upper slopes. This clear separation is no longer as apparent in 2021 (Table 7). These factors suggest that *D. keniodendron* is shifting off the slopes and ridges and recruiting in the valley bottoms. The shift is only according to topographic position, however, not elevation, as overall *D. keniodendron* shifted upward in elevation by 29 m (Table 2). *Dendrosenecio keniodendron* growth and reproduction depend strongly on adequate cover—either vegetation or rock talus—particularly in the dry season (Smith & Young, 1994). The shift to the valley bottom may therefore be a response to soil moisture changes, even as the slight upward shift in elevation may be a response to temperature changes.

The change in the population structure of *D. keniodendron* is perhaps the biggest change observed between the two periods. The plots in 2021 were characterised by many more young, and fewer older, individuals compared to 1980. In the 1980 study, it was found that most plots were even-aged stands of different ages (see Figure 2 in Young & Peacock, 1992). The authors attributed the even-aged population structure to the infrequent pulse reproduction that would allow one generation to grow and thrive as a cohort, suppressing intra-specific recruitment until a later cohort eventually established underneath senescent stands (Young & Peacock, 1992). In 2021, on the other hand, most plots were characterised by an uneven-aged distribution—inverse J-shaped curve—with a high abundance of smaller individuals (Figure 5). These smaller individuals were single-branched, representing pre-reproductive status. This population structure suggests recruiting populations of *D. keniodendron*.

4.3 | *Dendrosenecio keniodendron* as keystone species

Temperature and moisture are not the only forces affecting plant communities. In alpine environments, both facilitate and competitive processes are known to occur and can vary according to abiotic gradients as well as the species concerned (Anthelme et al., 2014; Cavieres, 2021). In the 1980 study, Young and Peacock (1992) found that the most important environmental factors driving plant community composition—for their 45 plots—were % vegetation cover (by inference soil moisture, see Young, 1994), altitude (by inference temperature) and mean *D. keniodendron* height (by inference facilitation/competition) (Young & Peacock, 1992). Across the 35 repeat plots, the situation is similar, with some minor differences. In both years, the first axis is associated with both elevation and live vegetation cover, as the elevation and moisture gradients appear to be largely along the same axis (Table 6). This axis separates out a similar array of species in both years: the moist valley bottom species (*L. deckenii* subsp. *keniensis*, *D. keniensis*, *R. oreophytus* and *H. ruepelli*) from the dry ridge species (*A. alpina*, *L. telekii*, *Carduus platyphyllus* and *Senecio purtschelleri*). The second and third axes in both periods, however, correlate most strongly with *D. keniodendron* density and topographic position. The strong correlation with *D. keniodendron* community characteristics (the third axis in 1980 and the second

axis in 2021) suggests that *D. keniodendron* continues to play an important role in shaping plant communities—and perhaps even more so in 2021. Looking at the shifts from 1980 to 2021 with respect to these underlying environmental factors, it is evident that some of the shifts are correlated with *D. keniodendron* characteristics and not elevation or live vegetation cover (Figure 6).

The importance of *D. keniodendron* in driving plant assemblages can be seen in the associations with the other dominant species. Young and Peacock (1992) hypothesized that *D. keniodendron* functions as a foundation or keystone species that creates micro-habitats and facilitates the establishment of other species, while suppressing others. Studies of other giant rosette species in South America have shown that they alter soil temperatures, creating micro-climates more favourable for other plants (Mora et al., 2019). Facilitation has long been recognised as a component of tropical alpine environments enabling complex plant communities to develop in harsh environments (Anthelme et al., 2014; Cavieres, 2021; D'Odorico et al., 2013; Hupp, 2016).

This facilitation effect can be seen in the positive relationship between *D. keniodendron* mean stand height and *Alchemilla* spp. frequency (Figure 7), which was also noted in the 1980 study (Young & Peacock, 1992). In contrast, in the case of *Helichrysum* spp., it appears competition is the dominant plant interaction, with an inhibitory effect on the abundance of *Helichrysum* spp. There were strong correlations (both positive and negative) between *D. keniodendron* height and many of the other dominant species as well—for instance, *L. telekii*, *D. keniensis*, and *H. rueppelli* – and in fact most of these correlations are stronger in 2021 than they were in 1980 (Table 7). Interestingly, for *A. johnstonii* the nature of the effect has shifted. While in 1980 *D. keniodendron* height was positively associated with both *Alchemilla* species, in 2021 this was no longer true for *A. johnstonii*. This may be a function of the lack of older stands in 2021 that are more effective in altering microclimates. These changes can lead to other indirect effects, as *Alchemilla* species themselves can have a facilitative or competitive effect on other species (Rehder et al., 1988).

The changes in *D. keniodendron* distribution from 1980 to 2021 may therefore explain some of the other species' changes seen in Table 2. The species with the largest decrease in frequency and the largest declines in elevation were mostly the low-lying cushion plants and acaulescent rosettes. These are the plants most likely to take advantage of the facilitative benefits of *D. keniodendron*. If this species has shifted from its original range it may leave some of these species vulnerable. On the other hand, the increases in *Helichrysum cymosum* may be explained by freedom from competition with *D. keniodendron*, since *D. keniodendron* appears to inhibit *Helichrysum* spp. growth (Young & Peacock, 1992) (Figure 7).

