Modelling landscape-scale occurrences of common grassland species in a topographically complex mountainous environment

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Abstract

Mountainous regions typically harbour high plant diversity but are also characterised by low sampling intensity. Coarse-scale species distribution models can provide insights into the distribution of poorly sampled species, but the required bioclimatic data are often limited in these landscapes. In comparison, several environmental factors that vary over relatively fine scales in mountain environments (e.g. measures of topography) can be quantified from remotely-sensed data, and can potentially provide direct and indirect measures of biologically-relevant habitat characteristics in mountains. Therefore, in this study, we combine field-sampled floristic data with environmental predictors derived from remotely-sensed data, to model the ecological niches of 19 montane plant species in the Maloti-Drakensberg mountains, South Africa. The resulting models varied considerably in their performance, and species showed generally inconsistent responses to environmental predictors, with altitude and distance to watershed being most frequently included in models. These results highlight the species-specificity of the forb species' environmental tolerances and requirements, suggesting that environmental change may result in re-shuffling of community composition, instead of intact communities shifting along gradients. Furthermore, while the relatively high importance of altitude (a proxy for temperature) and topographic wetness index (a proxy for soil moisture) suggest that the flora of this region will be sensitive to shifts in temperature and rainfall patterns, several non-climatic environmental variables were also influential. Our findings indicate that local response to climate change in mountains might be especially constrained by soil type and topographic variables, supporting the important influence of non-climatic factors in microclimatic refugia dynamics.

Keywords Ecological niche modelling · Linear models · Topography · Plant diversity · Altitude

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Introduction

To effectively protect biodiversity, it is important to identify areas where high numbers of rare, localised or endangered species are concentrated (Myers 2003). For plant biodiversity, the majority of these areas are located in montane regions (Muellner-Riehl et al. 2019), likely reflecting how mountains contain steep environmental gradients, often harbour unique geological strata, and have complex topography, which leads to a large diversity of niches within relatively small areas (Antonelli et al. 2018; Rahbek et al. 2019). Additionally, many individual mountain tops act as islands in the landscape because of their distinct climatic conditions and are thereby drivers of evolutionary radiation (Riebesell 1982). However, despite their relative isolation, montane ecosystems may face threats in the form of mining, over-grazing and climate change (Schmeller et al. 2022).

Our knowledge of plant diversity in mountains depends on herbarium collections gathered over many years. However, mountain regions are often poorly sampled as the terrain can be largely inaccessible, resulting in large parts of these areas remaining under-explored (Clark et al. 2006; Li et al. 2011; Sainge et al. 2017; Wursten et al. 2017). As a result, these herbarium collections can describe a regions' overall species diversity and inform broadly about the occurrence of rare and endemic species, but they only partially reveal distribution patterns in mountain environments, without actually characterising species environmental requirements, which is necessary for effective conservation efforts (Greve et al. 2016).

Conservation planning often considers rarity and endemism as criteria for target identification, but this approach overlooks important aspects of plant life in mountains. Accurate assessments of ecosystems must also include the distribution of common species since the functioning of many ecosystems and the associated ecosystem services are only directly influenced by rare species when they are locally abundant or their ecological role is unique (Dee et al. 2019). A focus on common plant species is thus necessary if we want to understand how plant species and their niches are distributed within mountain regions and how these species affect the ecological functioning on a larger scale. Such information will help in understanding plant distributions, but also in monitoring vegetation changes and predicting future floristic responses to climate change (Silveira et al. 2019). In addition, since species distributions are shaped by complex interactions between individual biological traits (e.g., growth forms, morphological adaptations, phylogenetic niche conservatism) and environmental constraints (Carscadden et al. 2020), comparing drivers of distribution across multiple species with different traits can provide important insights of how these components determine range size and niche breadth.

Ecological niche modelling is a tool used to predict suitable environments for a species on the basis of incomplete occurrence data by extrapolating the information from those limited occurrence data to the entire sampled region (Weber et al. 2017). This approach makes use of different statistical modelling algorithms and can be utilised even when complete data (including absence data for a species) is unavailable. It does, however, require detailed environmental data so that the occurrence of the species can be linked to environmental conditions, allowing projecting the species occurrence throughout space and time (Pearman et al. 2008). In the Drakensberg, previous efforts to apply niche models to understand species distributions (Bentley et al. 2019; Gwate et al. 2023) were mainly based on presence-only models, which can limit model evaluation and calibration (Drake 2014), and coarsely interpolated climatic data only, which may fail in representing the

topographical climate variation at the microhabitat level (Franklin et al. 2013).

Climatic conditions are among the most important explanatory factors that determine the distribution of plants in any environment at broader scales (Punyasena et al. 2008). Climate plays a particularly large role in mountain environments because there is a high amount of local variation in rainfall, temperature, evapotranspiration and wind direction and speed (Leuschner 2000; Scherrer and Körner 2011; Körner 2021). However, there is a lack of detail in climatic data in the mountains, as weather stations are sparse, and climatic gradients are very steep and not easily modelled (Barry 1992). Therefore, when extrapolations of climatic data are done for mountainous environments, they are typically coarse estimates and often not very reliable (Schmitt et al. 2013; Shahgedanova et al. 2021).

Topography has a large impact on local climatic conditions in mountains, across both large (e.g. temperature variation across elevation) and smaller scales (temperature variation on adjacent north vs. south-facing slopes; Kattel et al. 2015). For example, temperature generally declines with elevation (Montgomery 2006), but sheltering and shading in deep valleys and the effect of anabatic and katabatic airflows may strongly modify this pattern locally (Sturman 1987). Rainfall can have a complex pattern of local variation too, as it depends on the interaction of topography and prevailing wind directions. The effect of air forced to rise up mountain slopes often creates unstable conditions and orographic rainfall, but how this rainfall is distributed over different slopes depends on fine details in topography and air movement through valleys (Barry 1992; Neiman et al. 2002). Air movement in mountains is extremely complex as it involves daily fluctuations in air pressure as a result of differential heating of slopes and valleys, and this, in turn, has an effect on potential evaporation and temperature. In consequence, while we understand that climatic conditions can vary strongly across short distances within mountains, the characterization of this finer scale variation in temperature, rainfall and other variables is in practice limited by data availability and the development of microclimatic models (although see, e.g. Kearney et al. 2020).

As a result of the climatic and topographic heterogeneity, it is a particular challenge to provide realistic assessments of plant distributions within mountain ranges at the landscape scale. In this study, therefore, we link plant distributions directly to fine-scale topographical information that can be obtained from data layers that are directly available from satellite imagery or large-scale maps, assessing (1) the accuracy with which species distributions can be modelled using widely available environmental data in a region with limited botanical survey data and (2) which environmental variables are most frequently related to species occurrence patterns. By understanding the distributions of common species in

mountains, we can enhance our understanding of the environmental drivers affecting the occurrence of plants across mountain environments.

Methods

Study area

Our study region is the northern Maloti-Drakensberg mountains in eastern South Africa, adjacent to Lesotho, at the border of the Free State and KwaZulu-Natal provinces. This region is characterised by a temperate climate with warm summers and cold winters that are dry with regular frost and occasional snowfalls. It also experiences summer rainfall in the form of thunderstorms that arise from convective and orographic cloud formation.

