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REVIEW

History and evolution of the afroalpine flora: in the footsteps of Olov Hedberg

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Abstract

The monumental work of Olov Hedberg provided deep insights into the spectacular and fragmented tropical alpine flora of the African sky islands. Here we review recent molecular and niche modelling studies and re-examine Hedberg's hypotheses and conclusions. Colonisation started when mountain uplift established the harsh diurnal climate with nightly frosts, accelerated throughout the last 5 Myr (Plio-Pleistocene), and resulted in a flora rich in local endemics. Recruitment was dominated by long-distance dispersals (LDDs) from seasonally cold, remote areas, mainly in Eurasia. Colonisation was only rarely followed by substantial diversification. Instead, most of the larger genera and even species colonised the afroalpine habitat multiple times independently. Conspicuous parallel evolution occurred among mountains, e.g., of gigantism in *Lobelia* and *Dendrosenecio* and dwarf shrubs in *Alchemilla*. Although the alpine habitat was ~ 8 times larger and the treeline was ~ 1000 m lower than today during the Last Glacial Maximum, genetic data suggest that the flora was shaped by strong intermountain isolation interrupted by rare LDDs rather than ecological connectivity. The new evidence points to a much younger and more dynamic island scenario than envisioned by Hedberg: the afroalpine flora is unsaturated and fragile, it was repeatedly disrupted by the Pleistocene climate oscillations, and it harbours taxonomic and genetic diversity that is unique but severely depauperated by frequent bottlenecks and cycles of colonisation, extinction, and recolonisation. The level of intrapopulation genetic variation is alarmingly low, and many afroalpine species may be vulnerable to extinction because of climate warming and increasing human impact.

Keywords Afroalpine · Colonisation · Eastern African mountains · Evolution · Long-distance dispersal · Olov Hedberg

Introduction

The spectacular flora occurring on the tops of the tropical African sky islands has attracted the attention of generations of biogeographers because of its extreme fragmentation and iconic examples of gigantism and convergent evolution: the impressive plants of *Lobelia* and *Dendrosenecio* can rise up to 10 m above the otherwise low-growing alpine vegetation. These mountains provide an excellent example of a highly isolated system, where interaction between historical and contemporary processes has formed a flora rich in local endemics (Gehrke and Linder 2014; Gizaw et al. 2016a). The uppermost, afroalpine habitat is home to no more than ~ 520 species of vascular plants that are able to endure a peculiar and harsh climate: while the days can be very warm, the nights are often freezing cold, all through the year (Hedberg 1961; Gehrke and Linder 2014). This striking diurnal cycle has a great impact on the local

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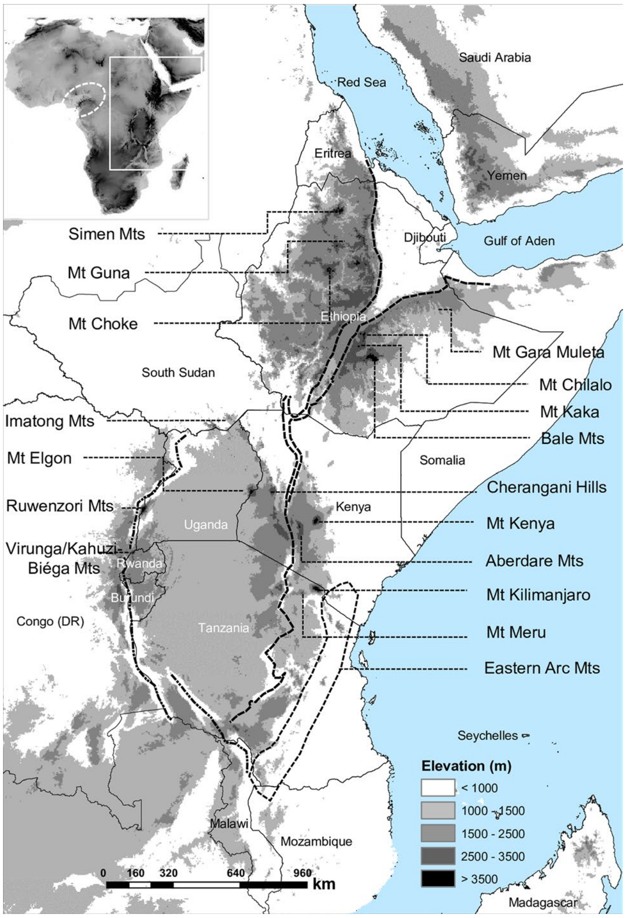

Fig. 1 Major mountains and mountain ranges that are sufficiently high to support an alpine habitat in eastern Africa under the current climate (the Eastern Arc Mts are also indicated although these do not harbour alpine vegetation). Fault lines of the Great Rift Valley are shown as stippled lines. The small West African afroalpine habitat patches are indicated with the white circle on the small map in the left top corner

biota, and stands in stark contrast to the seasonal climates at higher latitudes and to the warm climates of the adjacent tropical lowlands. Most species of the afroalpine flora are endemic to Africa (78%; Hedberg 1961), but almost as many (67%) are exclusive to these mountains (Gehrke and Linder 2014). Many of them also extend below the treeline into the species-rich afromontane region, one of the 36 global biodiversity hotspots (Mittermeier et al. 2011; CEPF 2016), and together, the afroalpine and afromontane floras can be referred to as the afrotemperate flora (White 1983; see Carbutt and Edwards 2015 for concept discussion and delimitation).

Most of the mountains that are high enough to support an afroalpine flora are found in Ethiopia and East Africa (here referred to as eastern Africa), but a few small patches with a depauperate afroalpine flora are also found in West Africa (Fig. 1; Gehrke and Linder 2014). In eastern Africa, these high mountains occur along one of the most prominent rift systems on earth, the East African Rift System (EARS), which is more than 3000 km long and transects the Ethiopian and Kenyan plateaus (Ring et al. 2018). It is divided into one older, volcanically active Eastern Branch and a younger, less volcanic Western Branch (Ring et al. 2018). The onset of mountain uplift is poorly dated, but it may have begun 45 Ma (Ebinger et al. 2000; Trauth et al. 2005; Ring et al. 2018). The associated volcanism resulted in the formation of the extensive mountain ranges in the Ethiopian highlands, where huge Miocene shield volcanoes are superimposed on much older flood basalts, and the scattered high mountains in East Africa, with origins ranging from the Miocene to the late Pliocene (Griffiths 1993). Most of the mountains appear to have been uplifted to sufficient elevation for developing alpine vegetation as late as the Pliocene or even Pleistocene, i.e., mainly during the last 5 Myr (reviewed in Gehrke and Linder 2014).

The exploration of the afroalpine flora started in the early 1800s (see, e.g., Richard 1847–1851; the term afroalpine was used for the first time by Hauman 1933). Many mountains were still unexplored when Engler (1892) published an early account of the East African mountain flora. Since then, many expeditions resulted in new knowledge of certain plant groups and individual mountain floras, such as the series of papers by Fries and Fries (e.g., 1922a, b, 1923, 1948). In 1948, the Swedish botanist Olov Hedberg participated in an East Africa Expedition and made numerous new collections from the afroalpine flora. In the following years, he studied all available herbarium material and published his monumental book '*Afroalpine Vascular Plants. A Taxonomic Revision*' in 1957 (Hedberg 1957), the first complete account since that of Engler (1892). This book provided a state-of-the-art taxonomy of the entire afroalpine flora in East Africa (but did not include Ethiopia or Cameroon), as well as a comprehensive appendix with detailed discussions and morphological measurements. Building on this solid taxonomic foundation, Olov Hedberg, partly together with his wife Inga Hedberg, continued to explore these mountains and published several insightful papers on the origin, evolution, taxonomy, ecology and biogeography of the afroalpine flora in the following decades. They also carried out or initiated taxonomic revisions of the entire Ethiopian flora (Hedberg 1983), leading to the publication of the Flora of Ethiopia and Eritrea in 1980–2009 (Demissew et al. 2011; Hedberg and Persson 2011). The Hedbergs also performed extensive cytological investigations, documenting the impact of polyploid evolution in the afroalpine flora (49% polyploidy; Hedberg and Hedberg 1977; vs 33% globally; Rice et al. 2019; and > 80% in polar desert; Brochmann et al. 2004).

Hedberg (1961, 1965, 1969, 1970, 1986, 1997) emphasised the importance of the harsh climate and recurring frosts in defining the afroalpine flora. He postulated that whereas some species, such as the giant senecios (Fig. 2) and giant lobelias, were differentiated from less specialized forms found at lower elevations, a large proportion of the flora instead has strong phytogeographic affinities to cold-adapted lineages in remote temperate areas of the world. Hedberg (1961) stated that '[the afroalpine flora] seems to have existed in tropical East Africa before the formation of the mountains now harbouring it, and to have been strongly isolated from other high-mountain (or temperate) floras for a long time'. In his taxonomic work, he stressed that earlier authors typically had exaggerated the level of intermountain allopatric ('vicarious') speciation, reducing many described single-mountain endemics into synonymy (e.g., Hedberg 1955, 1957). He hypothesized the existence of habitat bridges between certain mountains under past climates, at least for plants that are able to grow in the montane zone. However, he thought that the mountain top populations must have remained isolated from each other even during glacial periods, as supported by his finding that the proportion of endemic species increased with their ascending lower altitude limit. He, therefore, emphasised the importance of long-distance dispersal (LDD), in particular by cyclones. He noted that direct habitat connection among mountains is inconsistent with the striking differences in species composition of ecologically similar plant communities in different mountains, such as the *Dendrosenecio* forests and *Alchemilla* shrublands, suggesting that the communities were synthesized on each mountain separately after independent LDD of the constituent species.

In this review, we revisit Hedberg's views on the history and evolution of the afroalpine flora and review recent work using molecular and niche modelling tools that were unavailable to him. We concentrate on the afroalpine flora, but also touch upon plant groups and themes representing the wider afrotemperate flora. We put particular emphasis on dated phylogenies and phylogeographic results based on range-wide sampling, and place these in the context of the geological and climatic history of the region. The new insights and large body of evidence accumulated since Hedberg's era point to an emerging scenario of a young, unsaturated, fragile and vulnerable island flora, with unique taxonomic and genetic diversity that seems to be severely depauperated by frequent bottlenecks and cycles of colonisation, local extinction, and recolonisation.

Plio-Pleistocene LDDs prevail in colonisation of the emerging sky islands

Botanists from temperate regions often feel somewhat lost in tropical forests, but more happily at home if they take on the laborious task of climbing beyond the treeline. Hedberg (1961, 1965, 1986) analysed the phytogeographic connections of the afroalpine flora and estimated that an astonishing proportion of the species (48%) belong to temperate elements, 10% to a South African element, and 3% to a Himalayan element (data from Hedberg 1986). He assigned only one third of the afroalpine species to an endemic afromontane element, among them the giant senecios and lobelias, which he thought originated from montane forest ancestors. Because of the high level of endemism, Hedberg (e.g., 1961, 1986) believed that the afroalpine flora was old, and that even the afroalpine populations of widespread species such as *Arabis alpina* had been isolated from their northern counterparts for at least some millions of years.

