Island biogeography of tropical alpine floras

Petr Sklenář¹*, Inga Hedberg² and Antoine M. Cleef³

¹Department of Botany, Charles University, 128 01, Prague, Czech Republic, ²Department of Systematic Biology, Uppsala University, SE-75236, Uppsala, Sweden, ³Paleoecology & Landscape Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1098 XH, Amsterdam, The Netherlands

ABSTRACT

Aim We analysed the effects of alpine area, geographical distance between mountains and isolation due to topography on mountain plant species richness, regional species turnover and patterns of species distribution.

Location Equatorial mountains of East Africa, South America and New Guinea.

Methods We collated lists of alpine species and estimated the extent of alpine area for seven mountains in each geographical region to construct species–area curves. We tested the observed frequency distribution of species among mountains against the expected distribution (assuming random dispersal) by means of a log-likelihood test. We compared species turnover among mountains using species accumulation curves. We expressed floristic similarity between mountain pairs as chi-square distance between observed and expected numbers of shared species and tested its correlation with geographical distance using the Mantel test.

Results Samples of East African, South American and New Guinean alpine floras contained 371, 489 and 279 species, respectively. Andean genera tended to be more species rich than genera in the other regions. Species richness of the mountains correlated with log-transformed area except in East Africa. Species distributions among mountains significantly deviated from random in all regions. Species turnover was lowest among East African sites and highest among South American sites, and the slopes of the cumulative species–area relationship were significantly different. Floristic similarity between mountains significantly declined with log(distance) in all regions, and the slope of the relationship was steepest in South America.

Main conclusions The flora of the Andean páramo is confirmed to be the most species rich of the tropical alpine regions. Páramo genera tend to be richer in species than afroalpine and tropicalpine Asian genera. There is higher species turnover in the Andes and the floras of individual mountains are therefore quite distinct. In contrast, the floras of the East African mountains are more uniform and possess a relatively large number of widespread species.

Keywords Afroalpine, Andes, equatorial mountains, habitat islands, New Guinea, páramo, plant species diversity, species–area relationships, tropicalpine.

INTRODUCTION

Mountainous regions of equatorial South America, East Africa and New Guinea host diverse alpine floras with a high proportion of endemic species (Smith & Cleef, 1988). The flora of the Andean páramo is the richest of these, with more than 500 genera and 3500 species of native vascular plants, of which as many as 60% may be endemic (Luteyn, 1992, 1999; Sklenář et al., 2005). In contrast, the afroalpine flora of tropical East Africa consists of only about 370 species in 140
Pleistocene changes also modified the elevational distribution (Hedberg, 1957, 1969). The tropical alpine flora of New Guinea comprises over 1100 species in 226 genera (van Royen, 1980–83; Johns et al., 2006). The tropical alpine plants inhabit a belt 1000–1500 m wide situated above the upper forest line, i.e. usually at 3500–4000 m a.s.l. but occasionally at 3000 m a.s.l. (Hedberg, 1951; Miehe & Miehe, 1994). The vegetation of this belt consists mainly of dense shrubby thickets, extensive grasslands and open herb-fields, but distinct vegetation types are also present on the shores of glacial lakes, in bogs and mires, on rocky screes, etc. (Hedberg, 1964; Cuatrecasas, 1968; Hope, 1976, 1980; Cleef, 1981).

The alpine belts of equatorial mountains are often considered to form ‘islands’ of cold climate in the warm tropics (Hedberg, 1964; Vuilleumier, 1970). In East Africa, the mountains are solitary peaks that rise from a plateau 1000–2000 m high (Hedberg, 1951; Coe, 1989). In contrast, the equatorial Andes are a structural complex of mountain ranges – cordilleras – topped by isolated peaks and ridges rising as much as 2000 m above the surrounding land (Kroonenberg et al., 1990; Claperton, 1993; Graham, 2009; Hoorn et al., 2010). A similar setting is found in New Guinea, where the principal mountain range is divided into numerous elevated plains and smaller ranges, crowned by high non-volcanic domes and volcanic peaks (Löffler, 1980).