The Drakensberg massif is an erosional mountain range that represents the remaining areas of basalt that were deposited after a period of massive volcanic activity following the breakup of Gondwanaland (McCarthy and Rubidge 2005) This mountain range has very steep slopes towards its eastern face, where it rises c. 2000 m above the coastal province of KwaZulu-Natal. The Free State province is situated on an inland high-altitude plain in the interior of South Africa that was formed during a period of uplift at the end of the Cretaceous. The eastern escarpment of the plateau intersects with the Drakensberg escarpment (Fig. 1), and the area around this intersection, therefore, has a topography that is characterised by plains of three different elevations intersecting: inland KwaZulu-Natal at about 1200 m altitude, the eastern Free State at around 1700 m altitude and the Lesotho Highlands at around 3000 m altitude. Rainfall in this area is primarily orographic, coming from the Indian Ocean in the east. Less commonly, cold fronts also sweep in from the west. There are weather stations in several towns in the foothills of the mountains, but only a single weather station in the high mountains (around Sentinel Peak) that was run for a short period of time (Nel et al. 2010). For most of the area, the weather is complex and unpredictable.

Field sampling

Thirty common grassland forbs were chosen for this study (Table 1; Fig. 1). These species were selected using the following criteria: (1) they should be found regularly in the area, and their distribution should not be confined to a single mountain or valley, (2) they should have a high detectability and be reliably identified, without any confusion with other forbs in the area, and (3) they should remain in this recognisable state throughout the flowering season, either because they flower for a long period, or because their vegetative form is conspicuous and easily recognised. These species

covered a broad range of growth forms, including geophytes, succulent forbs and dwarf shrubs. Of the 30 target species, only 19 species were recorded in more than 10 plots, with subsequent data analysis limited to this subset of species.

Transects were laid out in the mountains around the town of Phuthaditjhaba, either following contour lines or moving upslope in valleys or along ridges between 1800 and 2600 m a.s.l. These transects were accessed by foot during the summer growing seasons (November to March) of 2016, 2017 and 2020, and a 10×10 m plot was surveyed every 100 m along each transect, in which the occurrence of each of the thirty target species was recorded. Altitude, rock cover, vegetation cover, vegetation height, slope angle and slope aspect were additionally quantified in the field for each plot. Prior to analysis, slope aspect was decomposed into a measure of northness (i.e. $1 =$ north-facing, $-1 =$ south-facing, $0 =$ east- or west-facing) and eastness (following, e.g., Guisan et al. 1999). This means there are six predictor variables that were assessed in the field. A total of 231 plots were surveyed along eight transects.

Desktop predictor variables

Additional predictor variables were assessed from desktop studies: solar radiation, topographic wetness index, distance from watershed, and the categorical variable soil type.

To determine the solar radiation potentially received at each plot in the study area, the "solar radiation analysis tool" from ArcGIS 10:8.2 (ESRI 2023) was used. The tool maps the potential incident solar radiation over a geographic area for specific time periods. It accounts for atmospheric effects, site latitude and elevation, slope steepness and aspect, daily and seasonal shifts of the sun's angle, and effects of shadows cast by surrounding topography (ESRI 2023). The tool requires a Digital Elevation Model (DEM) of the study area. Therefore, a 30 m DEM for South Africa and Lesotho was obtained from the Shuttle Radar Topography Mission (SRTM; Drusch et al. 2012) and clipped to the study area. The "solar radiation analysis tool" with the following parameters was selected: output files were created for each month; a sky value of 512 (which is recommended as sufficient for calculations at point locations where calculation time is less of an issue and where you are using monthly averages); a viewshed of 32 (due to the complexity of the landscape in the study area); 32 calculation directions (due to the complex terrain); and finally, ground level was selected for reading height.

Topographic wetness index (TWI) was calculated following the methods of Dadjou (2021). The TWI shows a measure of wetness conditions at the catchment scale. It combines local upslope contributing area and slope using the digital elevation model to represent increased soil moisture where the landscape area contributing runoff is large and slopes
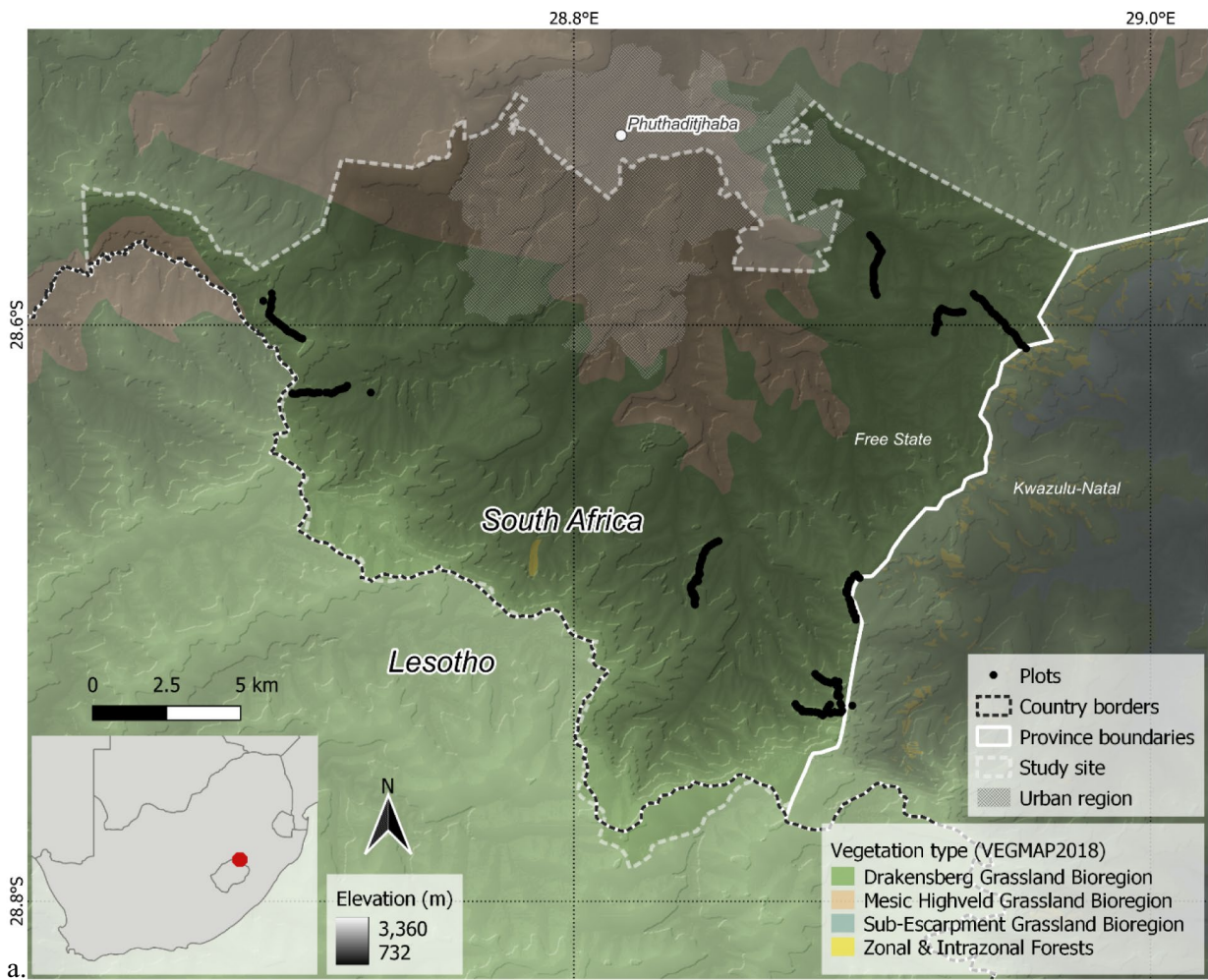
◀**Fig. 1 a** Survey sites in the northern Maloti-Drakensberg mountains in South Africa, bordering Lesotho, showing dominant vegetation types (Mucina and Rutherford 2006). The photographs below show some of the selected species that were recorded in this study: **b** *Gladiolus crassifolius*, **c** *Cyperus sphaerocephalus*, **d** *Helichrysum chionosphaerum*, **e** *Ajuga ophrydis*

