



The enigmatic tropical alpine flora on the African sky islands is young, disturbed, and unsaturated

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Tropical alpine floras are renowned for high endemism, spectacular giant rosette plants testifying to convergent adaptation to harsh climates with nightly frosts, and recruitment dominated by long-distance dispersal from remote areas. In contrast to the larger, more recent (late Miocene onward) and contiguous expanses of tropical alpine habitat in South America, the tropical alpine flora in Africa is extremely fragmented across small patches on distant mountains of variable age (Oligocene onward). How this has affected the colonization and diversification history of the highly endemic but species-poor afroalpine flora is not well known. Here we infer phylogenetic relationships of ~20% of its species using novel genome skimming data and published matrices and infer a timeframe for species origins in the afroalpine region using fossil-calibrated molecular clocks. Although some of the mountains are old, and although stem node ages may substantially predate colonization, most lineages appear to have colonized the afroalpine during the last 5 or 10 My. The accumulation of species increased exponentially toward the present. Taken together with recent reports of extremely low intrapopulation genetic diversity and recent intermountain population divergence, this points to a young, unsaturated, and dynamic island scenario. Habitat disturbance caused by the Pleistocene climate oscillations likely induced cycles of colonization, speciation, extinction, and recolonization. This study contributes to our understanding of differences in the histories of recruitment on different tropical sky islands and on oceanic islands, providing insight into the general processes shaping their remarkable floras.

tropical alpine habitats | age of flora | molecular dating | extinction

The enigmatic floras restricted to high mountains in the tropics provide a unique opportunity to study the timing and impact of dispersal, establishment, and diversification, allowing us insight into the evolution of whole floras. These unique, often startlingly rich floras contrast starkly in growth forms and species compositions with those found in the tropical climes closer to sea level (1, 2). Across the tropics, the upper elevations of the high mountains in South America, Southeast Asia, and Africa (3) experience similar harsh environmental conditions: year-round high insolation and extreme diurnal rather than seasonal variation in temperature (4). The archetypical dwarf shrub forms (e.g., *Alchemilla* and *Lachemilla*) and giant rosette forms (e.g., *Dendrosenecio* and *Epeletia*) typically found in these habitats provide classic examples of convergent adaptations independently derived in distantly related plant groups (5, 6).

Whereas most mountains that harbor tropical alpine floras are the result of recent uplift [late Miocene, 11.6 Ma onward (7, 8)], the high mountains in tropical Africa vary in age from about 40 Ma to 1 Ma (9), with the origins of volcanoes in the rift zone of East Africa and Ethiopia likely resulting in isolated alpine conditions from the early Miocene (23 Ma) onward (10). This places maximum bounds on the ages of present-day species communities but leaves open questions as to the rate with which plants colonized the emerging high-elevation niches and the relative roles of dispersal leading to successful establishment, in situ diversification, and extinction in generating present-day species diversity and endemism (11, 12).

These factors can be expected to differ markedly between tropical mountainous regions that differ in age, spatial extent, and degree of connectivity through time. The rich flora of the high Andes extends thousands of kilometers through the Americas, with the potential for north–south exchange with “flickering connectivity” across wide areas caused by climatic change (13). By contrast, the much less species-rich afroalpine flora (Fig. 1A) is typically restricted to solitary mountains isolated from each other by vast expanses of tropical lowland vegetation (14). These lowland barriers, in place since the origins of the mountains, largely persisted throughout the glaciations, despite the

Significance

Resilience is required to withstand or mitigate the effect of human-induced climate change. Today whole ecosystems are affected by climate change, but our understanding of their evolution and natural response is limited, often restricted to individual populations or species. The enigmatic flora on the tops of the African sky islands is isolated and unique, showing striking adaptations to the harsh tropical alpine conditions. Here we analyze genome data from a large fraction of afroalpine plants and show that this remarkable flora has a dynamic history with frequent colonizations and extinctions, most likely caused by previous natural climate changes during the ice-age cycles. The flora will be particularly vulnerable to human-induced climate warming, reducing alpine habitat into successively smaller areas.