The contrasting topographies of the equatorial mountain regions, especially the continuous Andean cordilleras versus the solitary East African mountains, are believed to have determined differences in plant species richness and distribution patterns (van der Hammen, 1974; Cleef, 1983; Hedberg, 1992). The chains of the Andean cordilleras presumably provided suitable pathways for migrations of alpine plants particularly during Pleistocene cold periods, when many páramo ‘islands’ merged into large treeless areas (Fig. 1) (Simpson, 1974, 1975, 1983; Cleef, 1979; Cuatrecasas, 1986; van der Hammen & Cleef, 1986; Hooghiemstra et al., 2006). Pleistocene climatic oscillations also affected the mountain vegetation in East Africa (Coetzee, 1967; Livingstone, 1967; Schüler et al., 2012), but the isolated alpine belts apparently never came into direct contact (Harmsen et al., 1991; Hedberg, 1992); plant migration was thus mainly possible through occasional dispersal across warm tropical lowlands (Hedberg, 1969, 1992; Coe, 1989; Harmsen et al., 1991; see also Brühl, 1997). Although the picture is less clear for New Guinea, Pleistocene changes also modified the elevational distribution of the alpine belts there (Hope, 1980, 2009).

The high species richness of páramo compared with tropical alpine East Africa and New Guinea is due to the large geographical extent of the Andes (Smith & Cleef, 1988; Hedberg, 1992). Beyond that obvious fact, however, patterns of species richness in the three regions remain poorly explored. In this study, we compared plant species diversity and distribution among seven East African, seven Andean and seven New Guinean mountains of comparable sizes. Because the East African mountains have been much more effectively isolated than the Andes and New Guinea, we predicted that: (1) there is higher species turnover among the East African mountains, which implies lower between-mountain similarity; (2) species are distributed more randomly among East African mountains; and (3) the East African mountains are less species rich than comparably large mountains elsewhere.

### Materials and Methods

#### Study sites

All seven East African mountains reaching into the afroalpine belt were included in the study (Fig. 1a) – the Virunga volcanoes, Ruwenzori, Mount Elgon, Aberdare, Mount Kenya, Kilimanjaro and Mount Meru; all but Ruwenzori are of volcanic origin (Hedberg, 1951). In order to have an equal number of mountains, seven Andean and seven New Guinean mountains with well-documented alpine floras were selected. In the Andes, those sites are: Antisana, Chimborazo and Cajas in Ecuador; Los Nevados, Sumapaz and Sierra Nevada del Cocuy in Colombia; and Sierra Nevada de Mérida in Venezuela (Fig. 1b). The Ecuadorian sites, along with Los Nevados, are of volcanic origin, and the remaining sites are of non-volcanic origin. In New Guinea, the Snow Mountains, Oranje Mountains, Star Mountains, Mount Gipuzwe, Mount Wilhelm (Bismarck Range), Sarawaket Range and Owen Stanley Range were selected (Fig. 1c); all but Gipuzwe are of non-volcanic origin. Although the distances between the sites vary in the ranges 69–919 km, 135–1553 km and 132–1205 km in East Africa, the Andes and New Guinea, respectively (see Appendices S1–S3 in Supporting Information), the distances between mountains do not differ significantly between regions (Kruskal–Wallis ANOVA by ranks, $P = 0.49$).

The extent of the alpine belt of each mountain was obtained from data from SRTM version 4 (Shuttle Radar Topography Mission; available at: http://srtm.csi.cgiar.org/). Surface area was calculated employing DEM SURFACE TOOLS 2.1.254 (Jenness, 2010) implemented in ArcMAP 10 (ESRI, Redlands, CA, USA, 2011). The elevational limits of the afroalpine belt of individual mountains were extracted from Hedberg (1951) and varied between 3600 and 3800 m, except for Kilimanjaro where it was 4000 m; for the elevational delimitation of the Andean superpáramo and alpine New Guinea, see below.

#### Species lists

We used species lists that have been collated from original data sets and from published works. We compared the flora of the afroalpine belt with the flora of Andean superpáramo above 4100–4200 m and with alpine New Guinea above 3800 m. For our purposes, the superpáramo belt appears best for several reasons: (1) the superpáramos are isolated and there is no direct connection to nearby peaks; (2) this belt has been well studied and species lists are available for the sites; and (3) the vegetation is largely free from human
Figure 1 Geographical location of the study sites in (a) equatorial East Africa, (b) South America, and (c) New Guinea. The approximate extent of alpine belts at the Last Glacial Maximum (LGM) is delimited by the 2200 m contour line (left or lower panel) and its current extent by the 3500 m contour line (right or upper panel); the extent of glaciers was ignored. The LGM lower limit of the alpine belt is based on Haberle (1998), van ’t Veer & Hooghiemstra (2000), Kiage & Liu (2006) and G.S. Hope (Australian National University, Canberra, pers. comm., 2012).
Species diversity and distribution