A series of studies have now tested Hedberg's hypotheses on the origin of the flora using molecular phylogenetic and phylogeographic tools to infer the ancestral lineages and ages of afroalpine species. The general patterns that begin to emerge might partly have surprised but certainly also excited Hedberg. Many afromontane clades of plants and animals are indeed old and many of them have their closest relatives in tropical lowland forests, with long-term climatic stability being a major factor generating and maintaining species diversity (e.g., Fjeldså and Lovett 1997; Lovett et al. 1988; Couvreur et al. 2008; Voje et al. 2009; Tolley et al. 2011; Dimitrov et al. 2012; Loader et al. 2014; Mairal et al. 2015). Afromontane clades, therefore, typically demonstrate niche convergence in their adaptation to higher elevations, consistent with the Out of the Tropical Lowlands (OTL) hypothesis (Qian and Ricklefs 2016; cf. also Merckx et al. 2015). Afroalpine species and clades, in contrast, tend to be much younger (Plio-Pleistocene) than believed by Hedberg, but in accordance with his view many of them originated after LDD from various remote temperate regions (cf. Linder 2014 and references below). Thus, many afroalpine lineages demonstrate niche conservatism in the sense that they were already adapted to cold climates, but they demonstrate niche convergence in the sense that their establishment in the afroalpine region required an adaptive shift from seasonal to diurnal cold climates (Nürk et al. 2018). It is possible, therefore, that many of the afroalpine lineages that arrived from temperate regions first established at lower, montane elevations (where many of them still occur today) before entering the true alpine zone with its nightly frosts (Gehrke 2018). Compared to temperate alpine floras, tropical alpine floras show stronger phylogenetic clustering relative to their surrounding floras; that is, on average, tropical alpine species are more closely related to each other than are species at lower elevations (Qian et al. 2021). This is probably caused by strong environmental filtering in combination with phylogenetic niche conservatism as suggested by Qian et al. (2021), but may also reflect that

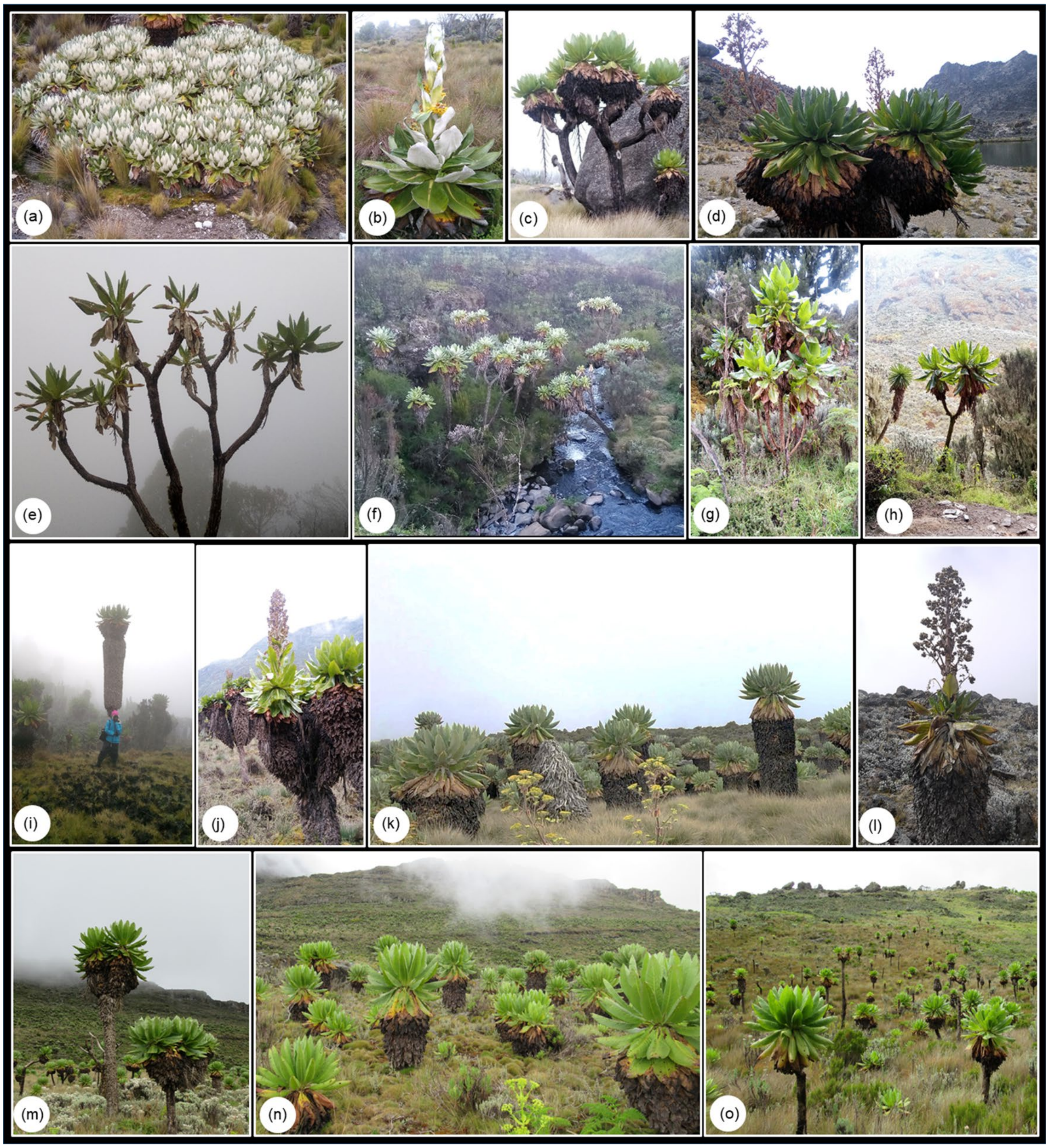

Fig. 2 The afroalpine flagship genus *Dendrosenecio* shows conspicuous and intricate variation in growth form and morphology, resulting from parallel altitude/habitat adaptation on different mountains combined with occasional long-distance dispersal and hybridization (Tusiime et al. 2020; Gizaw et al. in press; photos: Abel Gizaw). **a**–**d**: Growth form differentiation in high-altitude habitats on Mt Kenya. *Dendrosenecio keniensis* **a**, **b** is a low-growing (< 1.5 m), procumbent plant that branches close to the ground and occurs on constantly water-saturated soils, whereas *D. keniodendron* **c**, **d** is an erect giant with tall stems (up to 7 m) that branch high above the ground and occurs on well-drained soils. **e**–**h**: Plants at lower altitudes tend to have thin stems with only few old leaves kept for insulation, exemplified by plants of *D. battiscombei* on Mt Kenya (**e**, **f**) and *D. erici–rosenii* on Mt Ruwenzori (**g**, **h**). **i**–**o** Plants at higher altitudes tend to have thick stems with a prominent layer of insulating old leaves, exemplified by plants of *D. adnivalis* in the Ruwenzori Mts (**i**, **j**), *D. kilimanjari* on Mt Kilimanjaro (**k**, **l**) and *D. elgonensis* on Mt Elgon (**m**–**o**). Adopted from Tusiime et al. (2020)

a high proportion of the species in tropical alpine floras are derived from remote rather than local species pools.

Quite a few of the afroalpine species that Hedberg (1986) attributed to the endemic afromontane element seem rather to have originated after recent dispersal from temperate regions (e.g., all *Alchemilla* spp., Gehrke et al. 2016; some *Carex*, Box 1, Gehrke 2011; Gizaw et al. 2016b). *Helichrysum*, on the other hand, one of the most species-rich genera in the afroalpine flora, colonised the tropical alpine zone at least five times independently from local ancestors at lower elevations (Galbany-Casals et al. 2014). This genus originated in Southern Africa and spread via the Drakensberg Mountains into the montane and alpine regions of eastern Africa. In *Lobelia*, the tropical alpine zone was occupied independently by montane ancestors in the Western and Eastern Rifts (Knox and Palmer 1998). The giant lobelias arrived in East Africa from eastern Asia in the Miocene, and spread from there across the Congo basin in the early Pliocene to West Africa, across the deserts of northern Kenya at the Pliocene–Pleistocene transition to Ethiopia, and even to South America (Brazil; Knox and Li 2017; Perez and Yu 2021). The lineage radiated throughout the Pliocene to the late Pleistocene (Knox and Li 2017). In *Dendrosenecio*, the situation is not yet fully clarified, but a recent study based on high-throughput sequencing (Hyb-Seq) suggests that the lineage diversified from the Late Miocene and well into the Pleistocene (Gizaw et al. in press), and the current species diversity seems to result from parallel altitude/habitat adaptation in four mountain groups (Tusiime et al. 2020). Knox and Palmer (1995) suggested, contrary to Hedberg (1986) and others that the giant senecios originated at high altitudes on Mt Kilimanjaro. This is, however, highly unlikely given the young (Pleistocene) age of Mt Kilimanjaro and the new dating results of Gizaw et al. (in press). The genus *Hypericum* seems to have a complex history in Africa. It most likely originated there and dispersed to Eurasia and elsewhere, preferring temperate and often mountain habitats. It re-established in Africa multiple times independently in lower montane areas, from where it colonised the afroalpine habitat at least twice (Nürk et al. 2015).

Many studies have now documented temperate origins of afroalpine species. The widespread *Arabis alpina* colonized the afroalpine region twice during the middle and late Pleistocene, in both cases from the Balkans/Middle East (Box 2, Koch et al. 2006; Assefa et al. 2007). Western Eurasian origins have been inferred for *Anthoxanthum* (Box 3; late Pliocene; Pimentel et al. 2013), *Lychnis* (Box 4; late Miocene–early Pliocene; Popp et al. 2008; Gizaw et al. 2016a), and most likely *Alchemilla* (probably Pleistocene; Gehrke et al. 2016). The eastern African *Swertia* species belong to two different clades, both originating from the Himalayas (Chassot et al. 2001). Eurasian origins have also been inferred for some *Carex* and *Ranunculus* (Gehrke and Linder 2009). Southern African mountain origins have been inferred for most afroalpine lineages of *Senecio* (Box 5, Kandziora et al. 2016), and, astonishingly, the afroalpine fine-leaved *Festuca* clade was inferred to have originated from northern South America (Box 6; Messinian–Pliocene; Minaya et al. 2017).

The model plant *Arabidopsis thaliana* has an intriguing history. Hedberg considered this species to be indigenous to the afroalpine flora in his 1957 book (Hedberg 1957), and assigned it to the northern temperate element (Hedberg 1986). This was long disregarded by the scientific community, who assumed that this otherwise intensively studied plant is native only to western Eurasia. *Arabidopsis thaliana* diverged from its primarily western Eurasian sister clade in the early Pliocene according to Hohmann et al. (2015). It was surprising, therefore, when Durvasula et al. (2017) and Fulgione and Hancock (2018) found that the African populations are older and more diverse than the Eurasian ones. They inferred that the species originated in Africa, possibly somewhere in northern Africa, in the middle Pleistocene (1.2–0.8 Ma) associated with a transition from outcrossing to selfing. Colonisation of the eastern African mountains occurred during the last glaciation (90 ka), and the current lineages in Eurasia arrived from Africa as recently as 45 ka.