are low. This process also uses the SRTM-DEM developed for the solar radiation calculation. Once the TWI layer was calculated the survey points were overlayed and a TWI value for each survey plot could be determined.

Soil data were obtained from the Soil and Terrain database for Southern Africa (SOTERSAF version 1.0) at a scale of 1:2 million (Batjes 2004). The vector layer was imported into ArcMap in order to obtain the data appropriate for each plot. This led to the categorization of soils as one of three types: Lithic leptosols, Eutric leptosols or Paraplinthic Acrisols.

The distances for each plot from the both watersheds (Lesotho border and Free State-KwaZulu-Natal border) were calculated because these are a proxy for orographic rainfall, with the distant plots receiving less rainfall than the proximate plots. The tool for calculating this distance was gDistance() function from the rgeos R package version 0.6-2 (Rundel and Bivand 2013), using a base raster layer of 30 m resolution.

Species distribution models

All continuous environmental variables were examined for collinearity using Pearson correlation tests. Due to strong collinearity between potential incident solar radiation across most months, only solar radiation values for June and December were retained for subsequent analyses. Variance inflation factors (VIF) showed that soil type (the only categorical predictor) was not strongly correlated with any of the other predictors. After removing vegetation cover and distance from the Lesotho border, there were 11 candidate predictor variables retained, all with $r < |0.6|$ and VIF < 2.2 (see Online Appendix; Fig. A1). Vegetation height was log-transformed prior to analyses.

To test if quadratic terms should be considered for each of the continuous predictor variables (i.e. to account for non-linear and/or unimodal species–environment relationships), each predictor was fitted to each species' occurrence data using a generalised linear model with a binomial distribution. Two models were fitted for each species-predictor combination, a linear model and a quadratic model, and a quadratic term was only considered useful when the quadratic model had a lower AIC score than the associated linear model and the quadratic model improved the deviance explained (% DE) by the linear model for the species by $> 5\%$. Quadratic terms only met these two criteria for > 1

species for altitude, rock cover and distance from watershed. As a result, quadratic terms were only considered further for these three predictor variables.

A best subsets model building approach was then used to identify the best combination of predictor variables (from 11 predictors and 3 quadratic terms) for each species, with transect identity included as a random effect to account for the spatial structure of the sampling design. Species occurrence was modelled using a generalised linear mixed effect model with a binomial distribution, with all resulting models ranked using AIC. Model fit was assessed using the area under the curve of a receiver operating characteristic plot (AUC; Fielding and Bell 1997) and the true skill statistic (TSS; Allouche et al. 2006), based on three repeats of three-fold cross-validation (with random division of the dataset). Relative variable importance was then calculated for each variable included in each species' top ranked model, using the approach of Niittynen and Luoto (2018). As variable importance cannot be determined for random effects, two analytical approaches were used when assessing model fit and variable importance: transect identity was dropped from the model (likely overestimating the relative importance of the remaining predictors, and underestimating model fit) or was treated as a fixed effect (potentially overestimating its importance and overestimating model fit).

All statistical analyses were run in R statistical software v 4.2.2 (R Core Team 2022), with additional functions from the corrplot (Wei et al. 2022), biomod2 (Thuiller et al. 2023), car (Fox and Weisberg 2018), glmmTMB (Brooks et al. 2017) and modEvA (Márcia Barbosa et al. 2013) libraries.

Model projection

The best-performing models were used to project the occurrence of species across the entire study region using the function "predict" from the R package "terra" version 1.7-39 (Hijmans et al. 2022). Since some variables used to model the presence of some species were not available for areas beyond the sampled plots, we restricted this step to species in which the top-performing models included only predictors which could be derived from DEMs: elevation, slope, northness, eastness, solar radiation in June, solar radiation in December, TWI, and distance to the watershed. For elevation, we used the same 30 m resolution SRTM-DEM used in the previous step. The solar radiation data was obtained from the Photovoltaic power potential (PVOUT) raster published by the Global Solar Atlas dataset version 2.0 (ESMAP 2019) under the resolution of 250 m. For the Topographic Wetness Index, we used the Africa Soil Information Service (AfSIS): Topographic Wetness Index (TWI) (Vagen 2010) under 90 m resolution. For topographic eastness and northness, we used the DEM raster and the functions "raster.east" and "raster.north" available on the package "red" version

Table 1 Species selected for this study

Species	Family	Growth form	Occurrences
Agapanthus campanulatus	Agapanthaceae	Geophyte	40
Ajuga ophrydis	Lamiaceae	Forb	43
Crassula vaginata	Crassulaceae	Succulent forb	46
Cyperus sphaerocephalus	Cyperaceae	Graminoid	26
Dianthus basuticus	Caryophyllaceae	Forb	25
Gladiolus crassifolius	Iridaceae	Geophyte	23
Helichrysum aureum	Asteraceae	Forb	156
Helichrysum chionosphaerum	Asteraceae	Creeper	91
Helichrysum oreophilum	Asteraceae	Forb	63
Helichrysum pallidum	Asteraceae	Forb	79
Hermannia gerrardii	Malvaceae	Creeper	63
Lotononis lotononoides	Fabaceae	Dwarf shrub	70
Moraea huttonii	Iridaceae	Geophyte	24
Searsia discolor	Anacardiaceae	Suffrutex	69
Scabiosa columbaria	Dipsacaceae	Forb	77
Schistostephium crataegifolium	Asteraceae	Dwarf shrub	19
Senecio macrocephalus	Asteraceae	Succulent forb	84
Senecio rhomboideus	Asteraceae	Succulent forb	32
Zaluzianskya microsiphon	Scrophulariaceae	Forb	14

1.5.0 (Cardoso 2023). All raster resolutions were resampled to 30 m resolution using bilinear interpolation and cropped to the extent of the study site using the R package "terra". The predicted suitable area for each species was calculated using a threshold based on a fixed sensitivity value of 0.9 (Liu et al. 2005; Bean et al. 2012). The model sensitivity was calculated using the presence and absence values from the sampled sites with the function "evaluate" from the package "dismo" version 1.3-9 (Hijmans et al. 2017). We used the calculated thresholds to reclassify the projections into presence/absence maps using the function "classify" in the R package "terra". Finally, the extent of the suitable area for each species was calculated using the function "expanse" in the same package.