The number of species present on each mountain was calculated and the species–log(area) relationship was graphed for each region; ANCOVA was used to test for differences between the slopes using the **S**ystat 5 (Systat Software, Evanston, IL, USA). For each species, we calculated the number of mountains where it was found and then those counts were used to construct a frequency histogram of species by the number of mountains on which they occur. This observed frequency distribution was compared to a distribution obtained by 1000 randomizations. For each mountain within the region, species were randomly drawn from the regional species pool with the constraint that the number of drawn species was equal to the number of observed species. The number of mountains occupied by each species was calculated for each run. Differences between the observed and expected (assuming random distribution) numbers of occupied mountains were compared by means of a log-likelihood test (Sokal & Rohlfs, 1995).

Species turnover among mountains was measured by means of species accumulation curves (i.e. sample-based rarefaction curves) that were constructed for each region. The curves were obtained with the software package **Estimates** (Colwell, 2004), and the species numbers (Mao tau estimate) were plotted against cumulative mountain area obtained by 1000 randomizations. Total species diversity of the regions, i.e. the regional species pool or gamma diversity ($\gamma$), was partitioned into the within-mountain (alpha, $\alpha$) and between-mountains (beta, $\beta$) components. The alpha component was calculated as the mean species richness of the mountains and beta component was obtained by dividing $\gamma$ by $\alpha$ (Whittaker, 1970; Jost, 2007).

The floristic similarity between each pair of mountains was expressed as the difference between the observed number of shared species and the expected number of shared species under the assumption that the mountains were colonized randomly (Connor & Simberloff, 1978; Sklenář & Balslev, 2005; see also Spence & Pócs, 1989). The expected number of shared species was calculated as $\alpha_1 \times \alpha_2 / \gamma$, where $\alpha_1$ and $\alpha_2$ are the numbers of species found on each of the mountains (Connor & Simberloff, 1978; Simberloff et al., 1981). Chi-square ($\chi^2$) between observed and expected numbers was used as a measure of floristic similarity. The correlation between the matrix of geographical distances and the matrix of floristic similarity was measured by means of Mantel tests, within R **Package** (Legendre & Vaudor, 1991); a $P$-value was obtained by 499 randomizations.

**RESULTS**

Our samples from the tropical alpine flora of East Africa, the South American Andes and New Guinea included a total of 371, 489 and 279 species distributed in 141, 135 and 90 genera, respectively. *Helichrysum* was the most species-rich East African genus (23 species in the sample), whereas *Draba* (27 species) was the richest genus in the Andes, and *Rhododenron* (21 species) was the richest in New Guinea. In general, the genera inhabiting the Andean high-elevation páramo were found to be more species rich than genera in the other two alpine regions (Fig. 2). Genera with a single species made up 57% of genera in East Africa, 52% of genera in New Guinea and 42% of genera in the Andes.

The mean species richness for the East African, Andean and New Guinean mountains was 174.4, 155.6 and 113.6, respectively. In East Africa, Mount Meru was the least diverse, containing only 93 species, whereas Mount Elgon was the richest of all mountains, with 243 species. Slightly less variation was found in the other two regions, with the species number ranging from 100 (Sumapaz) to 198 (Anti-sana) among Andean sites, and from 83 (Owen Stanley Range) to 170 (Snow Mountains) among New Guinean sites (Appendices S1–S3). Species richness correlated with the log-transformed geographical area of the mountains in two.
regions (Fig. 3). A significant correlation was found in the Andes \( (r = 0.820, P = 0.02) \) and New Guinea \( (r = 0.871, P = 0.01) \), whereas the correlation for East African sites was marginally non-significant \( (r = 0.724, P = 0.07) \). Although the slope of the richness–area relationship seemed to be steeper for East African sites, the difference between the regions was not significant \( (F = 1.55, P = 0.76, \text{d.f.} = 2,15) \).