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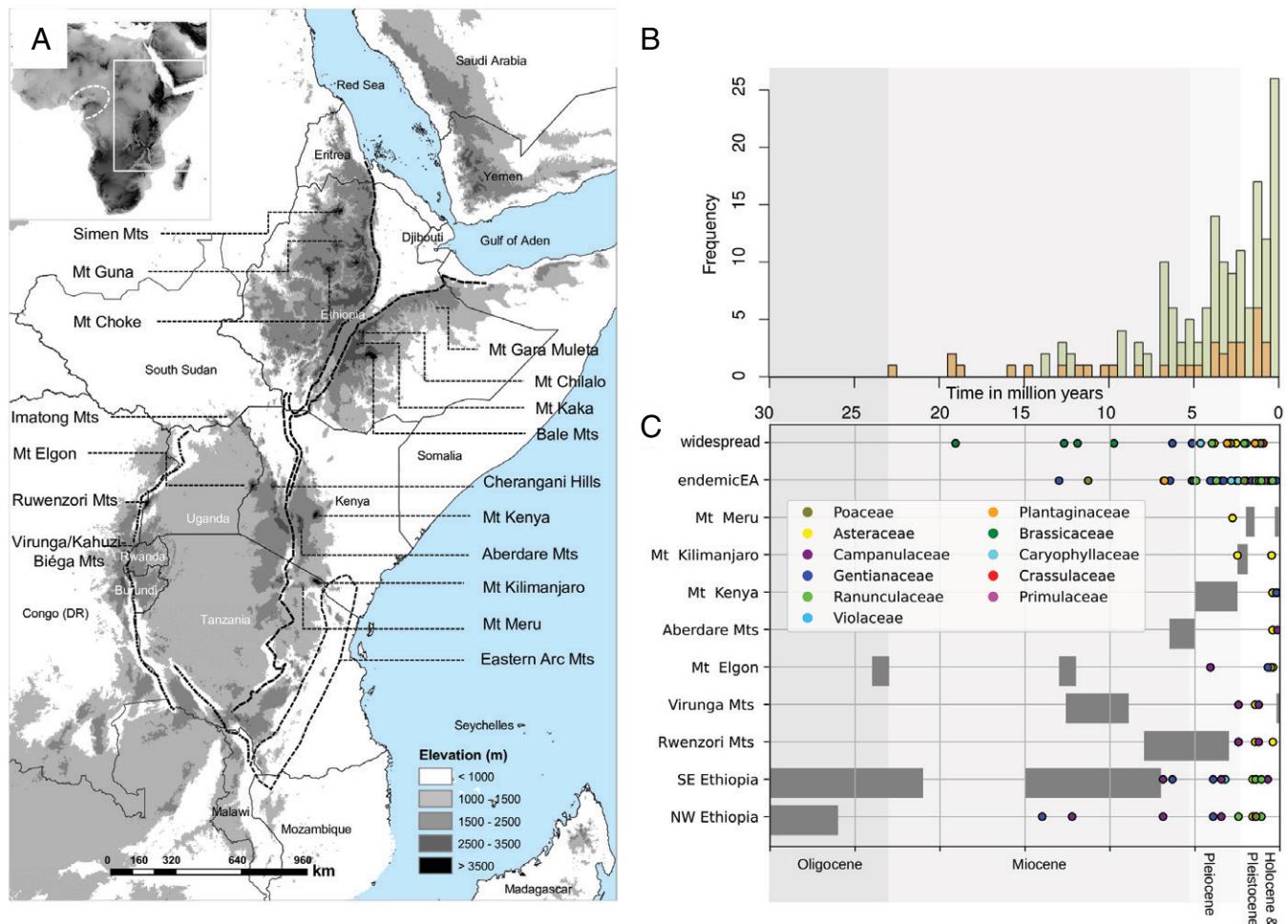