Results

Occurrence models varied strongly in performance, with mean AUC scores from cross-validation ranging from 0.68 to 0.94 and mean TSS scores from 0.22 to 0.80 (when including Transect as a fixed effect; AUC scores were on average 0.03 units lower and TSS scores 0.07 units lower when Transect was excluded from models; Table 2). All predictor variables (and their associated quadratic terms) were included in at least one species' best fit model, with altitude (13 species), distance to watershed (13 species) and rock cover (8 species) being included in the most best-fit models (Table 2; Fig. 2). None of the predictors that were included in more than one best-fit model had consistent signs

for their coefficients (i.e. the nature of the occurrence-predictor relationship was not consistent across all of the species where that predictor was included in the best-fit model). For example, altitude showed positive (3 species), negative (4 species), humped-shaped (3 species) and valley-shaped (2 species) relationships with the occurrence of the modelled species.

Variable importance was highest for distance to the watershed, soil type, and altitude (Table 3). Northness also had a high average variable importance, but this was driven by northness being the only variable included in the best-fit model for *Schistostephium crataegifolium*. Repeating the variable importance analysis including transect identity as a fixed effect did not alter these results (with transect being the 5th most important variable; Online Appendix Table A1).

Habitat suitability and distribution across the mountain region projected by the occurrence models varied considerably across species. Only in the cases where rock cover and vegetation height did not play a major role, could spatial distributions of species be modelled onto a digital elevation model (11 species; see Fig. 3). Some species influenced by similar combinations of variables (e.g., elevation and distance to watershed in *Crassula vaginata* and *Lotononis lotononoides*) showed similar response curves, and differed only in terms of the relative contribution of each variable to the overall explanatory power of the model (e.g. the relative importance of distance to watershed was 91% for *C. vaginata* and 46% for *L. lotononoides*). The response maps also show that some species, such as *Helichrysum aureum* and *Senecio rhomboideus*, were predicted to be approximately

Table 2 Best-fit occurrence model for each species, indicating the model fit (AUC = area under the curve, TSS = true skill statistic), and the variables included in the best model and their coefficients (+ = positive linear relationship; − = negative linear relationship; ∩ = hump-shaped quadratic; U = valley-shaped quadratic)

Species	AUC (mean±SD)	TSS (mean±SD)	Altitude	Height	Slope	Northness	Eastness	Rock cover	Solar rad: June	Solar rad: December	Distance to watershed	TWI	Soil type
Agapanthus campanulatus	0.89±0.07	0.66±0.14	U		+			U		−	−	+	**Eu > Li > Pa**
Ajuga ophrydis	0.84±0.05	0.51±0.09	U	+			+	−			U		
Crassula vaginata	0.83±0.10	0.53±0.19	−								U		
Cyperus sphaerocephalus	0.75±0.08	0.35±0.20	+		−						−		**Eu > Pa > Li**
Dianthus basuticus	0.84±0.10	0.51±0.24	+								∩		**Li > Eu > Pa**
Gladiolus crassifolius	0.80±0.06	0.46±0.16	∩		−		+	U		+	+		**Pa > Li > Eu**
Helichrysum aureum	0.72±0.03	0.31±0.08	+			+		−	−		−	−	**Pa > Li > Eu**
Helichrysum chionosphaerum	0.69±0.07	0.31±0.15	−	−				∩				−	
Helichrysum oreophilum	0.76±0.04	0.34±0.05								−	−		**Eu > Pa > Li**
Helichrysum pallidum	0.87±0.08	0.70±0.22									U	+	
Hermannia gerrardii	0.79±0.05	0.42±0.12	∩							−			
Lotononis lotononoides	0.94±0.04	0.80±0.06	∩				+			−	−		
Moraea huttonii	0.84±0.05	0.43±0.14				−	+				−		
Searsia discolor	0.70±0.11	0.23±0.22	∩				+	+					**Eu > Li > Pa**
Scabiosa columbaria	0.77±0.13	0.38±0.27						+			U		
Schistostephium crataegifolium	0.85±0.03	0.59±0.09				+							
Senecio macrocephalus	0.80±0.09	0.43±0.15	−			+	−	+					**Eu > Li > Pa**
Senecio rhomboideus	0.78±0.04	0.43±0.09	−	+							∩	+	
Zaluzianskya microsiphon	0.84±0.03	0.57±0.06		+			+				−	−	
Best models:			13	4	3	5	7	8	1	5	13	6	8

The last row summarises the number of species for which a variable was included in the best-fit model

Height vegetation height, *Slope* slope steepness, *Solar rad* potential direct incident radiation, *TWI* topographic wetness index, *Li* Lithic Leptosols, *Eu* Eutric Leptosols, *Pa* Paraplinthic Acrisols
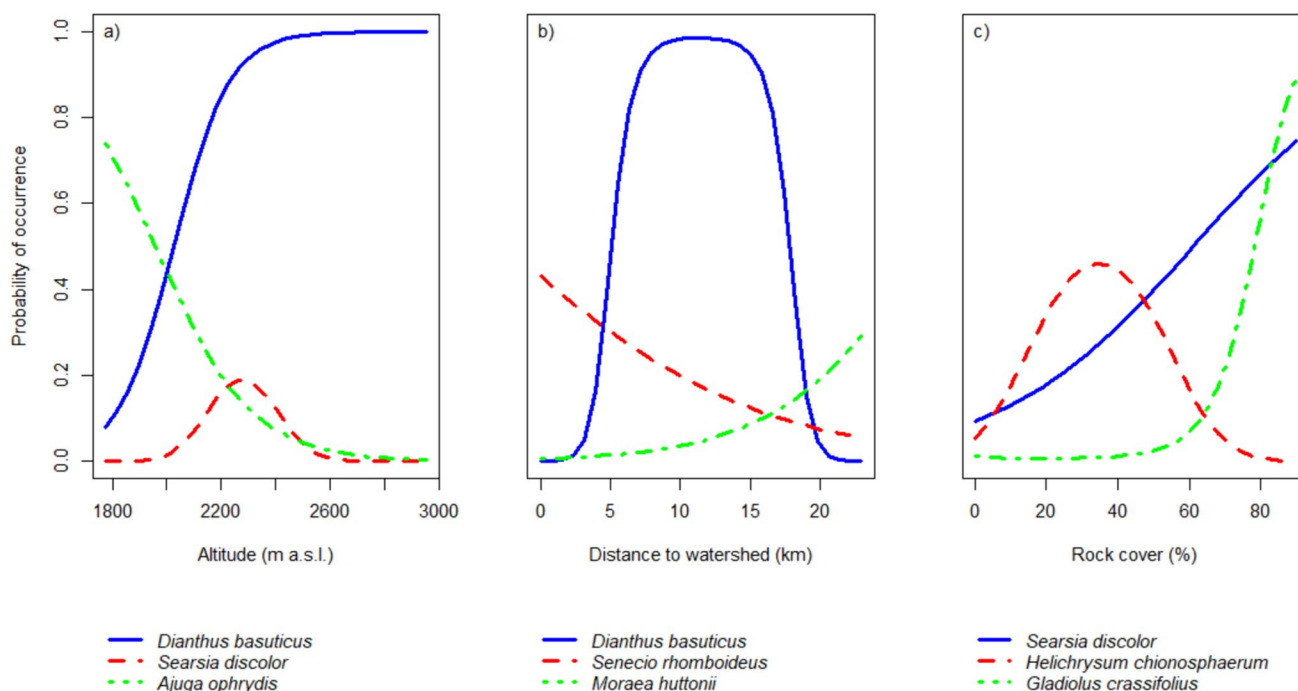
Fig. 2 Exemplar response curves illustrating contrasting species responses to **a** altitude, **b** distance to the watershed, and **c** rock cover. See Online Appendix B for all response curves for all species