Some afroalpine lineages have been inferred to have connections both to western Eurasia and to southern Africa. Eastern African *Erica* are related to the western European and Mediterranean species as well as to those in the Drakensberg Mountains in southern Africa (Box 7, Pirie et al. 2019). In the Late Pliocene, sub-Saharan Africa was colonized by two divergent lineages of *Anthoxanthum*, one from southeast Asia to southern Africa, and one from western Eurasia to eastern Africa (Pimentel et al. 2013). Intriguingly, these currently allopatric lineages were inferred to have met in East Africa during the Pleistocene and produced an allopolyploid (Box 3, Tusiime et al. 2017).

Ongoing work based on high-throughput sequencing of ~ 100 afroalpine species points to continuous and in fact accelerating establishment of lineages arriving from temperate areas through the last 5 Myr (Kandziora, Gehrke, Popp, Gizaw, Brochmann and Pirie, unpubl.). Thus, the eastern African sky islands can be viewed as a strongly isolated archipelago that is still young and experiencing repeated disturbance. It is characterized by open and unsaturated environments that continue to diversify topographically and ecologically and that increasingly recruit more cold-adapted immigrants arriving with the occasional ‘seed rain’ from temperate areas. The Pleistocene climate cycles probably induced high community turnover and extinction rates, opening up niches for colonisation by new lineages. The general dynamic model of oceanic island biogeography predicts that immigration increases during the first part of an island’s life (Borregaard et al. 2016; Whittaker et al. 2017), and this might apply to volcanic continental islands as well (see also Vidal and Clark 2019; Flantua et al. 2020). The glacial periods potentially had even more dramatic and disturbing impact on continental islands than on typical oceanic islands, where the climate is thermally stabilized by the ocean (Cronk 1997) although heavily influenced by sea level changes (Fernández-Palacios et al. 2016). In the sky islands, the propagule pool arriving from temperate regions has probably been at its maximum during the glacials, because these lasted much longer than the interglacials, because of reduced distances to source regions, and because of considerably larger size of the target area (Fig. 3; the afroalpine habitat was estimated to be eight times larger during the LGM; Chala et al. 2017; see also van der Hammen and Cleef 1986 for similar inference for the Andean Páramo flora). Successful establishment after immigration may also have been more likely during glacial periods because of increased availability of empty niches following extinctions, altitudinal shifts, and accompanying disruption of entire communities such as bogs, which need thousands of years to re-establish (cf. van der Hammen and Cleef 1986; Smith 1986). The climate oscillations in eastern Africa were, however, particularly complex because of a lack of synchrony between changes in temperature and rainfall. Major drought periods may have caused massive extinctions on mountains harbouring a flora adapted to constantly humid conditions, such as present-day Ruwenzori.

Frequent immigration, limited diversification

The level of endemism at the species level is high in the afroalpine flora: 67% of the 520 native species that regularly occur above 3200 m are endemic to these sky islands (Gehrke and Linder 2014). Many of the endemics are widespread (Hedberg 1957); according to the updated species list of Gehrke and Linder (2014), only 15% are endemic to a single mountain (or a group of closely adjacent mountains). In many cases, the evolution of endemic species was probably linked to adaptive shifts from seasonally cold climates (or, more rarely, from the milder climate at lower elevations) to a strongly diurnal climate with recurrent night frosts (Gehrke 2018). There are only four endemic genera (*Dendrosenecio*, *Haplosciadium*, *Hedbergia* (cf. Scheunert et al. 2012), and *Oreophyton*; the former endemic genus *Uebelinia* is embedded in *Lychnis*; Popp et al. 2008).

The high level of species endemism is, however, not associated with substantial diversification of lineages establishing in the afroalpine region. There is much less diversification than implied by the early explorers who tended to over-describe new taxa (cf. Hedberg 1957), and much less than might be inferred solely from the number of species per genus. More than half of the 191 genera in the afroalpine flora are represented by a single species, and just 14% of them are represented by more than five species (Gehrke and Linder 2014). Phylogenetic studies show that many congeneric species result from independent migrations into the afroalpine region rather than diversification. Multiple immigrations have been inferred for *Carex* (at least 13 times; Gehrke and Linder 2009, 2011), *Ranunculus* (4 times; Gehrke and Linder 2009, 2011; Hörandl and Emadzade 2011), *Senecio* (4–14 times; Kandziora et al. 2016), *Helichrysum* (at least 5 times; Galbany-Casals et al. 2014), *Cardamine* (4 times; Carlsen et al. 2009), *Hypericum* (at least 2 times; Nürk et al. 2015), *Swertia* (2 times; Chassot et al. 2001), and *Anthoxanthum* (2 times; Tusiime et al. 2017).

Notable exceptions are *Alchemilla*, the giant *Lobelia* lineage, *Dendrosenecio*, and *Senecio*. In *Alchemilla*, a single immigration resulted in 17 afroalpine species, most of them with restricted distributions; these species probably evolved by allopatric speciation in different mountains or mountain groups after initial adaptation to the diurnal climate (Gehrke et al. 2016). The giant *Lobelia* lineage in eastern Africa diversified into 21 species to occupy a range of habitats in montane forests and the afroalpine zone (Knox and Palmer 1998), representing a combination of adaptive radiation and intermountain allopatric speciation. In *Dendrosenecio*, parallel altitudinal adaptation in different mountain groups, in a few cases combined with adaptation to different habitats

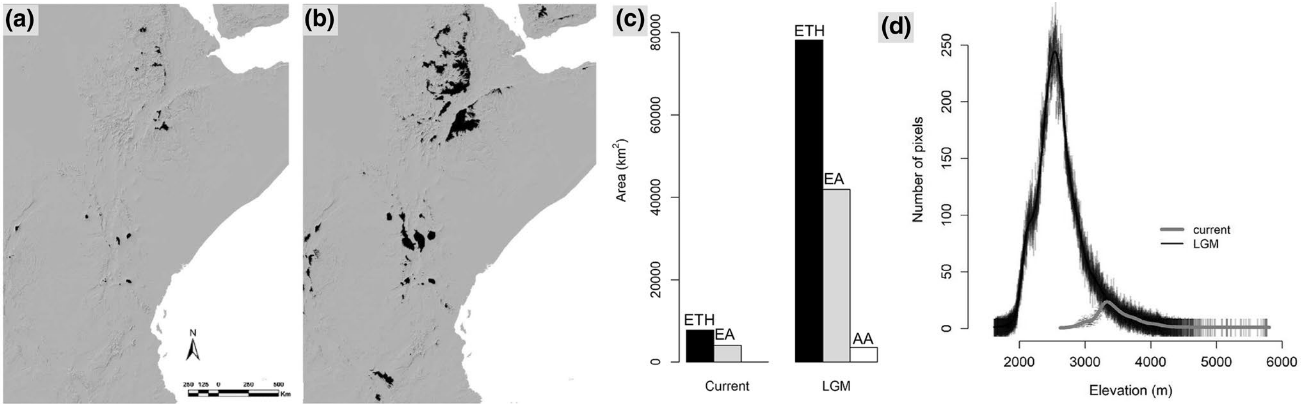

Fig. 3 Extent of the afroalpine habitat in eastern Africa under **a** current and **b** LGM (Last Glacial Maximum, ~21 ka) climate; alpine habitat is indicated in black. **c** Spatial extent of the alpine habitat in different regions: AA—Yemen (araboalpine), EA—East Africa (Kenya, Tanzania and Uganda), ETH—Ethiopia. **d** Extent of alpine habitat at different elevations; the y-axis represents 1 km × 1 km grid cell count. Adopted from Chala et al. (2017)

within individual mountains, seem to have resulted in 5–10 species (Tusiime et al. 2020; Gizaw et al., in press; note, however, that Knox 2005 and in particular Hedberg 1957, 1969 accepted more species). In *Senecio*, the most species-rich genus in the afroalpine flora, one of the independent immigrations resulted in seven species (Kandziora et al. 2016). In most cases, diversification was more limited and typically resulted in only two or a few allopatric species (e.g., *Carex monostachya* and *C. runssoroensis*; Gizaw et al. 2016b; Fig. 4; Box 1).

In addition to limited time since colonisation, it is possible that the level of intermountain gene flow is sufficiently high to prevent allopatric divergence into distinct species, rendering the afroalpine flora poor in single-mountain endemics. Phylogeographic studies show that although many afroalpine species are represented by distinct genetic groups in different mountains, there is often only subtle morphological differentiation between them or none at all, and there is increasing evidence for intermountain LDD and hybridisation (see below). This might be surprising in an island system with such strong geographic isolation, especially among the distant peaks in East Africa. Limited adaptive radiation within individual mountains is, however, expected given the limited size of their afroalpine habitat. This is probably the main reason why the tropical alpine Andean Páramo with its much larger and more connected areas of alpine habitat shows vastly greater species richness and many lineages showing extreme and rapid radiation (Madriñán et al. 2013; Sklenář et al. 2014; Hughes and Atchison 2015; Kolář et al. 2016a, b; Lagomarsino et al. 2016). Mountain ruggedness combined with degree and frequency of past connectivity are central concepts in the ‘flickering connectivity system (FCS)’ proposed by Flantua and Hooghiemstra (2018) as a major driver of species richness and endemism in mountains. The combination of extreme fragmentation and small extent of the alpine patches has probably resulted in much less expression of the FCS system in eastern Africa than in the Andes.

Parallel adaptation: giants, dwarfs and cushions

Hedberg was fascinated by the classical examples of convergent (or parallel) evolution provided by the enigmatic giant rosette plants of tropical alpine environments, such as the giant *Lobelia* and giant *Dendrosenecio* in Africa and *Puya* and *Espeletia* in South America. These lineages are distantly related but have independently developed strikingly similar morphological, physiological and life history traits in response to the tropical alpine climate (Hedberg 1964, 1969; Nagy and Grabherr 2009; Givnish 2010). They have large leaf rosettes which often fold up during the night to protect the buds, and they retain old leaves for insulation, accumulate large amounts of water to counteract temperature shocks, and grow taller with increasing altitude to escape the low temperatures close to the ground (Hedberg 1964; Smith and Young 1987; Fetene et al. 1998).