Fig. 1. Geographic distribution and recruitment to the afroalpine flora (>3,500 m). (A) Major mountains and mountain regions in eastern Africa. The Great Rift Valley is shown as stippled lines. (B) Numbers of afroalpine colonization (orange) and in situ diversification (olive) events per 0.5-Ma time bin. Colonizations, here represented by stem nodes, must be interpreted as maximum age estimates for events that are more recent to an unknown degree. (C) Stem age estimates of afroalpine species in relation to mountain orogeny [gray bars; Gehrke et al. (9)]. Species are colored according to family. Local endemics (species restricted to one or two mountains) are mapped to individual mountains; the remaining species are classified as “eastern African endemics” (endemicEA) or as “widespread.” Age estimates in B and C represent both Bayesian median node ages of individual seed plant clades.

eight times greater than present-day area of afroalpine habitat inferred for the Last Glacial Maximum (14). Population genetic studies of several afroalpine plant species have shown strong intermountain isolation of populations with genetic exchange limited to rare long-distance dispersal events rather than ecological connectivity (15). The pattern of recruitment to the floras on such isolated continental “sky islands” might be most similar to that on oceanic islands such as Hawaii (11).

The key to inferring the sequence and timing of the dispersal and speciation events that founded a biome is comprehensively sampled time-calibrated phylogenetic trees. The afroalpine flora is dominated by genera that are well known from their numerous species distributed across both northern and southern temperate regions. Case studies [e.g., *Alchemilla*, *Carex*, *Helichrysum*, and *Ranunculus* (15)] have begun to paint a picture of multiple independent colonizations from the late Miocene *ca.* 10 Ma onward, particularly from remote northern as well as southern temperate areas, followed by limited in situ diversification (15). A deeper understanding of the process of recruitment to tropical alpine floras requires a broad comparison of multiple independent groups (12), but past comparisons in the afroalpine region (11) have been limited by the state of phylogenetic knowledge across the flora. Here, we address this limitation, analyzing multiple lineages

from the afroalpine flora based on new field-collected material and data from high-throughput sequencing.

Results

We collected new material during field expeditions to all major mountains in East Africa and Ethiopia and gathered novel sequence data for 92 species belonging to 33 genera and 13 families (*SI Appendix*, Table S1). The species were selected to represent 1) both local and regional endemics as well as more widespread species, 2) species-rich as well as species-poor lineages in the afroalpine flora, 3) different habitats, and 4) those not previously included in phylogenetic studies. We used genome skimming (16) to retrieve high-copy chloroplast genomes and nuclear ribosomal cistron, obtaining 1.8 to 9.8 million reads per sample (NCBI Sequence Read Archive [SRA] database under the BioProject ID PRJNA766027).

We used an analytical pipeline to update alignments from published analyses of 1) >35,000 species of seed plants represented by two chloroplast markers (17) and 2) individual seed plant clades with chloroplast and/or nuclear sequence data (refs. 6 and 18–29 and *SI Appendix*, Table S3). Our approach (*SI Appendix*, Appendix 1) allowed us to supplement the new

data with similar sequences from GenBank, thus increasing the number of afroalpine species to a total of 102 (19 of which were represented with two or more accessions; *SI Appendix*, Tables S2–S4), representing 20% of the 515 species, 18% of the 90 genera, and 26% of the 50 families known from the flora (9) plus nonafroalpine outgroups (*SI Appendix*, Table S3). To infer time windows for colonization of the afroalpine region and in situ diversification within it, we used molecular dating analyses, of which most were calibrated using fossil evidence. We summarized ages for stem and crown nodes of afroalpine species and clades. To test the robustness of the results we compared these two datasets and two different molecular dating methods: seed-plant-wide analyses with penalized likelihood (PL) and individual seed plant clades with both PL and Bayesian statistics [the latter incorporating phylogenetic uncertainty; matrices and phylogenetic trees in text format are available via the Open Science Framework (30) and figure format phylogenies are presented in *SI Appendix* S2]. Thus, we obtained up to three stem age estimates for each of the 102 afroalpine species (*SI Appendix*, Table S2), depending on differences in sampling across datasets, with each approach delivering 91 to 93 dated

nodes (representing common ancestors of afroalpine species/populations and their closest relatives).