equally common across the study region. Species belonging to similar growth forms (Table 1) have yet very different distribution patterns.

Projected suitable habitat across the study area varied strongly between species, ranging between c. 40 and 100% of the area (Fig. 4). Species such as *Agapanthus campanulatus*, *Dianthus basuticus* and *Senecio macrocephalus* are predicted to be relatively range restricted, while *Helichrysum aureum*, *Helichrysum pallidum* and *Senecio rhomboideous* show large suitable areas.

Discussion

For the majority of species, elevation strongly affected species' occurrence, combined with various other topographic factors, often including rock cover, distance from the watershed, and/or soil type. The impact of altitude on species distribution has been highlighted in many studies (e.g. Wang et al. 2003), as altitude is linked to temperature and often also to orographic rainfall, wind intensity and/or cloud cover (Körner 2007). Interestingly, in this study, some species seem to have a bimodal distribution with regards to altitude. This may indicate a preference for habitats such as relatively flat mountain tops or crests that occur at low altitude on sandstone and again at high altitude on basalt.

In this system distance from the watershed also correlates with the amount of orographic rainfall, as the escarpment

edge (i.e. the watershed) is where moist air from the Indian Ocean is forced up due to the steep incline of the topography. Rock cover was an important factor for the occurrence of several species, likely reflecting a gradient of decreasing soil depth, increasing light availability, and greater microclimatic variation. As a result, areas of higher rock cover potentially offer, for example, opportunities for species that are less competitive in a dense grass layer. The influence of soil type is probably predominantly through its effect on nutrient status and hydrological properties of soils. Many studies have emphasized the importance of soil and other edaphic factors in mountain grasslands and, along with topography (including slope, aspect, altitude), are the most important environmental factors driving species occurrence patterns (Pickering and Green 2009; Huo et al. 2015; Buri et al. 2020).

While there tends to be pronounced variability in the environmental variables that are most strongly related to species occurrence patterns, and variation in the nature of the effect of those predictors on species occurrence, some predictors did show strong trends. For example, both eastness and the amount of solar radiation received during summer demonstrated predominantly consistent correlations with the occurrence of the species in which they were included in the top-ranked models (positive and negative correlations respectively). Both of these metrics relate to the solar inputs at site, with west-facing slopes in this system experiencing more direct incident radiation during warmer

Table 3 Variable importance (%) for each fixed effect predictor included in the best model for each species (excluding Transect as a predictor)

Species	Altitude	Height	Slope	Northness	Eastness	Rock cover	Solar rad: June	Solar rad: December	Distance to watershed	TWI	Soil type
Agapanthus campanulatus	13		9			6		14	25	11	23
Ajuga ophrydis	51	10			11	11			16		
Crassula vaginata	9								91		
Cyperus sphaerocephalus	6	1	<1	<1	4	<1	17	1	11	<1	59
Dianthus basuticus	15								19		67
Gladiolus crassifolius	30		3		5	8		5	28		20
Helichrysum aureum	33			7		6	10		24	2	19
Helichrysum chionosphaerum	48	3				38				10	
Helichrysum oreophilum								6	30		64
Helichrysum pallidum									47	40	14
Hermannia gerrardii	67							33			
Lotononis lotononoides	49				3			2	46		
Moraea huttonii				1	17				82		
Searsia discolor	23				18	17					
Scabiosa columbaria						<1			>99		42
Schistostephium crataegifolium				>99							
Senecio macrocephalus	41			20	6	<1					34
Senecio rhomboideus	6	5							87	2	
Zaluzianskya microsiphon		27			13					61	
Mean:	30%	9%	4%	26%	9%	10%	14%	10%	47%	18%	38%

Each row sums to 100%, so the values in each row represent the relative contribution to the explanatory power of that model (irrespective whether the % DE values are high or low; see Table 1). Values in the bottom row represent the mean variable importance across all species. For variable importance values where transect was included as a fixed effect, see Online Appendix Table A2

Height vegetation height, *Slope* slope steepness, *Solar rad* potential direct incident radiation, *TWI* topographic wetness index
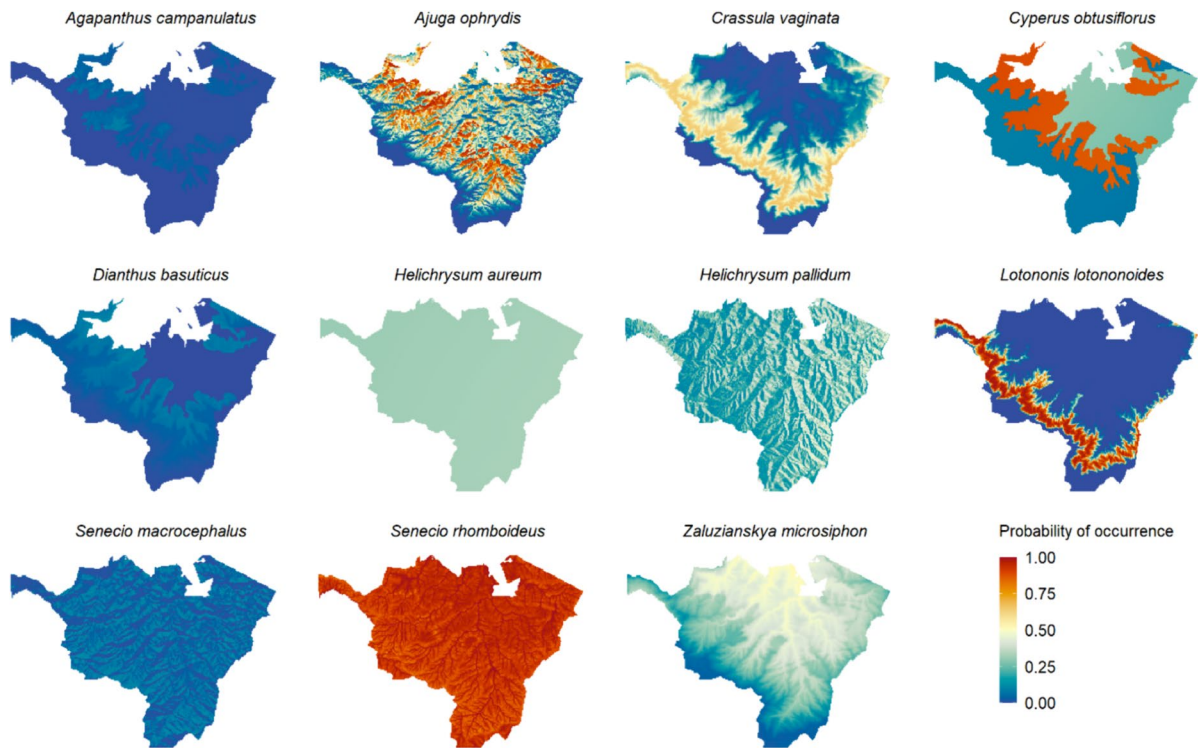
Fig. 3 Examples of species' projected occurrence probabilities across the study area. Dark red tones indicate higher predicted probabilities of occurrence, while dark blue tones indicate lower probabilities. All projections are in WGS84 and 30 m resolution