There is now convincing molecular evidence for parallel evolution also among mountains in eastern Africa, not only of gigantism in *Lobelia* (Knox and Palmer 1998; Knox and Li 2017) and *Dendrosenecio* (Knox and Palmer 1995;

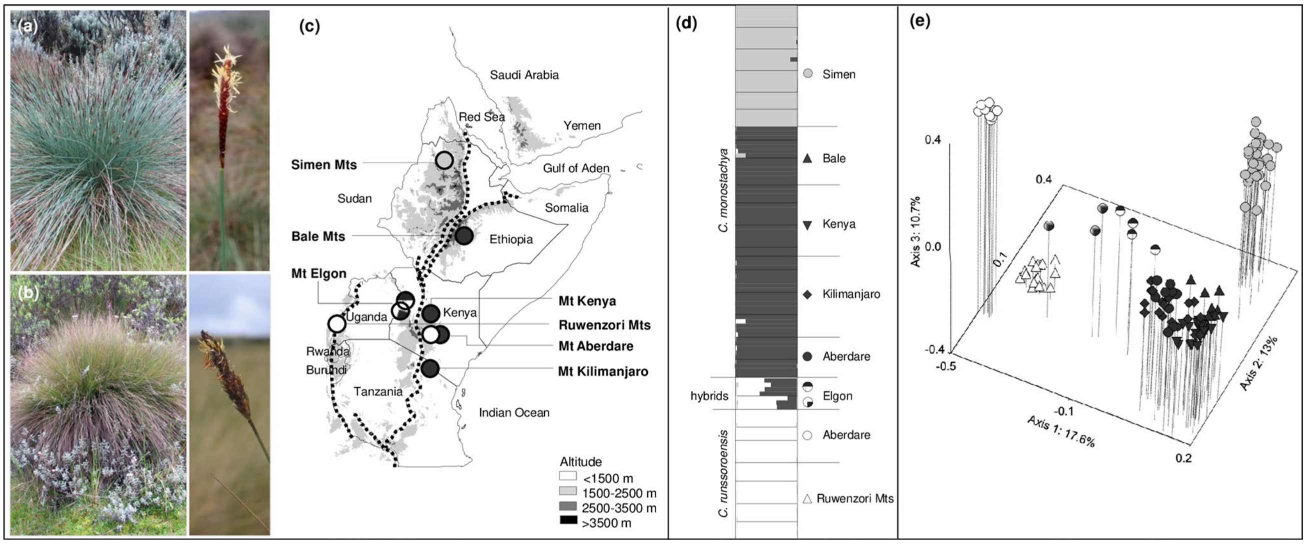

Fig. 4 AFLP-based phylogeographic analysis of the afroalpine endemics **a** *Carex runssoroensis* (29 plants from 7 populations; white symbols) and **b** *C. monostachya* (84 plants from 19 populations; black and grey symbols). **c** Geographic distribution of the three main genetic groups inferred from Bayesian clustering. **d** Graphical representation of the assignment pattern. **e** Principal Coordinates Analysis (PCoA) based on Dice’s coefficient of similarity between genotypes. Photos: **a** Abel Gizaw (spike) and Berit Gehrke (tussock); **b** Berit Gehrke. **c**–**e**: Reproduced from Gizaw et al. (2016b)

Tusiime et al. 2020; Gizaw et al. in press) but also of dwarf shrubs and perennial cushions, life forms typical of harsh arctic and alpine environments. After the single dispersal of *Alchemilla* to the eastern African mountains, herbaceous ancestors developed secondary woodiness independently in Ethiopia and East Africa (Gehrke et al. 2016). The widespread perennial, cushion-formed high-altitude plants described as *Swertia lugardae* evolved independently in five Ethiopian mountains from annual, erect low-altitude plants described as *S. abyssinica*; their genotypes grouped according to mountain, not to the described species (Bekele 2006).

Recent, parallel adaptive evolution (Pleistocene, and even Holocene) has now been convincingly documented in a number of animal and plant groups in other parts of the world, in particular along steep environmental clines which drive repeated and rapid evolutionary diversification, for example along altitudinal gradients in mountains (e.g., Kolář et al. 2016a, b; Bertel et al. 2018; Konečná et al. 2019) and development of secondary woodiness on continental and oceanic islands (Nürk et al. 2019). Recent genomic studies show that there are several molecular mechanisms that can facilitate adaptation to extreme cold and other abiotic stresses, and that many genes can be involved (Birkeland et al. 2020; Nowak et al. 2020). Three plant lineages of the Brassicaceae, which colonized the Arctic independently, have evolved similar suites of adaptations by modifying different components of similar stress response pathways, implying that there are many genetic trajectories for adaptation to extremely cold environments (Birkeland et al. 2020). In *Dendrosenecio*, high-altitude plants typically have larger stems and leaves than low-altitude plants, and show stronger physiological adaptations ensuring frost tolerance and avoidance (Hedberg 1964; Mabberley 1986; Beck 1986). Whereas high-alpine and low-alpine plants on the same mountain tend to be conspicuously different in morphology, they are genetically more similar to each other than they are to plants on other mountains (Knox and Palmer 1995; Tusiime et al. 2020; Gizaw et al. in press). Many of the numerous taxa of *Dendrosenecio* described over the years are only poorly differentiated genetically, and the genetic variation within mountains and mountain groups is often more or less continuous, consistent with recent ecoclinal or ecotypic differentiation in the presence of gene flow (Tusiime et al. 2020). It seems that only in a few cases, ecotypes may be recognised as morphologically distinct subspecies, and only on one or possibly two mountains as distinct species.

The time is obviously ripe to re-address the timing, mechanisms and patterns of parallel adaptation in the afroalpine flora using genomic approaches. Recent genomic studies of the Andean lineages *Espeletia* and *Lupinus* show that diversification often has occurred exceptionally fast via ecological speciation during the last glacial cycles of the Pleistocene, and that small-scale ecological divergence may have occurred along multiple niche dimensions (Nevado et al. 2018, 2019; Pouchon et al. 2020).

Migration corridors among the sky islands: do they, or did they exist?

As noted above, many members of the afroalpine flora are widespread, occurring on more than one mountain or mountain group, in spite of the extreme fragmentation of this system. How, and how often, did or do they spread among the mountains? Based on topographic, floristic and ecological analyses, Hedberg (1969) predicted that the montane forest expanded to form corridors among some adjacent mountains during the warm and humid interglacials. Studies of several montane forest plants and animals have provided evidence consistent with this prediction, some of them even for montane forest corridors between East and West Africa (e.g., Kadu et al. 2011, 2013; Mihretie et al. 2015; Mairal et al. 2015, 2017; Chartier et al. 2016; Gichira et al. 2017; Migliore et al. 2020), and in some cases found that such forest bridges disappeared only recently due to anthropogenic impact (e.g., Kebede et al. 2007; Hemp and Hemp 2018). Hedberg (e.g., 1970) did not believe, however, that past climates had enabled high alpine species to migrate gradually among mountains, and assumed that their ranges must have been established solely based on LDD. He found that whereas adaptation to endozoochorous dispersal with birds was virtually non-existent in the afroalpine flora, one third of the species were adapted to wind-dispersal and two thirds to ectozoochorous dispersal, but believed that cyclones in any case might be crucial for their long-distance dispersal.

Paleoecological, niche modelling, and phylogeographic studies have provided new insights into these questions raised repeatedly by Hedberg. Geological and pollen analytical work has shown that glaciers were present on the highest peaks during the LGM (Coetzee 1964; Hamilton 1982; Messerli and Winiger 1992; Umer et al. 2007). The glacial climates led to a considerable downward shift of afroalpine plant communities, and they oscillated along the elevational gradient in response to the frequent Pleistocene cycles. The paleoecological evidence suggests that the extent of the alpine habitat increased during the glacials, but not enough to create direct connections between the main mountains (Sepulchre et al. 2006; Bonnefille 2010; Hendrickx et al. 2014).

Using niche modelling, Chala et al. (2017) addressed whether suitable habitats shifted far enough downslope under past colder climates to form bridges enabling gradual migration, taking into account that only one third of the species in the afroalpine flora are exclusively alpine, and that the other species extend to varying degrees into grasslands and open forests at lower elevations. They mapped the extent of the current alpine habitat and projected it to the LGM