Our phylogenies revealed that the closest relatives of afroalpine lineages were geographically distant, nested within wider temperate clades, from which we assumed that afroalpine colonization occurred after divergence of afroalpine lineages from their most recent common ancestors. We found evidence for divergent lineages (supported nonmonophyly) within some afroalpine species (*SI Appendix*, Table S4) and more independent dispersals into the afroalpine region than expected if each genus only dispersed once (*SI Appendix*, Table S5). Each of the genera *Lobelia*, *Ranunculus*, and *Swertia*, for example, colonized the afroalpine region at least twice independently.

The molecular dating results enabled us to place the assemblage of multiple afroalpine plant lineages into a unified time-frame (Fig. 2). Stem node ages may thus substantially predate dispersals (31), but we nevertheless found a range of ages concentrated toward the present (Fig. 1 B and C). Of a total of 43 stem nodes of species and clades representing the maximum bounds for times of colonization of the afroalpine, 58%, 68%, and 83% fell within the last 5 My (individual seed plant clades

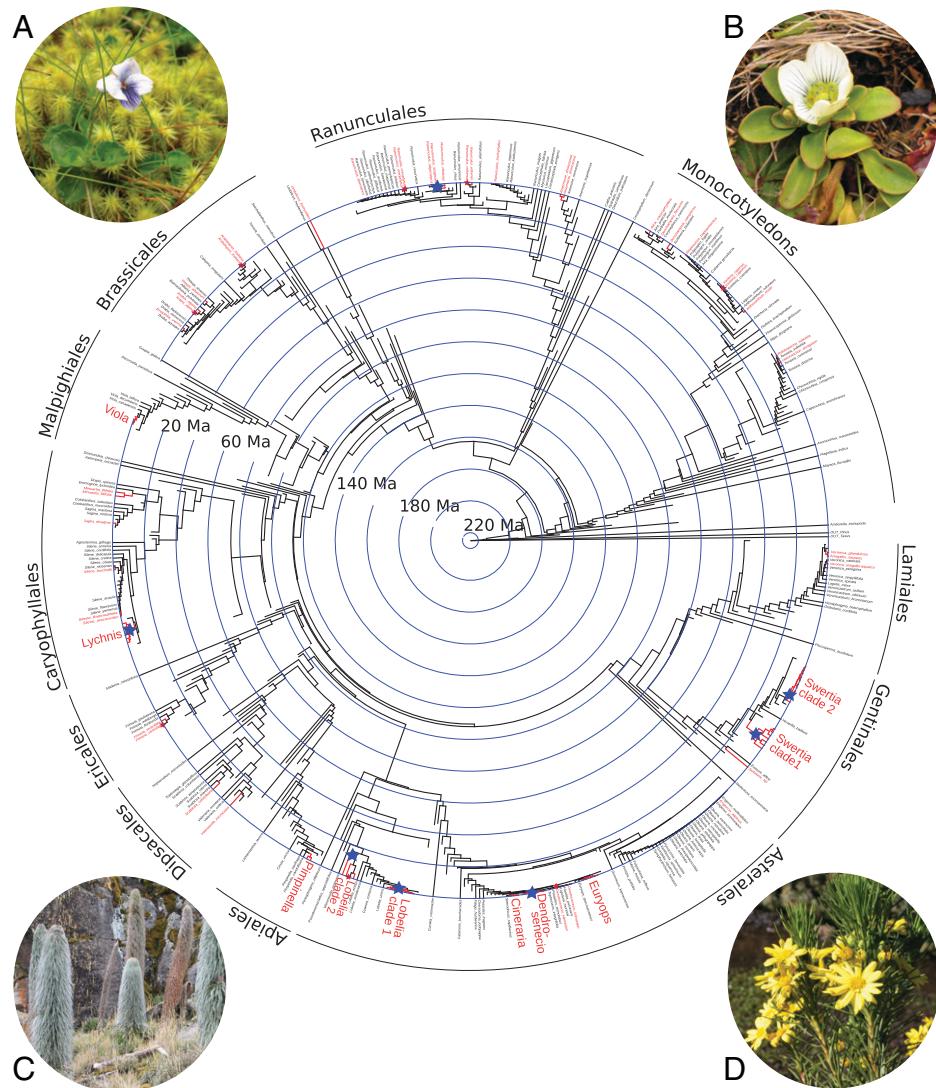


Fig. 2. Seed-plant-wide dated phylogeny based on our new data combined with the original matrix of Janssens et al. (17) with afroalpine species indicated in red type and those of the original dataset further indicated with a red star. Clades not including afroalpine species are pruned to crown clade nodes to increase readability. Afroalpine clades supported by posterior probability ≥ 0.95 in the BEAST2 analyses of the individual seed-plant clades are indicated with blue stars. Circles indicate time in million years before the present. Photographs show examples of afroalpine species: (A) *Viola eminii*, (B) *Swertia crassiuscula*, (C) *Lobelia telekii*, and (D) *Euryops brownei*. Image credit: B. Gehrke, available under a creative commons CC-BY-NC license at <https://www.inaturalist.org/>.

BEAST2 and PL and seed-plant-wide PL) and 72%, 89%, and 88% within in the last 10 My. None were consistently older than 15 My (*SI Appendix*, Table S6). Similar to Rabosky et al. (32), we found no obvious relationship between the timing of arrival in the afroalpine region and subsequent in situ diversification, as illustrated by the diversifications of both early- and late-arriving lineages of *Lobelia* and of *Swertia* (*SI Appendix*, Fig. S1).

We found that most afroalpine lineages diverged from their nonafroalpine relatives after the end of the major mountain uplifting processes (Fig. 1B, the number of colonization events). More than 80% of those included in the analyses of individual seed plant clades diverged within the last 5 My, with a maximum of only 7 of our 102 sampled species dating back to the early phases of afroalpine habitat existence (*SI Appendix*, Table S7). Those with narrow distributions typically