Fig. 4 Estimated suitable area for each species that had explanatory models using only topographic variables (i.e. excluding rockiness and vegetation height) across the study region (see Fig. 1)
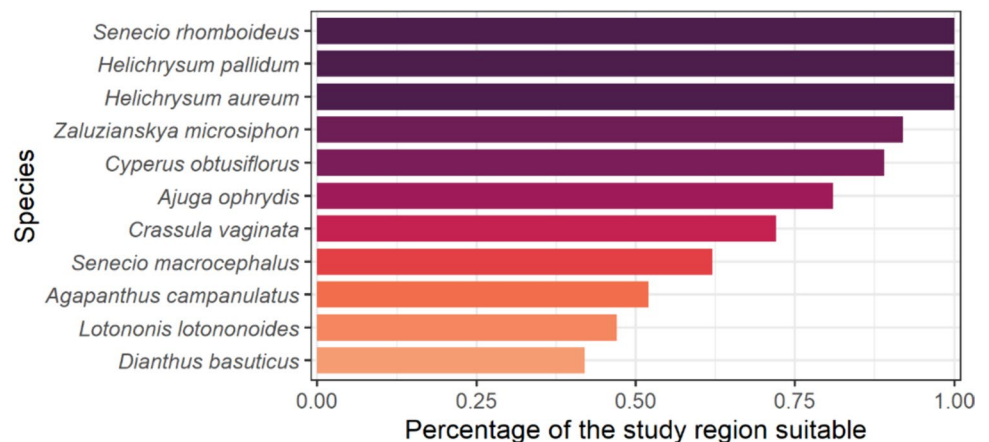
afternoon times (and with east-facing slopes often having reduced solar inputs due to morning mist). This suggests that in this system many, but not all, species benefit from cooler, less sunny microsites, having a higher probability of occurrence in locations with lower solar inputs. This finding is in strong contrast to observations from most other systems, where warmer, sunnier microsites are typically associated with higher plant richness and more complete vegetation cover (Kulonen et al. 2018). This depends a lot on the choice of species of the study. The ecologically most dominant species, the grasses, are not included in the study and in warm

and sunny sites it is likely them that benefit from becoming more dominant. Large forbs and shrubs are typically dominant on scree slopes, drainage lines and rocky areas. There were no growth forms that showed similar responses here but the sample sizes are too small to make definite statements about that.

Mountain ecosystems are particularly vulnerable to climatic changes (Thuiller et al. 2005). It is expected that vegetation will generally expand upslope if mountain habitats become warmer and that high-altitude endemic species will therefore be under specific threat (i.e. the 'escalator to

extinction' (Dirnböck et al. 2011; Pauli et al. 2012; Urban 2018). This is particularly relevant in our study system as elevation was an important predictor in most of the species' distribution models. Indeed, elevation has always been recognised as a major influence on vegetation patterns in the mountains, and the majority of species are expected to shift their range in response to warming temperatures (Vitasse et al. 2021; Zu et al. 2021). However, given that a diversity of occurrence-elevation patterns were observed (positive and negative, linear and non-linear), a community-wide upslope range shift is unlikely, and instead a more complex reshuffling of grassland composition may occur in response to changing temperatures (as observed by e.g. Le Roux and McGeoch 2008).

The pronounced topographic variation (and, e.g., the associated edaphic heterogeneity) often observed in mountainous areas may, however, also provide some degree of buffering against the impacts of climate change (Scherrer and Körner 2011; Niskanen et al. 2017). For example, aspects of topography, such as solar radiation and rock cover, will not be impacted as a result of global climate change, even though there is a tendency for more rocky places towards higher altitudes. Given that many of the variables identified in this study as being important drivers of forb occurrence patterns will not be directly impacted by changes in rainfall or temperature regimes, these findings suggest variation in susceptibility to change across our study species (in agreement with, e.g., Moeslund et al. 2013). This differential susceptibility to changes in climate could, therefore, cause large differences in the degree to which species ranges shift, potentially leading to a greater mixing of species and an overall homogenisation of vegetation across altitudinal bands (Savage and Vellend 2015; Cramer et al. 2022).

Importance for conservation

Despite study species being selected on the basis of their 'commonness' in the region's mountain grasslands, there was still a wide range in the predicted range of these species within the study region. This variation in species predicted occupancy likely reflects the predictor variables selected in this study (and their resolution), but also differences in species biology. The species that have strong habitat specialisation tend to occur in specific, limited environments. The number of variables involved in determining such habitats cannot be determined at the scale this study operated on. If a species occupies unique or rare environmental conditions, it may respond strongly to the arbitrary choice of threshold, resulting in a smaller predicted area (Boulangeat et al. 2012; Carscadden et al. 2020).

The predicted size of a species occupancy within a specific area does not have to correspond with the actual

frequency with which that a species is encountered in the field (Crisfield et al. 2024). The predicted area size indicates the 'potential' habitat but because of biotic factors (e.g. presence of competition or the absence of mutualists) and dispersal constraints, the species may not occur in all the places that are indicated as potential habitat. Also, when species have a large potential distribution, neutral models apply and this may lead to a small actual distribution after a series of random dispersal and competition events over several generations, despite the equal tolerance for environmental conditions among all species (Hubbell 2001). This emphasizes why we need to be careful with the interpretation of the predicted range sizes as they do not necessarily reflect the rarity of species on the ground nor give an understanding of the specific threats that a species faces.

When rarity arises due to habitat specialisation and these habitats are at risk, it can help in prioritising which species inhabiting topographically complex mountainous environments require most attention for conservation and known existing populations of such species need to be monitored. Following the procedure outlined in this paper can help in setting such conservation priorities as it becomes evident which species are occurring in a narrow niche, even while they may still be commonly encountered. There are many studies that highlight conservation priorities of mountainous regions (for example Hou et al. 2010) but none of them focus on the landscape-scale of particular mountains and slopes. Knowing the distributions of species within mountain areas is particularly important when we consider the pressures that mountainous regions are subjected to in the face of climatic changes.