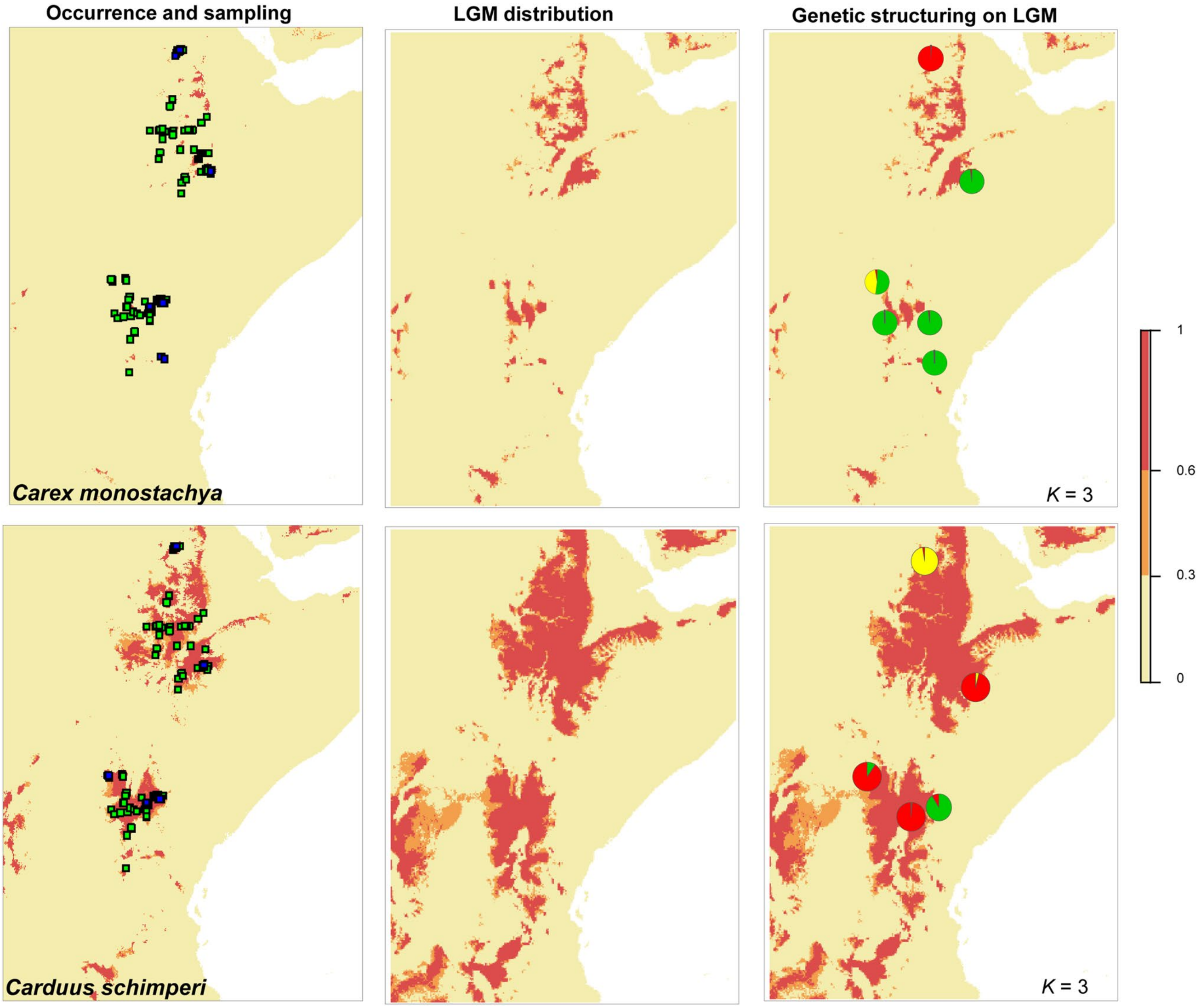

Fig. 5 Realized and potential distribution of one exclusively afroalpine species (*Carex monostachya*) and one non-exclusively afroalpine species (*Carduus schimperi*) and geographic structuring of their genetic (AFLP) diversity. The first column shows the modelled potential distribution under the current climate and the occurrence points used in the models, reflecting realized current distribution (most of the occurrence points are based on own field work and herbarium material verified by us (green and blue); a few added from GBIF (black)). The second column shows the modelled distribution under the Last Glacial Maximum (LGM) climate. The third column shows genetic structuring (genetic groups inferred from Bayesian analyses) mapped on the LGM distribution. Map colors indicate habitat suitability based on agreement among pixels from three binary maps constructed using different algorithms (0.0–0.3—yellow, habitat unsuitable with high certainty; 0.3–0.6—orange, habitat suitability uncertain; > 0.6—red, habitat suitable with high certainty). In both species, the southeastern Ethiopian populations belong to the same genetic group as East African populations, in spite of lack of habitat connectivity. In *C. schimperi*, putative ecological connectivity across the Rift Valley both in Ethiopia and East Africa during the LGM did not result in genetic connectivity. Genetic data: Gizaw et al. 2016b and Wondimu et al. 2014; modelling: Chala, unpublished data)

climate to assess whether gradual migration was possible for exclusively alpine taxa during this glacial period, and thus potentially also during earlier glaciations. The LGM treeline was estimated to be about 1000 m lower, which is consistent with estimates from pollen records (Coetzee 1964; Maitima 1991; Zech 2006; Schüler et al. 2012), and the alpine habitat to be eight times larger than today (Fig. 3). At the LGM, most of the alpine habitat of the Ethiopian highlands was interconnected except across the Rift Valley, whereas the solitary mountains of East Africa remained isolated for exclusively alpine species. Chala et al. (2017) also modelled land cover under current and LGM climates to assess whether grassland and open forests could have served as migration corridors for alpine taxa that today extend into lower vegetation belts. Notably, they found that for drought-tolerant species, gradual migration may have been possible during the dry glacial periods, and possibly also under the current climate before agriculture transformed the low-lying landscapes.

In contrast, molecular data, partly in combination with niche modelling for individual species, do not provide support for gradual migration of any afroalpine species among mountains (although the possibility for gradual migration among closely adjacent mountains has not yet been analysed in detail). The molecular studies rather identify many LDD episodes across vast lowland barriers. This implies that although some potential migration corridors may have existed (Chala et al. 2017), they do not seem to have resulted in effective intermountain gene flow. It turns out that geographic distance is often a poor predictor of genetic distance in the afroalpine flora. In accordance with Hedberg's (1970) view, morphological adaptations to bird and wind dispersal may play a subordinate role in LDD relative to truly unpredictable 'chance dispersal' with non-standard vectors (Berg 1983; Alsos et al. 2007, 2015; Nathan et al. 2008). Wondimu et al. (2014) used AFLPs to infer the history of two species with different dispersal adaptations, but similar geographic ranges and habitats: the wind-dispersed *Carduus schimperi* and the supposedly short-distance-dispersed *Trifolium cryptopodium*. In both species, populations from opposite sides of the narrow Rift Valley barrier in Ethiopia were genetically more distant than those from opposite sides of the vast Ethiopia–East Africa barrier. The surprising pattern of high genetic similarity between populations from the Bale Mts in Ethiopia and the distant East African mountains has also been identified in several other species (Ehrich et al. 2007; Gizaw et al. 2013, 2016b; Masao et al. 2013; Chen et al. 2015; Wondimu et al. 2017). It is still a mystery why the vast Ethiopia–East Africa barrier seems to be more permeable—at least for some species—than the narrow Rift Valley barrier within Ethiopia, which is found to be a major biogeographic barrier for both animals (reviewed in Komarova et al. 2021) and plants.

Based on dated phylogenies, extreme Pleistocene LDD episodes have been inferred between the afroalpine habitats on the opposite sides of tropical Africa for *Lychnis abyssinica* (< 300 ka; Gizaw et al. 2016a) and *Festuca abyssinica* (two LDDs, 860 ka and 520 ka; Mairal et al. 2021). For *Festuca*, three small patches of suitable LGM habitat were identified between East and West Africa, potentially acting as stepping stones. In *Carex*, allopatric speciation resulting in one eastern (*C. monostachya*) and one western species (*C. runssoroensis*) in East Africa was followed by LDD of the western species across the vast Ugandan lowland gap, resulting in secondary contact and admixture (Gizaw et al. 2016b).

Geographic distance among mountain groups appears to be a better predictor of floristic distance than intraspecific genetic distance. Gehrke and Linder (2014) analysed similarities among the mountain floras and identified four geographic groups: West Africa, Ethiopia/Sudan (with eastern and western subgroups, separated by the Rift Valley), western East Africa and eastern East Africa. They showed that this pattern is better explained by geographic isolation than by environmental filtering. They further showed (Gehrke and Linder 2011, 2014) that species richness—as in oceanic islands—can be explained by a model including age, area size, elevation and isolation, whereas levels of endemism are best explained by species richness in combination with area and isolation.

In ongoing work, we address the relative roles of LDD and past habitat connectivity based on genotypes of 28 afroalpine species (a subset of the species in Table 1, i.e., those occurring on at least two mountains) and modelling individual species ranges during the LGM and for 1 kyr time slice intervals until today (Gizaw, Chala, Popp, Zimmermann, Brochmann et al., unpublished data). Most species show distinct, but highly variable genetic structuring among mountains, reflected by large variation in median pairwise population differentiation both among (Φst 0.24–0.47) and within species (Φst 0.03–0.78). Many of the species had considerably larger potential ranges during colder climates (e.g., the non-exclusively alpine *Carduus schimperi*; Fig. 5). However, the correlation between ecological and genetic distances was virtually constant through time in all species and lower than that between geographic and genetic distances, suggesting that LDD has always been the main driver shaping genetic structure. Geographic distance and species characteristics such as dispersal adaptations only explained part of the variation, suggesting a major role of stochasticity associated with LDDs. Genetic and floristic distances were, however, correlated, suggesting that initial colonisation of mountains and subsequent intermountain gene flow are both driven by similar LDD events. Additional evidence for high levels of stochasticity in community assembly in the afroalpine flora is provided by our ongoing work assessing genetic diversity of 38 species (Table 1) versus total species diversity in 100 m × 100 m plots analysed in five major habitat types (rock outcrop, bog, *Alchemilla* shrubland, grassland, and *Dendrosenecio* woodland; Dimitrov, Gizaw, Chala, Brochmann et al., unpublished data). Whereas the meta-analysis of Vellend et al. (2014) found that correlations between species diversity and genetic diversity are generally positive (but see, e.g., Taberlet et al. 2012), we find no correlation in these afroalpine habitats, probably reflecting LDD stochasticity combined with frequent habitat disturbance caused by the Pleistocene climate oscillations.

Table 1 Average within-population Nei's gene diversity (*D*; estimated as the average proportion of pairwise differences among genotypes, Kosman 2003) inferred from Amplified Fragment Length Polymorphism (AFLP) analyses of field-collected material of 3756 plants of 38 species from the eastern African mountains

Taxon	Family	No of plants	No of pops	No of loci	Dispersa mode	Pollination vector	*D*	Reference
Carduus schimperi Sch. Bip.	Asteraceae	108	24	339	W	Insect	0.054	Wondimu et al. 2014
Crepis dianthoseris N. Kilian, Enke, Sileshi & Gemeinholzer (syn. *Dianthoseris schimperi* A. Rich.)	Asteraceae	129	31	368	W	Insect	0.083	Unpubl.
Dendrosenecio Hauman. spp.	Asteraceae	460	109	455	W	Insect	0.081–0.094	Tusiime et al. 2020
Dichrocephala chrysanthemifolia (Blume) DC.	Asteraceae	151	31	368	S	Insect	0.075	Unpubl.
Haplocarpha rueppellii (Sch. Bip.) Beauverd	Asteraceae	191	38	539	S	Insect	0.071	Unpubl.
Helichrysum formosissimum (Sch. Bip.) Sch. Bip. ex A. Rich.	Asteraceae	143	32	411	W	Insect	0.084	Unpubl.
Helichrysum forskahlii (J.F. Gmel.) Hilliard & B.L. Burtt	Asteraceae	220	48	545	W	Insect	0.083	Unpubl.
Arabis alpina L.	Brassicaceae	224	33	254	S	Insect (self?)	0.051	Ehrich et al. 2007
Cardamine obliqua Hochst. ex A. Rich.	Brassicaceae	148	34	151	S	Insect (self?)	0.049	Unpubl.
Lobelia giberroa Hemsl.	Campanulaceae	195	25	173	S/W	Sunbird	0.061	Kebede et al. 2007
Lobelia rhynchopetalum Hemsl.	Campanulaceae	102	21	175	S/W	Sunbird	0.117	Chala et al. 2016
Lobelia telekii Schweinf.	Campanulaceae	108	24	276	S/W	Sunbird	0.091	Unpubl.
Lobelia wollastonii Baker f.	Campanulaceae	44	11	232	S/W	Sunbird	0.194	Unpubl.
Umbilicus botryoides Steud. ex A. Rich	Crassulaceae	30	7	97	S	Insect	0.204	Unpubl.
Carex monostachya A. Rich.	Cyperaceae	88	20	239	S	Wind	0.089	Gizaw et al. 2016b
Carex runssoroensis K. Schum.	Cyperaceae	32	8	156	S	Wind	0.049	Gizaw et al. 2016b
Erica arborea L.	Ericaceae	59	11	106	S/W?	Insect (wind?)	0.080	Gizaw et al. 2013
Erica trimera (Engl.) Beentje	Ericaceae	110	20	106	S/W?	Insect (wind?)	0.076	Gizaw et al. 2013
Trifolium cryptopodium Steud. ex A. Rich.	Fabaceae	66	17	174	S	Insect	0.061	Wondimu et al. 2014
Swertia abyssinica Hochst. (incl. *S. lugardae* Bullock)	Gentianaceae	121	24	316	S	Insect	0.092	Unpubl.
Geranium arabicum Forssk. (incl. *G. kilimandscharicum* Engl.)	Geraniaceae	211	45	327	S	Insect	0.072	Wondimu et al. 2017
Hypericum revolutum Vahl	Hypericaceae	227	33	152	S	Insect	0.150	Unpubl.
Luzula abyssinica Parl.	Juncaceae	172	41	73	S	Wind	0.096	Unpubl.
Anthoxanthum nivale K. Schum.	Poaceae	125	35	376	S	Wind	0.155	Tusiime et al. 2017
Deschampsia cespitosa (L.) P. Beauv. (incl. *D. angusta* Stapf & Hubbard)	Poaceae	33	9	128	S	Wind	0.125	Masao et al. 2013
Festuca abyssinica A. Rich.	Poaceae	122	34	479	S	Wind	0.175	Unpubl.
Koeleria capensis (Steud.) Nees	Poaceae	93	24	202	S	Wind	0.042	Masao et al. 2013
Rytidosperma subulata (A. Rich.) Cope	Poaceae	44	10	112	S	Wind	0.106	Unpubl.