arrived or diverged from their sister lineages after the final uplift of the mountain(s) to which they are currently restricted (Fig. 1C). The distribution of node ages within independent afroalpine lineages, as summarized across independent clades, showed increase toward the present (Fig. 1B and C). Species accumulation increased exponentially over time: Fitting our data to an exponential distribution revealed high R^2 values (individual clades BEAST2: 0.98; individual clades treePL: 0.97; seed-plant-wide treePL: 0.96; Fig. 3). The data showed distinct changes in accumulation rates through time that were not apparent in modeled curves (Fig. 3 and *SI Appendix*, Fig. S2). According to an exponential diversification model, we would only expect a change in rates close to the present, but we also detected changes that occurred earlier. Depending on the dating method, changes began around 6 to 5 Ma and became more frequent within the last 2.5 My (Fig. 3).

Discussion

Although the final uplift of some of the tropical African high mountains date back to the Oligocene (>30 Ma), and although our stem node ages constitute a considerably conservative estimate for estimating the timing of colonization of afroalpine plant lineages, we found that most lineages must have colonized the afroalpine during the last 5 or 10 My. Based on estimated ages of 20% of the afroalpine flora, we show that the assembly of this flora accelerated toward the present, with a rate of species accumulation within the flora increasing exponentially (Fig. 3). This suggests that the afroalpine region remains below its carrying capacity for species diversity.

We might expect colonization events to accumulate steadily over the time that habitat is available, or even to tail off toward the present as niches are filled. Our finding of concentrations of both afroalpine colonization and in situ diversification events toward the present (Fig. 1B) appears, therefore, to point to a substantial impact of extinction on the composition of the flora. The pattern we observe is consistent with the extremely low intrapopulation genetic diversity and recent intermountain population divergence reported for many individual afroalpine species (15). Palynological and macrocharcoal records from the Bale Mountains in Ethiopia show a marked reduction of afroalpine communities around 12.5 ky B.P. (33) and paleoenvironmental data from lake cores imply a major climatic incursion in tropical East Africa around 11.5 ky B.P. (34), suggesting climate-induced extinction of afroalpine plants after the last glaciation. Our results thus provide evidence from across the flora in line with the emerging view of the afroalpine flora as the product of cycles of colonization, speciation, extinction,

and recolonization induced by the Pleistocene climate oscillations, resulting in unsaturated, fragile communities of species depauperated by frequent genetic bottlenecks (15).