The method applied in this study offers an approach to modelling species distributions in montane regions at a landscape level, and can be used to identify species and areas for monitoring that may be most strongly impacted by environmental change. In this approach, the presence of species' presences and several environmental predictors' values were directly sampled on-site instead of derived from other geographic databases. This partially overcomes the limitation of the coarse resolution and the uncertainties associated with the low geographic coverage of mountain systems by the global climatic databases (Thornton et al. 2022). Even though some projections include variables that can be considered proxies for climate data derived from weather stations, removing this bias from the model training refines the results compared to models trained using spatially biased datasets.

Species distribution modelling at an intermediate scale can give a good indication of the way in which plant species are distributed within a mountain landscape. This reveals that different plant species, even if they are equally common across the mountain range, may have entirely different habitat requirements and will therefore respond differently to

future changes. How plants respond to a complex of environmental predictors in a mountainous landscape is of crucial importance for the conservation of these species.

Declarations

Competing interests The authors declare they have no competing interests.

References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Antonelli A, Kissling WD, Flantua SG, Bermúdez MA, Mulch A, Muellner-Riehl AN, Kreft H, Linder HP, Badgley C, Fjeldså J (2018) Geological and climatic influences on mountain biodiversity. Nat Geosci 11:718–725

Barry RG (1992) Mountain weather and climate. Psychology Press, London

Batjes NH (2004) SOTER-based soil parameter estimates for Southern Africa (ver. 1.0). Report 2004/04, ISRIC—World Soil Information, Wageningen. https://isric.org/sites/default/files/isric_report_2004_04.pdf

Bean WT, Stafford R, Brashares JS (2012) The effects of small sample size and sample bias on threshold selection and accuracy assessment of species distribution models. Ecography 35:250–258

Bentley LK, Robertson MP, Barker NP (2019) Range contraction to a higher elevation: the likely future of the montane vegetation in South Africa and Lesotho. Biodivers Conserv 28(1):131–153. https://doi.org/10.1007/s10531-018-1643-6

Boulangeat I, Lavergne S, Van Es J, Garraud L, Thuiller W (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. J Biogeogr 39:204–214

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Buri A, Grand S, Yashiro E, Adatte T, Spangenberg JE, Pinto-Figueroa E, Verrecchia E, Guisan A (2020) What are the most crucial soil variables for predicting the distribution of mountain plant species? A comprehensive study in the Swiss Alps. J Biogeogr 47:1143–1153

Cardoso P (2023) Package 'Red' BAT imports

Carscadden KA, Emery NC, Arnillas CA, Cadotte MW, Afkhami ME, Gravel D, Livingstone SW, Wiens JJ (2020) Niche breadth: causes and consequences for ecology, evolution, and conservation. Q Rev Biol 95:179–214

Clark JL, Neill DA, Asanza M (2006) Floristic checklist of the Mache-Chindul mountains of Northwestern Ecuador. Contributions from the United States National Herbarium, pp 1–180

Cramer MD, Hedding DW, Greve M, Midgley GF, Ripley BS (2022) Plant specialisation may limit climate-induced vegetation change to within topographic and edaphic niches on a sub-Antarctic island. Funct Ecol 36:2636–2648

Crisfield VE, Guillaume Blanchet F, Raudsepp-Hearne C, Gravel D (2024) How and why species are rare: towards an understanding of the ecological causes of rarity. Ecography 2024(2):e07037

Dadjou F (2021) How to calculate topographic wetness index (TWI), in ArcGIS? https://www.researchgate.net/post/how_to_calculate_topographic_wetness_index_TWI_in_ArcGIS/604b730e0af47c129700ba71/citation/download

Dee LE, Cowles J, Isbell F, Pau S, Gaines SD, Reich PB (2019) When do ecosystem services depend on rare species? Trends Ecol Evol 34:746–758

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

Drake JM (2014) Ensemble algorithms for ecological niche modeling from presence-background and presence-only data. Ecosphere 5(6):76. https://doi.org/10.1890/ES13-00202.1

Drusch M, Del Bello U, Carlier S, Colin O, Fernandez V, Gascon F, Hoersch B, Isola C, Laberinti P, Martimort P, Meygret A (2012) Sentinel-2: ESA's optical high-resolution mission for GMES operational services. Remote Sens Environ 120:25–36

ESMAP (2019) Global Solar Atlas 2.0 technical report. World Bank, Washington, DC

ESRI (2023) An overview of the Solar Radiation toolset. https://pro.arcgis.com/en/pro-app/latest/tool-reference/spatial-analyst/an-overview-of-the-solar-radiation-tools.htm

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv 24:38–49

Fox J, Weisberg S (2018) An R companion to applied regression. Sage Publications, Thousand Oaks

Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? Glob Change Biol 19(2):473–483. https://doi.org/10.1111/gcb.12051

Greve M, Lykke AM, Fagg CW, Gereau RE, Lewis GP, Marchant R, Marshall AR, Ndayishimiye J, Bogaert J, Svenning J-C (2016)

Realising the potential of herbarium records for conservation biology. S Afr J Bot 105:317–323

Guisan A, Weiss SB, Weiss AD (1999) GLM versus CCA spatial modeling of plant species distribution. Plant Ecol 143:107–122

Gwate O, Canavan K, Martin GD, Richardson DM, Clark VR (2023) Assessing habitat suitability for selected woody range-expanding plant species in African mountains under climate change. Trans R Soc S Afr 78(1–2):87–101. https://doi.org/10.1080/0035919X.2023.2205368

Hijmans RJ, Phillips S, Leathwick J, Elith J, Hijmans MRJ (2017) Package 'dismo'". Circles 9:1–68

Hijmans RJ, Bivand R, Forner K, Ooms J, Pebesma E, Sumner MD (2022) Package 'terra.' Maintainer, Vienna, Austria

Hou M-F, Lopez-Pujol J, Qin H-N, Wang L-S, Liu Y (2010) Distribution pattern and conservation priorities for vascular plants in Southern China: Guangxi Province as a case study. Bot Stud 51:377–386

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Huo H, Feng Q, Su Y-H (2015) Shrub communities and environmental variables responsible for species distribution patterns in an alpine zone of the Qilian Mountains, northwest China. J Mt Sci 12:166–176

Kattel DB, Yao T, Yang W, Gao Y, Tian L (2015) Comparison of temperature lapse rates from the northern to the southern slopes of the Himalayas. Int J Climatol 35:4431–4443

Kearney MR, Gillingham PK, Bramer I, Duffy JP, Maclean IMD (2020) A method for computing hourly, historical, terrain-corrected microclimate anywhere on earth. Methods Ecol Evol 11:38–43

Körner C (2007) The use of 'altitude' in ecological research. Trends Ecol Evol 22:569–574

Körner C (2021) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer Nature, Cham

Kulonen A, Imboden RA, Rixen C, Maier SB, Wipf S (2018) Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. Divers Distrib 24:252–261