The estimate for *Dendrosenecio* is given as the range for the four main genetic groups inferred by Tusiime et al. (2020), which correspond to the four main mountain regions; their analyses included all 11 species recognized in the latest taxonomic treatment of the genus (Knox 2005). Dispersal type is given as W – wind dispersal or S – short-distance dispersal (i.e. no morphological dispersal adaptations, or adaptations to local dispersal only); W? indicates potential regular dispersal with wind because of small seed size. The average *D* over all 38 species is 0.087. Average *D* was higher for short-distance-dispersed plants (0.099) than for wind-dispersed plants (0.068). Wind- and sunbird-pollinated plants show higher average *D* (0.105–0.116) than insect-pollinated plants (0.077). Notably, these values are in most cases much lower than the averages reported for plant species elsewhere by Nybom (2004), ranging from $D = 0.27$ for wind-dispersers and outcrossers to $D = 0.12$ for selfers. Unpublished data provided by Gizaw, Brochmann et al.

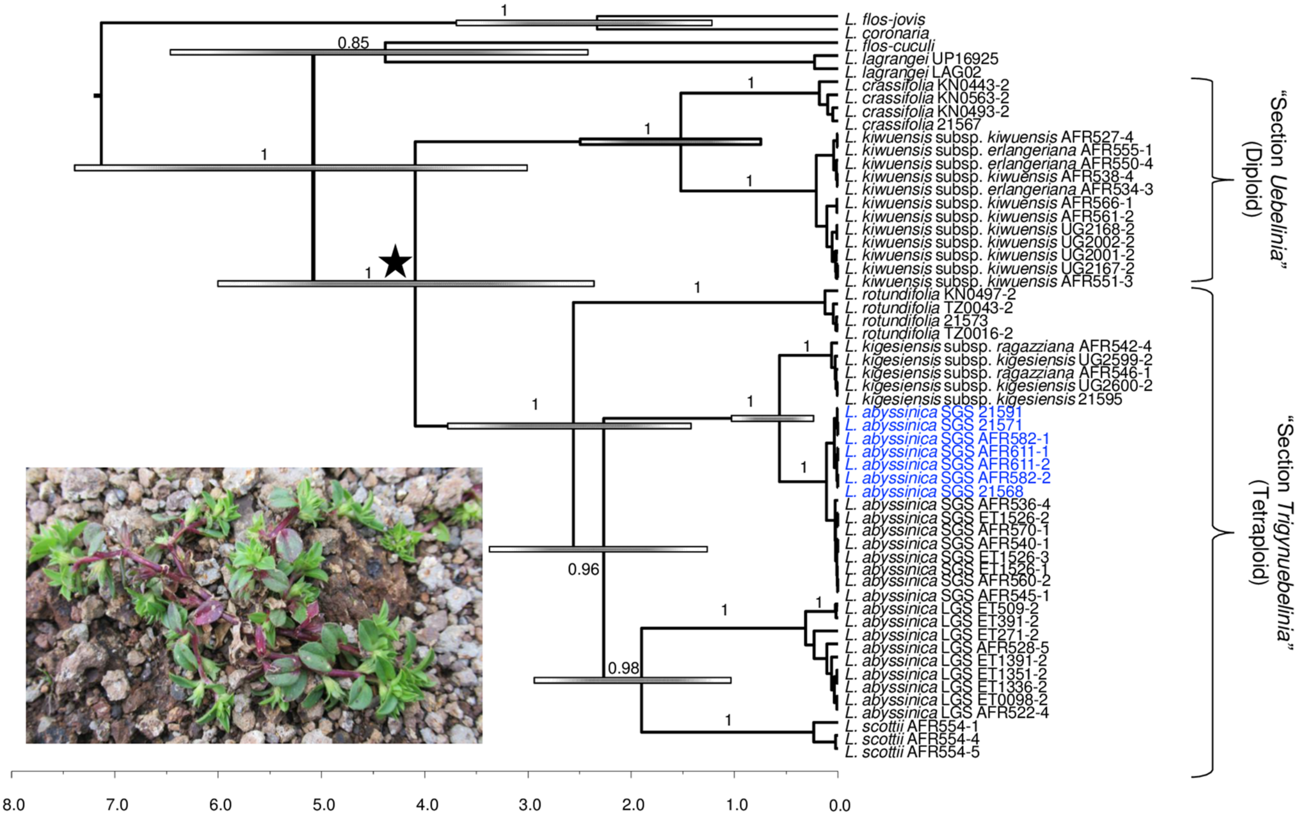

Fig. 6 Single-locus tree for *Lychnis* inferred from sequences of a combined *rps16/psbE-petL* pDNA data matrix. Node bars represent 95% highest posterior density (HPD) age intervals. Time scale in million years. The star denotes the afromontane/afroalpine clade. *Lychnis abyssinica* LGS and *L. abyssinica* SGS denote large-genome-size and small-genome-size variants, respectively. Blue fonts depict the West African accessions. Adopted from Gizaw et al. (2016a). Photo: *Lychnis abyssinica* by Abel Gizaw

Afroalpine plant populations are genetically depauperate and prone to extinction

It is of considerable conservation concern that most afroalpine plant species studied so far harbour very little intrapopulation genetic variation, most likely because of repeated bottlenecks induced by frequent climatic and vegetational shifts and long-distance colonisation by few propagules. Table 1 presents average within-population Nei's gene diversity (*D*) based on published and unpublished AFLP data sets for 3756 plants of 38 afroalpine species. Average diversity over all 38 species is 0.087, ranging from 0.042 to 0.204 for individual species. Thus, afroalpine plant species tend to contain much less within-population genetic diversity than reported for plant species occurring elsewhere by Nybom (2004), who found averages ranging from 0.27 for wind-dispersed and outcrossing species to 0.12 for selfing species. In our set of species, both wind-dispersed and supposedly short-distance-dispersed species have low diversity (0.068–0.099). Sunbird- and wind-pollinated species, which are likely to be outcrossing, have slightly higher genetic diversity (0.105–0.116) than species with insect-pollination syndromes (0.077), of which some are likely to be primarily selfing. Extremely little within-population genetic diversity have also been reported for some high alpine species in the Andes, attributed to genetic drift caused by founder effects, lack of gene flow, and/or autogamy (Vásquez et al. 2016; Sgorbati et al. 2004).

These data imply that afroalpine plants may be extremely vulnerable and prone to extinction, in particular because of the compounding effects of ongoing habitat destruction (e.g., overgrazing, human-induced fires) and climate change. The plants inhabit a narrow band of suitable conditions that already is limited to the upper extremes of the mountains. Chala et al. (2016) modelled

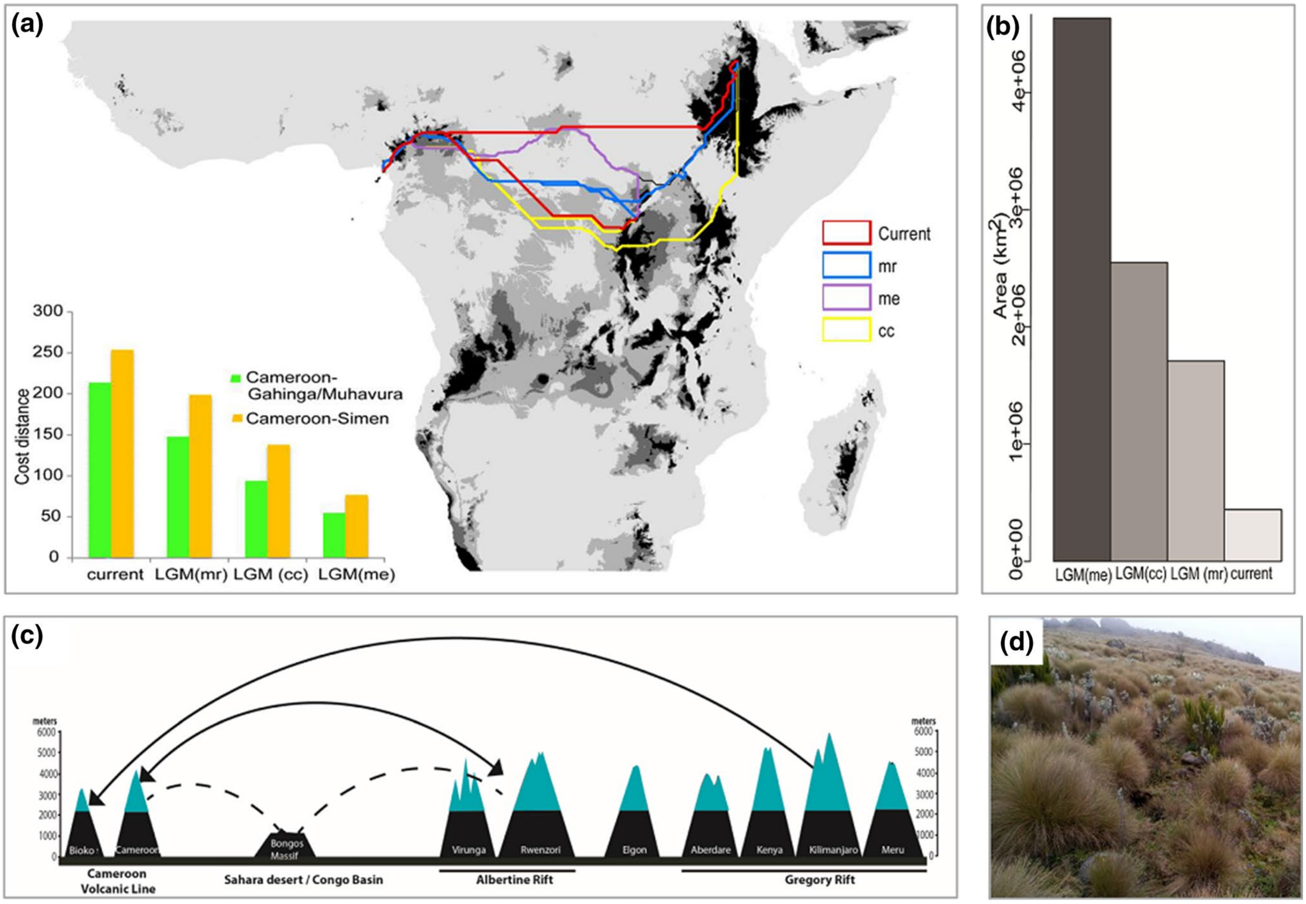

Fig. 7 Likelihood analysis of dispersal routes in *Festuca abyssinica*. **a** Least-cost paths between western and eastern African high mountains under current and three LGM climate models [MIROC-ESM (mr), MPI-ESM-P (me), and CCSM (cc)]. The paths are plotted on a habitat suitability map produced by averaging predicted probability values from nine LGM habitat suitability maps (three algorithms *three climate models), with increasing suitability indicated as increasing darkness of grey to black. The cost raster was produced by assigning different cost values for the ensemble habitat suitability classes. Pixels which were unsuitable with high certainty were assigned a resistance cost of 10, pixels with uncertain suitability a cost of 5, and pixels which were suitable with high certainty a cost of 1. The accumulated cost to migrate between Cameroon and Gahinga/Muhavura is shown in green columns, and the accumulated cost to migrate between Cameroon and Simen is shown in yellow columns. Cost distance refers to the accumulation of these costs to migrate from source to destination across a resistance cost surface. **b** Spatial extent of suitable habitats for this species under current and the three LGM climate models. **c** Schematic representation of the distribution of *F. abyssinica* during the LGM (in blue), showing the supported transcontinental dispersal events (continuous lines) and a potential stepping-stone pathway through Central Africa—Sudan (dashed line) (adopted from Mairal et al. 2021). **d** *F. abyssinica* grassland on Mt Kenya. Photo: Abel Gizaw