The occurrence of several spikes in species accumulation through the last 7 My (Fig. 3A, row 2) suggests that net species accumulation across lineages within the flora may have been impacted by common factors such as climate change and mountain uplifting. The precision of our age estimates is not, however, sufficient to address the effect on in situ diversification in more detail. Future analyses could narrow down such estimates through a combination of denser taxon sampling, coalescence-based dating of species (35), and dating the evolution of key adaptive traits (36) and could incorporate model-based biogeographic analysis to assess lag times between origins of habitat, colonizations, and in situ diversification in individual clades (37).

How does the recruitment of the afroalpine flora compare to that of other tropical alpine floras, and to that of comparably isolated oceanic island floras? The stages of mountain building that pushed colonizable substrate out of the tropical climate zone were mostly recent in South America and Southeast Asia, taking place from the mid-Miocene onward (7, 8). Global cooling cycles that further contributed to shaping current day occurrence patterns of tropical-alpine plants intensified since the start of the Quaternary glaciations about 2.6 Ma (38). This is consistent with recent dating studies from the tropical alpine flora in South America (39). Here we show that most of the afroalpine flora also dates to the Plio-Pleistocene (Fig. 1), despite the much more variable ages of the individual African high mountains, with only few earlier-arriving lineages.

Thus, endemic alpine species diversity is recent in origin across the tropics, making these regions evolutionary cradles of biological diversity (12, 39). The Andean tropical alpine flora is, however, much richer in species than the afroalpine flora and includes hyperdiverse clades such as *Calceolaria*, *Epeletia* s.s., *Lupinus*, and *Pentacalia* (40). Such large in situ species radiations are virtually absent from the afroalpine flora, probably reflecting the much smaller spatial extent and greater fragmentation of the tropical alpine habitat in Africa. The high species turnover across the Andean Páramos versus the homogeneity of species compositions across the isolated fragments of afroalpine habitat is consistent with the hypothesis that periodic connectivity drives diversification (13). An equivalent analysis of species accumulation in the Páramo is needed to further compare patterns of past extinction and resilience for tropical alpine floras in general.

The history of recruitment and evolution of the afroalpine flora also differs from that of comparable oceanic islands. The Macaronesian archipelagos show lower levels of endemism (20%) than tropical alpine regions (>60%), probably because they are closer to the source of their floristic diversity, northern Africa. Contrary to the afroalpine flora but similar to the tropical Andean flora, Macaronesia shows striking species radiations following establishment in many clades [e.g., *Aeonium* and *Echium* (41, 42)], perhaps due to a combination of greater age and lower extinction rates given more stable oceanic climates (43). The islands of Hawaii are more similar to the afroalpine mountains in terms of their degree of isolation, but the estimated <500 km² of vegetation at high elevation in Hawaii, home to just 13 tropical alpine species, is much smaller (11). This is despite a potentially greater age of the Hawaiian flora, which may originate from older, now submerged, islands of the chain (44).

The differences between the afroalpine flora and other island- and alpine-like floras across the tropics serve to highlight their unique histories and unique diversity. These floras, with