Le Roux PC, McGeoch MA (2008) Rapid range expansion and community reorganization in response to warming. Glob Change Biol 14:2950–2962

Leuschner C (2000) Are high elevations in tropical mountains arid environments for plants? Ecology 81:1425–1436

Li R, Dao Z, Li H (2011) Seed plant species diversity and conservation in the northern Gaoligong Mountains in western Yunnan, China. Mt Res Dev 31:160–165

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393

Márcia Barbosa A, Real R, Muñoz AR, Brown JA (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. Divers Distrib 19:1333–1338

McCarthy T, Rubidge BS (2005) The story of earth & life: a southern Africa perspective on a 4.6 billion-year journey. Struik, Cape Town

Moeslund JE, Arge L, Bøcher PK, Dalgaard T, Svenning JC (2013) Topography as a driver of local terrestrial vascular plant diversity patterns. Nord J Bot 31:129–144

Montgomery K (2006) Variation in temperature with altitude and latitude. J Geogr 105:133–135

Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, SANBI, Pretoria

Muellner-Riehl AN, Schnitzler J, Kissling WD, Mosbrugger V, Rijsdijk KF, Seijmonsbergen AC, Versteegh H, Favre A (2019) Origins of global mountain plant biodiversity: testing the 'mountain-geobiodiversity hypothesis.' J Biogeogr 46:2826–2838

Myers N (2003) Biodiversity hotspots revisited. BioScience 53:916

Neiman PJ, Ralph FM, White A, Kingsmill D, Persson P (2002) The statistical relationship between upslope flow and rainfall in California's coastal mountains: observations during CALJET. Mon Weather Rev 130:1468–1492

Nel W, Reynhardt D, Sumner P (2010) Effect of altitude on erosive characteristics of concurrent rainfall events in the KwaZulu-Natal Drakensberg. Water SA. https://doi.org/10.4314/wsa.v36i4.58429

Niittynen P, Luoto M (2018) The importance of snow in species distribution models of arctic vegetation. Ecography 41:1024–1037

Niskanen A, Luoto M, Väre H, Heikkinen RK (2017) Models of Arctic-alpine refugia highlight importance of climate and local topography. Polar Biol 40:489–502

Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB, Coldea G, Dick J, Erschbamer B, Calzado RF (2012) Recent plant diversity changes on Europe's mountain summits. Science 336:353–355

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. Trends Ecol Evol 23:149–158

Pickering C, Green K (2009) Vascular plant distribution in relation to topography, soils and micro-climate at five GLORIA sites in the Snowy Mountains, Australia. Aust J Bot 57:189–199

Punyasena SW, Eshel G, McElwain JC (2008) The influence of climate on the spatial patterning of Neotropical plant families. J Biogeogr 35:117–130

Rahbek C, Borregaard MK, Antonelli A, Colwell RK, Holt BG, Nogues-Bravo D, Rasmussen CMØ, Richardson K, Rosing MT, Whittaker RJ, Fjeldså J (2019) Building mountain biodiversity: geological and evolutionary processes. Science 365:1114–1119

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Riebesell JF (1982) Arctic-alpine plants on mountaintops: agreement with island biogeography theory. Am Nat 119:657–674

Rundel C, Bivand R (2013) Package 'rgeos' interface to geometry—open source. R package version 0.6.2

Sainge MN, Onana J-M, Nchu F, Kenfack D, Peterson AT (2017) Botanical sampling gaps across the Cameroon Mountains. Biodivers Inform. https://doi.org/10.17161/bi.v12i0.6707

Savage J, Vellend M (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. Ecography 38:546–555

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J Biogeogr 38:406–416

Schmeller DS, Urbach D, Bates K, Catalan J, Cogălniceanu D, Fisher MC, Friesen J, Füreder L, Gaube V, Haver M, Jacobsen D, Le Roux G, Lin Y-P, Loyau A, Machate O, Mayer A, Palomo I, Plutzar C, Sentenac H, Sommaruga R, Tiberti R, Ripple WJ (2022) Scientists' warning of threats to mountains. Sci Total Environ 853:158611

Schmitt CB, Senbeta F, Woldemariam T, Rudner M, Denich M (2013) Importance of regional climates for plant species distribution patterns in moist Afromontane forest. J Veg Sci 24:553–568

Shahgedanova M, Adler C, Gebrekirstos A, Grau HR, Huggel C, Marchant R, Pepin N, Vanacker V, Viviroli D, Vuille M (2021) Mountain observatories: status and prospects for enhancing and connecting a global community. Mt Res Dev 41(2):A1

Silveira FAO, Barbosa M, Beiroz W, Callisto M, Macedo DR, Morellato LPC, Neves FS, Nunes YRF, Solar RR, Fernandes GW (2019) Tropical mountains as natural laboratories to study global changes: a long-term ecological research project in a megadiverse biodiversity hotspot. Perspect Plant Ecol Evol Syst 38:64–73

Sturman AP (1987) Thermal influences on airflow in mountainous terrain. Prog Phys Geogr 11:183–206

Thornton JM, Pepin N, Shahgedanova M, Adler C (2022) Coverage of in situ climatological observations in the world's mountains. Front Clim 4:814181

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. Proc Natl Acad Sci 102:8245–8250

Thuiller W, Georges D, Gueguen M, Engler R, Breiner F, Lafourcade B, Patin R (2023) biomod2: ensemble platform for species distribution modeling. R package version 4.2-4. https://CRAN.R-project.org/package=biomod2

Urban MC (2018) Escalator to extinction. Proc Natl Acad Sci 115:11871–11873

Vagen TG (2010) Africa soil information service: topographic wetness index (TWI). International Center for Tropical Agriculture - Tropical Soil Biology and Fertility Institute (CIAT-TSBF), World Agroforestry Centre (ICRAF), Center for International Earth Science Information Network (CIESIN), Columbia University, Nairobi, Kenya and Palisades, NY. http://africasoils.net/

Vitasse Y, Ursenbacher S, Klein G, Bohnenstengel T, Chittaro Y, Delestrade A, Monnerat C, Rebetez M, Rixen C, Strebel N (2021) Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. Biol Rev 96:1816–1835

Wang G, Zhou G, Yang L, Li Z (2003) Distribution, species diversity and life-form spectra of plant communities along an altitudinal gradient in the northern slopes of Qilianshan Mountains, Gansu, China. Plant Ecol 165:169–181

Weber MM, Stevens RD, Diniz-Filho JAF, Grelle CEV (2017) Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography 40:817–828

Wei T, Simko V, Levy M, Xie Y, Jin Y, Zemla J (2022) package 'corrplot': visualization of a correlation matrix (version 0.92). 2021

Wursten B, Timberlake J, Darbyshire I (2017) The Chimanimani Mountains. Kirkia 19(1):70–100

Zu K, Wang Z, Zhu X, Lenoir J, Shrestha N, Lyu T, Luo A, Li Y, Ji C, Peng S (2021) Upward shift and elevational range contractions of subtropical mountain plants in response to climate change. Sci Total Environ 783:146896