the habitat suitability of the Ethiopian endemic *Lobelia rhynchopetalum* and assessed how the range and genetic diversity of this enigmatic giant is affected under two climate models and four emission scenarios. They found that only 3.4% of its habitat may remain suitable by 2080, resulting in loss of 82% of its genetic diversity. Thus, specialized high-alpine giant rosette plants are likely to face very high risk of extinction following the ongoing climate change. These results also suggest that historical climate oscillations probably had dramatic effects on genetically depauperate afroalpine species and likely caused extinctions. There are similar concerns for afroalpine animals. The impressive Walia ibex (*Capra walie*) is restricted to a single population in the Simen Mountains in Ethiopia,

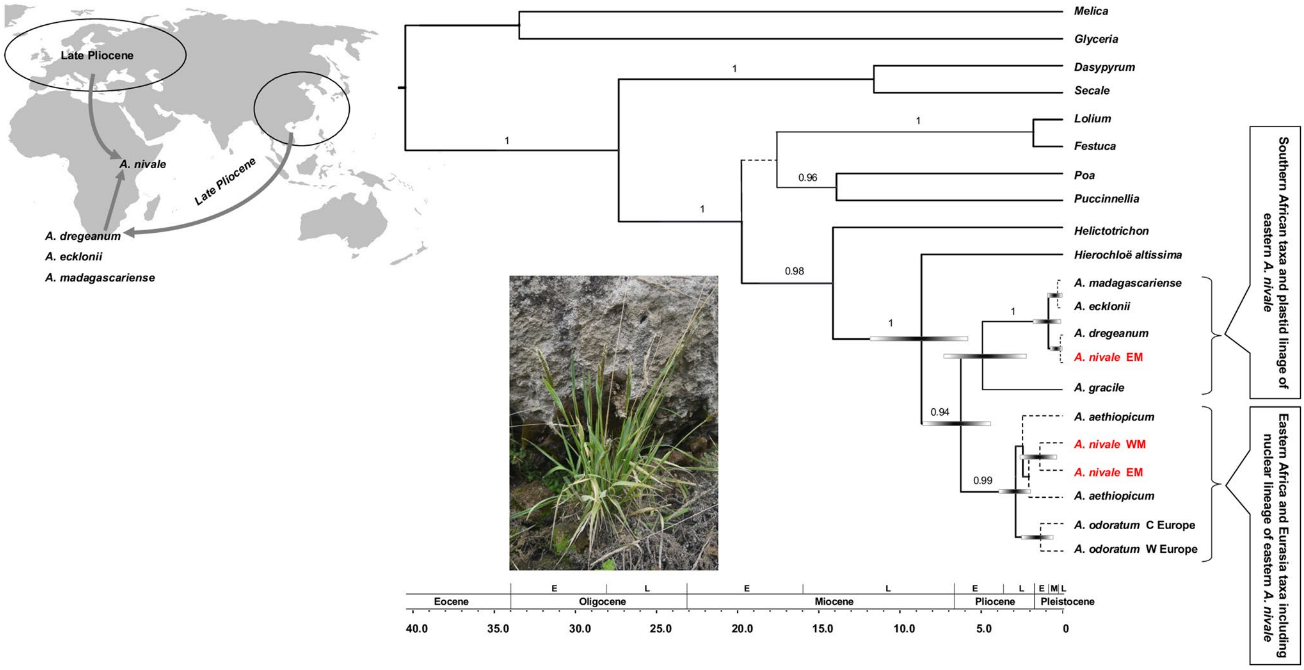

Fig. 8 Multi-labelled maximum clade credibility species tree of *Anthoxanthum* in sub-Saharan Africa obtained from a *BEAST analysis based on two nuclear (ITS and ETS) and two plastid (*trn*LF and *trn*TL) DNA regions. In *A. nivale*, the eastern mountain (EM) group is inferred to be hybridogeneous (hence represented twice in the tree). Dashed lines indicate branches with PP < 0.8. Bars show the 95% confidence interval for the age of the divergence. Adopted from Tusiime et al. (2017). The map shows the double migration scenario inferred by Pimentel et al. (2013) and Tusiime et al. (2017): a single migration from Eastern Asia resulted in the southern African lineage, and a single migration from western Eurasia resulted in the eastern African lineage (*A. nivale* and *A. aethiopicum*). These lineages are currently allopatric, but they met and hybridized in the eastern East African mountains in the late Pleistocene. Photo: *A. nivale* by Abel Gizaw

harbours the lowest genetic diversity ever recorded in a mammal, and competes with domestic goats for food plants, as shown by DNA metabarcoding of faeces using a DNA reference library constructed for the afroalpine flora (Gebremedhin et al. 2009, 2016). The peculiar and endangered Ethiopian wolf (*Canis simensis*) shows very little mtDNA diversity, attributed to its origin from Eurasian grey wolf ancestors as late as during the last glaciation and thus testifying extremely rapid adaptation to the afroalpine environment (Gottelli et al. 2004).

There is also some phylogenetic evidence suggesting that afroalpine plant populations are particularly prone to extinction. The most clear-cut evidence of extinction was found for *Anthoxanthum*; the currently allopatric southern and northern lineages once met in East Africa and produced an allopolyploid, but the southern lineage is absent from East Africa today (Fig. 8, Box 3;Tusiime et al. 2017). In the *Lychnis* phylogeny, the species are distinctly differentiated, but the terminal branches within species are typically very short and suggest not only recent colonisation of individual mountains, but also frequent local extinctions (Fig. 6, Box 4; Gizaw et al. 2016a). Similar findings of relatively old species that show recent interpopulational divergence and little intrapopulation genetic diversity are made in afromontane *Canarina* (Mairal et al. 2015, 2018). Thus, the afroalpine flora seems to represent a highly dynamic system characterized by cycles of colonisation, extinction, and recolonisation of individual sky islands during the Pleistocene climatic oscillations. A similar scenario has been suggested for the entire flora of the Cape Verde Islands (Brochmann et al. 1997), recently also for the flora of the easternmost islands in the Canarian archipelago (García-Verdugo et al. 2019); these are oceanic islands that are particularly prone to aridification. A promising avenue for further research into these questions is DNA metabarcoding of afroalpine lake sediments. Boessenkool et al. (2014) showed that this approach allows identification of past occurrences of taxa using a DNA reference library of the afroalpine flora.

Conclusions

We have shown that several of Hedberg's insightful inferences and hypotheses on the origin and evolution of the afroalpine flora now have been tested with abundant molecular data and niche modelling tools, in many cases providing evidence fully consistent with his views. In particular, his emphasis on LDD as a major factor both for the initial establishment of the flora and for intermountain colonisation and gene flow has been confirmed in many studies. Hedberg held his ground concerning this question at a time when the importance of LDD was heatedly debated and strongly believed to be negligible by a major part of the scientific community in Scandinavia (summarized in Brochmann et al. 2003 and Abbott and Brochmann 2003). It should also be highlighted that Hedberg (1970) felt 'inclined to believe that this [intermountain] dispersal may be due, not only to regular transport by the vectors mentioned above, but also to occasional catastrophic events, such as cyclones, which might easily carry away even those diaspores without any apparent adaptation for air flotation'. He thus anticipated what later became known as one of Berg's principles of plant dispersal (Berg 1983; Nathan et al. 2008): morphological adaptations to dispersal play a subordinate role in LDD relative to truly unpredictable 'chance dispersal' with non-standard vectors.

However, the new insights and large body of new evidence point to a much younger and more dynamic island scenario than envisioned by Hedberg. The afroalpine flora appears to be unsaturated, fragile and vulnerable, harbouring unique taxonomic and genetic diversity that is severely depauperated by frequent bottlenecks and cycles of colonisation, extinction, and recolonisation. The tropical African sky islands can be viewed as a strongly isolated archipelago that still is in its infancy, repeatedly disturbed by the Pleistocene climatic oscillations, and with accelerating recruitment of immigrants arriving from remote temperate areas. Most of the effective dispersal into this system as well as within it has probably occurred during the glacials, because they were long-lasting, the source regions were closer, and the target areas were larger. The major shifts in temperature and rainfall must have induced extinctions, elevational oscillations of species and disruption of plant communities, repeatedly opening up new niches available for colonisation. Today, it is of particular conservation concern that many afroalpine plant species harbour little intrapopulation genetic variation, much less than reported from elsewhere. Thus, afroalpine plants may be extremely vulnerable and prone to extinction, not only because climate warming forces them to move upwards beyond the highest summits, but perhaps more seriously by the accelerating and destructive impact of human activities at high altitudes in these spectacular sky islands.