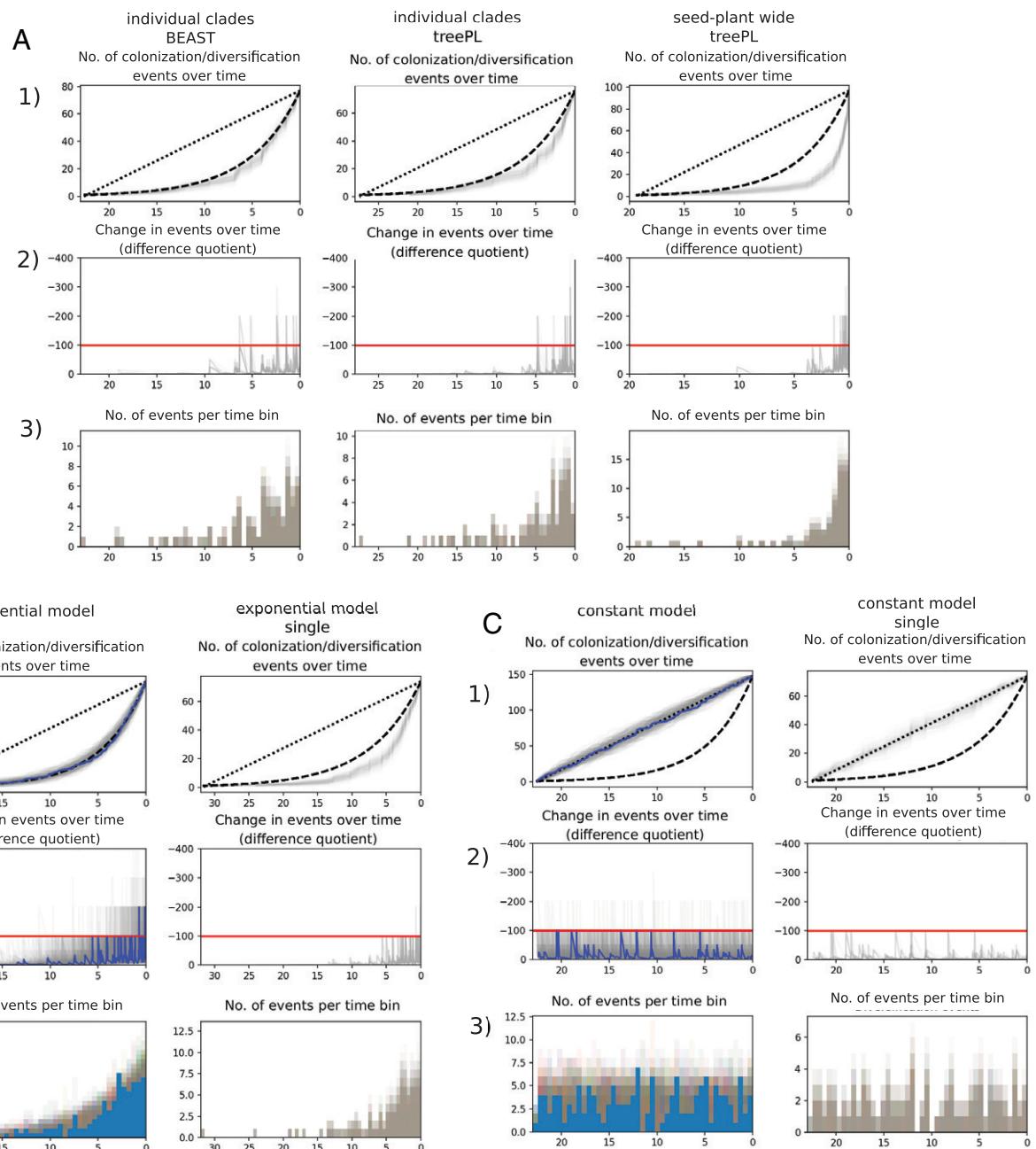


Fig. 3. Species accumulation over time in the afroalpine region based on historical lineage diversity estimates and relative branching times obtained from the time-calibrated phylogenies. These plots differ from standard lineage through time plots in that species accumulation in a region results from colonization events in addition to regional diversification of multiple independent lineages. Row 1: Number of colonization/diversification events over time. The black dotted line marks a constant rate model and the black dashed line an exponential model. Row 2: Change in number of colonization/diversification events over time calculated as a difference quotient (see main text). The red line shows the maximum difference of change in a constant model. Row 3: number of colonization/diversification events per 0.5-My intervals. Age estimates were subsampled to 50% 200 times. Results for our three different dating methods are shown in A. Simulated results are shown in B (exponential model) and C (constant model), with the left columns representing 200 iterations (one highlighted in blue) and right columns a single iteration subsampled to 50%.

their characteristic giant rosette plants and dwarf shrubs, have evolved independently in similar extreme environments against common backgrounds of climatic fluctuation and resulting species diversifications. Our results show that even in the older African mountains, the present-day tropical alpine flora has assembled remarkably recently, most likely repopulating habitats impacted by extinctions of earlier colonizers. However, the sheer speed and compounding impact of the current human-caused habitat destruction and climate change is unprecedented in this evolutionary context. The afroalpine flora inhabits a narrow band of suitable conditions that are already limited to the

upper extremes of the mountains, and it is susceptible to severe and increasing human-induced impacts such as overgrazing. The already decreasing extent of intact alpine habitat is projected to be pushed higher into smaller areas and might disappear altogether as the climate continues to warm (15, 45).