4.4 | Inertia in responses to climate change

Notwithstanding the changes discussed, we found relative stability within the plant communities in Teleki Valley over the past 40 years. The biggest changes appear to be a decline in species diversity and

a change in the population structure of the distinctive species, *D. keniodendron*. But for most plant species, changes in abundance and distribution have been muted or not evident. This may not be surprising given that alpine plants are usually long-lived, with slow life histories, and rare recruitment (Beck, 1986; Beck et al., 1984). These plants may also have a higher degree of resilience having adapted to such extreme weather conditions (Wahren et al., 2013). Similarly, arctic tundra systems often show little or no response to climate change, even though this non-response appears to be under-reported (Callaghan et al., 2022; Cirtwill et al., 2022). It is also possible that species ranges in these systems are limited by factors not directly related to the current climate (Schwartz, 2012), like glacial retreat or biotic drivers, or recruitment microsites (Smith & Young, 1994; Young, 1994). Where more dramatic changes in species ranges have been reported in afro-montane environments, this is often in the lower elevation zones (Hemp, 2009; Wesche et al., 2000), where disturbance regimes such as fire are more prevalent and can indirectly trigger rapid changes in plant communities. Other studies have predicted large shifts in species ranges based on climate models, not on empirical data (Chala et al., 2016; Kidane et al., 2019; Platts et al., 2013).

4.5 | The past and future of *Dendrosenecio keniodendron*

This study is limited by several factors. The resurvey only shows two points in time and therefore one has to make educated guesses about events in the intervening years or seasonal variation. The lack of precise (GPS) geo-locations also means that changes must be generalised to elevation and topographic positions. The limited spatial scope (limited to the Teleki Valley in both surveys) also does not allow generalisations across the broader alpine zone of Mount Kenya (or other East African mountains). Nonetheless, there are intriguing questions raised by this research which we hope will be investigated in the future.

The dramatic change in population structure of *D. keniodendron* suggests mortality of older individuals and recruitment of young. This is surprising as generally, local recruitment failure is a first indication of a climate-stressed species, while older, heartier individuals are more resilient (Silva et al., 2000; Strayer & Malcom, 2012), although increased recruitment in newly appropriate sites may also occur. The paucity of visible mortality (Table 5) presents a mystery, however. In these cold environments with slow rates of decay, dead individuals would be expected to be present on the landscape for a long time. Yet the dead individuals who were observed were few and distributed across all size classes. One possible explanation is fire. Fire would explain the lack of standing dead individuals as well as the dramatic shift in *D. keniodendron* size classes towards younger individuals. Several studies have documented the occurrence of fire in the lower alpine moorlands (Downing et al., 2017; Rehder et al., 1988; Smith & Young, 1994; Young, 2004), although rarely does fire reach the upper reaches of the valley (Downing et al., 2017). The FIRMS database of

fires, which goes back to 2000, does not record any incidence of fire in the study area (NASA FIRMS, 2023), and across the whole mountain incidences of fire above 4000m are rare (Henry et al., 2019). Therefore, while a fire might explain the localised loss of individuals, it probably does not—by itself—explain the valley-wide changes seen in this study. Other explanations include harvesting (even if only dead wood) by hikers/porters/rangers for firewood, and herbivory by animals such as elephants which have been known to frequent these areas and consume *D. keniodendron* (Mulkey et al., 1984).

Dendrosenecio keniodendron also appears to be shifting towards the valley bottom. This will put it in greater competition with *D. keniensis*, which currently occupies this habitat; historically the two species have occupied distinct topographic niches (Smith & Young, 1994). How these two species handle this new direct competition is therefore an important management question. Other questions arise concerning the specific causes and mechanisms for the shift of *D. keniodendron*: is the shift related purely to pressures of drying as suggested here or is there another factor involved? Finally, if *D. keniodendron* is indeed a keystone species, how will this shift impact the ecosystem as a whole? For example, there are a variety of vertebrate species that appear to rely on *D. keniodendron* stands for habitat (Young & Evans, 1993).

5 | CONCLUSION

The comparison of an ecological data set from 40 years ago to a resurvey in 2021 provides unique insights into plant community changes in a remote area that is threatened by climate change. We find suggestions of mortality, recruitment and movement for alpine species of the Teleki Valley over the past 40 years. Species diversity across the valley has declined, as has the frequency of several dominant species. There is tentative evidence of species' shifting as well as demographic changes in the iconic *D. keniodendron* species. On the other hand, there also appears to be considerable inertia in the dominant plant communities in the valley in the face of climate change, with relatively few significant changes over the 40-year period.

Two elevational trends are identified: a shift upward in elevation for some species and a shift towards the valley bottom for others, in particular *D. keniodendron*. The former shifts are likely a response to warming and more favourable temperatures at higher elevations, while the latter may be a response to increasing aridity, forcing some species to seek refuge in the moist valley bottom. *Dendrosenecio keniodendron* appears to be undergoing other changes associated with this geographic shift: total numbers have declined, and the stands that do exist are younger and concentrated in the valley bottoms. As *D. keniodendron* has been hypothesized to play a significant role in shaping plant communities in the valley (Young & Peacock, 1992), changes to this species may have far-reaching consequences for the biodiversity of the valley as a whole.

Climate change research has emphasised the upward movement along elevational gradients in response to global warming. Here our results suggest that moving down topographic (moisture) gradients

may also be a major species response to ecosystem drying, which could moderate (obscure) or even reverse upward movements. In fact, elevational niches (and vegetation zones) in general are likely determined as much by rainfall (soil moisture) as by temperature (Crimmins et al., 2011; O'Sullivan et al., 2021). Explicitly considering these conflating environmental pressures may produce more realistic and more useful models of biotic responses to global warming and climate change.

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CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data sets are available publicly on Figshare: <https://doi.org/10.6084/m9.figshare.21775973>.

ORCID

Timothy A. Downing  <https://orcid.org/0000-0002-3208-7492>

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