TEXT BOXES

Box 1

Carex—multiple Eurasian origins, limited diversification, LDDs and hybridisation (Figs. 4, 5). Gehrke and Linder (2009) used phylogenetic evidence to show that *Carex* colonized Africa 9–13 times independently. The genus originated in East Asia in the late Eocene, from where several migration events took place (e.g., Martin-Bravo et al. 2019). Several regions in the Northern Hemisphere have acted both as source and sink, and Africa and the Southern Hemisphere were colonized several times independently from Eurasia. All major lineages in *Carex* except the more warm-climate adapted subgenus *Vigneastra* colonized the afroalpine region, most of them probably during the Miocene, but they resulted in limited diversification (Gehrke and Linder 2009). Eight species reach afroalpine habitats, including the unusually tall *C. bequaertii* (Míguez 2018), several species of sect. *Spirostachyae* (Escudero and Luceño 2011), and the tussock-forming *C. monostachya* and *C. runssoroensis* (Gizaw et al. 2016b). The latter two sedges can form impressive tussocks up to 1.5 m high and dominate extensive afroalpine bogs, and are most closely related to the circumarctic/circumboreal *C. capitata* (Starr and Ford 2009; Gehrke 2011). Whereas *C. monostachya* is restricted to Ethiopia and eastern East Africa, *C. runssoroensis* occurs mainly in western East Africa but also in some eastern mountains, where the two species co-occur (Mt. Elgon, Mt. Kenya and the Aberdares). Gizaw et al. (2016b) addressed previous hybridisation hypotheses using AFLPs. The two species were distinctly differentiated, also in one of the mountains, where they co-occur, but the plants from Mt. Elgon were admixed. The results suggest initial allopatric divergence into one northern/eastern and one western lineage, which later spread across the vast Ugandan lowland gap. Surprisingly, one genetic group in *C. monostachya* was shared between the Ethiopian Bale Mountains and the distant East African mountains, testifying high dispersal capacity, but gene flow has nevertheless not prevented strong divergence in this species across the narrow Rift Valley in Ethiopia.

Box 2

Arabis alpina—double Eurasian origin, secondary contacts, local range shifts during glacial cycles. This arctic-alpine and afroalpine species is widespread in the eastern African mountains, where it reaches very high altitudes. Hedberg (1957) measured its morphological variation and concluded that the afroalpine populations belong to the same species as the arctic-alpine ones. He also performed artificial crosses between Kenyan and Swedish plants and found strong reduction in F_1 fertility, but almost full recovery in F_2 hybrids (Hedberg 1962). He thought that evolutionary diversification is slow in afroalpine Brassicaceae relative to other groups, and that *A. alpina* is a Tertiary relict in Africa (Hedberg 1965, 1969, 1970). Phylogeographic studies showed, however, that the species colonized the African mountains much more recently, and not only once. Based on synonymous mutation rates, Koch et al. (2006) found that two lineages of *A. alpina* migrated from the Balkans/Middle East into the eastern African mountains during the middle to late Pleistocene. The first migration probably occurred several glacial cycles ago; the second was more recent and resulted in secondary contact. Inferred from plastid DNA variation, the early-arriving lineage spread all over the eastern African mountains, whereas the late-arriving one seemed to be confined to Ethiopian mountains close to the Arabian Peninsula (Assefa et al. 2007). Ehrich et al. (2007) used AFLP data from 236 populations of *A. alpina* to test the prediction that the genetic consequences of range shifts in response to climate change during the Pleistocene differ among geographic areas. They found virtually no genetic diversity in the entire North Atlantic region, implying that plants from a single source population had recolonized vast areas after the last ice age. In contrast, genetic diversity was high and distinctly structured in the European Alps and the eastern African mountains, suggesting that range shifts in response to the glacial cycles were more local and served to preserve diversity. In the Alps, the genetic groups had patchy and partly overlapping distributions, whereas the genetic groups in the more fragmented African mountain system were clearly structured, although some LDDs were inferred. The AFLP data showed that the late-arriving lineage also dispersed from Ethiopia to the East African Mt Elgon, forming another secondary contact zone.

Box 3

Anthoxanthum—into Africa both from the north and southeast, limited diversification, secondary contact, polyploidization, local extinction (Fig. 8). In the Late Pliocene, sub-Saharan Africa was colonized by two divergent lineages of sweet vernal grasses, one from southeast Asia to southern Africa, and one from western Eurasia to eastern Africa (Pimentel et al. 2013). The nuclear phylogeny of Tusiime et al. (2017) shows that the two eastern African taxa originated after a single immigration from the north, confirming Hedberg's (1976) hypothesis of a close relationship to the *A. alpinum/odoratum* complex. The eastern African nuclear sequences formed three subclades, one with the Ethiopian *A. aethiopicum*, one with eastern East African *A. nivale*, and one with western East African *A. nivale*. Surprisingly, however, the plastid phylogeny placed eastern *A. nivale* together with the southern African taxa, and coalescent simulations rejected lineage sorting as explanation for the incongruence. Thus, although currently allopatric, the southern and eastern African taxa must have met and hybridized in the middle to late Pleistocene. It is likely that the nuclear genome of eastern *A. nivale* also contains DNA derived from the southern African lineage; the nuclear phylogeny of Tusiime et al. (2017) was inferred from ribosomal sequences, and southern African rDNA may have been eliminated via concerted evolution. This may resolve the conflicting morphology-based opinions of whether *A. nivale* has northern (Hedberg 1976; Phillips 1995) or southern affinities (Clayton 1970). It has both. Notably, mountains such as Mt Kilimanjaro and Mt Kenya are now quite well-explored, so it is likely that the southern African lineage went extinct there after the hybridisation event. Tusiime et al. (2017) also found western *A. nivale* to be low-ploid and eastern *A. nivale* to be high-ploid (cf. Hedberg 1976), suggesting that the latter is an allopolyploid in which the southern African lineage left its footprint. This Pleistocene hybridisation event is particularly intriguing given the deeper history of the two lineages. The southern African lineage belongs to a mainly southeast Asian, tropical-alpine group which itself originated via Miocene hybridisation between *Anthoxanthum* and *Hierochloë* (Pimentel et al. 2013). The East African allopolyploid thus has a double hybrid background spanning millions of years and widely different geographic affinities.

Box 4

Lychnis—single Eurasian origin, polyploidization, moderate diversification, recent LDD to West Africa (Fig. 6). The sky island taxa of *Lychnis* (formerly referred to the endemic genus *Uebelinia*) were considered as typical examples of vicarious speciation by Fries (1923), but Ousted (1985) rather recognised one very widespread, highly disjunct species (*L. abyssinica*), as well as five other, partly disjunct species. They originated after a single colonisation from Eurasia in the late Miocene or early Pliocene (5.2 Ma), followed by differentiation into one diploid and one tetraploid lineage (Popp et al. 2008; Gizaw et al. 2016a). Most of the 95% HPD of the estimated time of origin and initial diversification corresponds to a warm and moist period (Bonnefille 1995), consistent with the preference of these species for swampy areas and bogs. Subsequent speciation events occurred sporadically from the late Pliocene to the middle Pleistocene. Habitat fragmentation triggered by aridification and subsequent allopatric speciation may explain the diversification pattern, as the time estimates roughly fit with known arid periods. Notably, whereas the sky island species of *Lychnis* are distinctly differentiated, the terminal branches within species are typically very short and suggest not only recent colonisation of individual mountains, but also frequent local extinctions. Colonisations seem, for example, to have occurred during the last 0.3 Myr when the Ethiopian *L. kiwuensis* and *L. kigesiensis* dispersed to mountains in Uganda, and, most strikingly, when the Ethiopian *L. abyssinica* spread to the remote mountains in Cameroon and Nigeria.

Box 5

Senecio—multiple diverse origins, moderate diversification. *Senecio* (or Senecioneae; ragweeds) with its > 1250 species is possibly the largest genus of flowering plants (depending on generic concept; Pelser et al. 2007). This clade has an almost worldwide distribution despite its relatively young age (mid to late Miocene; Kandziora et al. 2017). The highest species diversity is found in Southern Africa and South America. Ragweeds display a wide range of growth forms and life histories, including small trees, shrubs, vines, succulents, epiphytes and herbaceous annuals, and occupy a multitude of habitats. Many species and lineages have hybridized, undergone polyploidization, and colonized diverse environments, often through rapid phenotypic divergence and adaptive radiation (Walter et al. 2020). There are at least five clades with afroalpine species, resulting from 4 to 14 independent colonisations (Kandziora et al. 2016). Most afroalpine lineages probably originated from southern African mountains, and some possibly from the Palearctic and South America. Colonisation of the afroalpine region often resulted in moderate in situ diversification. The most species-rich afroalpine clade includes seven species, much less than some clades of this genus in the tropical-alpine Andean Páramo. This difference is probably associated with the different spatial extents of the alpine habitat (Kandziora et al. 2016).

Box 6

Fine-leaved **Festuca**—single South American origin, moderate diversification, double Pleistocene dispersal between East and West Africa (Fig. 7). The fine-leaved fescues form conspicuous tussocks in afromontane and afroalpine grasslands. They belong to a single clade that seem to have originated at the Messinian–Pliocene transition, remarkably from northern South America (Minaya et al. 2017). Most taxa are reported as narrow endemics (note, however, that a critical taxonomic revision is needed), but *F. abyssinica* s. lat. is widespread on both sides of tropical Africa (Hutchinson et al. 1968; Clayton 1970). Mairal et al. (2021) studied these fescues by combining phylogenetic, phylogeographic and niche modelling approaches. Surprisingly, the western East African populations of *F. abyssinica* were genetically more similar to the West African than to the eastern East African populations. Dispersal models and ecological niche predictions supported multiple LDDs in eastern Africa and two LDDs between the two sides of Africa in the Pleistocene (0.86 Ma and 0.52 Ma), possibly facilitated by stepping stone(s) along a Central Africa–Sudan pathway during the coldest periods. This is supported by scenarios using a coalescence approach (pDNA) and correlations between genetic and geographic distances (AFLP), and by ecological niche modelling showing patches of LGM habitat suitability in the Marrah Mountains, Bongos Massif, and Adamawa Plateau, resulting in reduced least-cost path distances.

Box 7

Erica—connections both to the south and north. This genus comprises > 800 species, of which ~ 700 represent a single radiation in the Cape Floristic Region (Pirie et al. 2016). By contrast, just 23 species occur across the African high mountains, but these have a somewhat longer history, with occasional exchange with the ancestral range of the Ericeae clade to the north (western Europe and the Mediterranean) and with the younger Drakensberg Mountains lineage to the south (Pirie et al. 2019). Dispersal has typically occurred between adjacent, ecologically similar areas, but the pattern of regional endemic clades and near 100% regional species endemism implies that most of the African high mountain species evolved within the region. Most of them belong to a single clade that also includes the substantial Madagascan diversity. Two of them, *Erica arborea* and *E. trimera*, are unusual: both are phylogenetically isolated, relict lineages stemming back to the initial establishment of *Erica* in the afrotemperate region around 15 Ma. Both species are shrubs or small trees with tiny seeds, potentially capable of dispersal by wind over long distances, and both are widespread in the subalpine ericaceous zone, but with *E. trimera* restricted to higher altitudes than *E. arborea*. Gizaw et al. (2013) used pDNA and AFLP data to test the prediction that the more high-altitudinal *E. trimera* shows more distinct genetic structuring than the lower-altitudinal *E. arborea*, because inter-mountain migration of *E. arborea* may have been facilitated by habitat bridges under former climates. They found limited within-species diversity, but the genetic structuring was according to the prediction: *E. trimera* consisted of several distinct genetic groups with different pDNA haplotypes in different mountains, suggesting long-term isolation, whereas *E. arborea* showed virtually no geographic structuring at AFLP loci and only a single, widespread pDNA haplotype.

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