Materials and Methods

We collected plant material during field expeditions to all major eastern African sky islands (Ethiopia, Tanzania, Kenya, and Uganda). Vouchers and silica-dried leaf samples were deposited in herbaria in the countries of origin and in the

herbarium and DNABank at the Natural History Museum, University of Oslo (*SI Appendix*, Table S1). Our taxon sampling represents 102 species that occur in the alpine zone above 3,200 m (*SI Appendix*, Table S2) (9). We extracted DNA from silica dried leaves using Qiagen DNeasy Plant Mini Kits and constructed libraries using the TruSeq compatible genomic DNA library preparation kits for Illumina paired-end sequencing of 550 base pair inserts with multiplexing for 96 samples (Illumina). Sequencing was carried out on the Illumina HiSeq v2500 platform at the Norwegian Sequencing Centre (<https://www.sequencing.uio.no/>).

We inferred phylogenetic relationships of afroalpine species and clades based on plastid and nuclear ribosomal DNA sequence markers that have been widely sampled for phylogenetic studies by incorporating our new sequences into existing alignments of 1) all seed plants (17) and 2) individual seed plant clades (6, 18–29) (*SI Appendix*, Table S3); most of the latter are based on dense sampling of taxa, variable sequences, and shallow fossil calibrations. We used PhylUp (46) (<https://github.com/mkandziora/PhylUp/>), a Python workflow for finding and adding sequences to the target alignments using blast+ (47), to search both user-supplied data and GenBank. We first split concatenated matrices into single loci and used ncbiTAXONparser (<https://github.com/mkandziora/ncbiTAXONparser>) to link taxa to species names accepted by NCBI. We opted to add new sequences to the original alignments if the BLAST search returned a blast e-value of <0.001. Maximum sequence length was set to 2,000% to add potentially much longer matching plastid sequences, which were later trimmed to alignment length. Final alignments are available through the Open Science Framework (30).

We estimated ages of afroalpine species and clades based on the seed-plant-wide and individual seed-plant clade datasets using two different molecular dating methods: penalized likelihood as implemented in treePL (48) and Bayesian statistics under an uncorrelated lognormal relaxed clock model as implemented in BEAST2 (49). Apart from applying current versions of the software we aimed to match the age calibrations and other settings as reported in the original publications as closely as possible (*SI Appendix*, Table S8).

We summarized the age distribution of sampled colonization and in situ diversification events across the afroalpine flora as a whole and compared it to expectations given different models of diversification similar to the approaches in refs. 35 and 50. We analyzed the differences between consecutive node ages across phylogenies (for all individual seed-plant clades together and for the seed-plant-wide phylogeny), thus summarizing both colonization and diversification rate heterogeneity across lineages and through time. We used the difference quotient function incorporating a degree of phylogenetic and age uncertainty by 1) subsampling and 2) assessing separately results given the different age estimates obtained above (*SI Appendix*, Appendix 1). We compared the resulting distributions of densities of species accumulation through time, calculating the R^2 of the fit with

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those simulated assuming constant or exponential growth. Code used is available via data submission through the Open Science Framework (30). Detailed methods are presented in *SI Appendix*, Appendix 1.

Data Availability. DNA sequence reads from genome skimming are available from <https://www.ncbi.nlm.nih.gov/sra/PRJNA766027>. Code used for this study, alignments (including newly added sequences), phylogenetic trees, and analysis settings are available via the Open Science Framework (<https://osf.io/brmjg>), including reference to the respective original publications (6, 17–29) on which alignments and settings were based and respective initial publications are cited. All other study data are included in the article and/or *SI Appendix*. All contributions are cited in the main text and researchers that shared previously unavailable datasets from those publications are acknowledged.

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