The observed frequency distribution of species among mountains departed significantly from random in all three regions \( (P < 0.001, \text{d.f.} = 6 \text{ for all}) \). Many species in our sample were found on a single mountain and such one-mountain species accounted for nearly half of species in the Andes and close to one-third in East Africa and New Guinea (Fig. 4a). The number of species distributed on greater numbers of mountains gradually declined, although three-mountain species in East Africa, seven-mountain species in the Andes and five-mountain species in New Guinea all deviated from this general pattern. Whereas 33 species were found on all East African mountains, only 18 and 13 species were common to all Andean sites and all New Guinean sites, respectively. As a result, the floras of individual Andean mountains were quite distinct and were mostly composed of narrowly distributed species, whereas the floras of East African mountains contained a high proportion of widespread species (Fig. 4b). Species turnover (beta diversity) was thus lowest among East African sites \( (\beta = 2.1) \), higher in New Guinea \( (\beta = 2.5) \), and highest in the Andes \( (\beta = 3.1) \). This was illustrated well by species accumulation curves (Fig. 5), as species tended to accumulate more rapidly with area in the Andes than in East Africa and New Guinea, and the slopes of the species–log(area) relationship were significantly different \( (P < 0.001, F = 397, \text{d.f.} = 2,15) \).

The floristic similarity between pairs of mountains significantly declined with (log-transformed) geographical distance.
Species richness of tropical alpine floras

Owing to the large geographical extent of the Andes, the páramo flora is the most diverse of all tropical alpine regions (Smith & Cleef, 1988; Hedberg, 1992). The Andean páramo region is also the most species rich in our sample when the direct effect of area is accounted for. Although the East African alpine flora appears (on average) more species rich than the Andean superpáramo and New Guinean tropicalpine floras in a single-mountain comparison, the Andes are significantly more diverse at the regional scale. This is due to higher species turnover in the Andes (Figs 4 & 5), which can be related to several factors. There are a number of narrowly distributed (super)páramo species in diverse genera such as Espeletia s.l. (11 endemic species from Venezuela and the Colombian Cordillera Oriental in our sample), Draba, Gentianella, Senecio and Valeriana (Luteyn, 1999; Sklenár & Balslev, 2005). Moreover, the Andean sites span a greater distance than those in East Africa. Finally, there is an indirect effect of area – the larger the alpine region (cordilleras of the northern Andes) the richer the entire flora (superpáramo) and the more variable its samples (species occurring on individual mountains).

Immigration from outside the region has been an important source of diversity in all tropical alpine floras (Hedberg, 1965; Smith, 1977; Cleef, 1979; Wagstaff & Garnock-Jones, 2000; Albach et al., 2005; Wagstaff et al., 2006; Gehrke & Linder, 2009; Devos et al., 2010; Sklenár et al., 2011). In the páramo, about half of the entire species richness may be derived from plant lineages that immigrated from temperate regions (Sklenár et al., 2011). Numerous arrivals from northern temperate regions into montane and alpine East Africa have been documented (Galley & Linder, 2006; Assefa et al., 2007; Popp et al., 2008) – including multiple independent events in Carex and Ranunculus – but the contribution of immigrating taxa to recent species richness in the East African mountains remains to be quantified. It therefore remains unclear whether or not the smaller number of successful arrivals, owing to the smaller target area or its isolation (Hedberg, 1992), contributed to the relative poverty of the afroalpine flora. Nevertheless, it is important to note in this context the relatively low representation of the southern temperate element in the afroalpine flora and lesser representation of the northern temperate element in the New Guinean alpine flora (Smith & Cleef, 1988).

Andean genera tend to be more species rich than genera in East Africa or New Guinea (Fig. 2). The higher richness of the páramo flora might thus be due to enhanced speciation in the Andes, and multiple Pleistocene expansion–contraction pulses of the páramo belt offer a plausible scenario (van der Hammen & Cleef, 1986). Remarkably high speciation rates have been demonstrated in Andean genera such as Gentianella, Valeriana and Lupinus (von Hagen & Kadereit, 2001; Bell & Donoghue, 2005; Hughes & Eastwood, 2006), although there are also a number of relatively species-poor páramo groups (Luteyn, 1999). In East Africa, the high levels of plant endemism of individual mountains – up to 15% – are generally explained by a dispersal–speciation scenario, where successful overland dispersal was followed by speciation (Hedberg, 1957, 1969, 1992; Coe, 1989; Harmsen et al., 2011).
Species distribution patterns

Species richness increases with area (Fig. 3) and floristic similarity declines with geographical distance (Fig. 6) in tropical mountains, which is consistent with earlier observations and general biogeographical patterns (Smith, 1975b; Cuatrecasas, 1986; Hedberg, 1992; Lomolino et al., 2010). There are, nevertheless, distinct differences between the regions. Species richness appears to increase more rapidly with area in East Africa (although the relationship is marginally non-significant) and thus larger East African mountains tend to host more species than comparably large mountains in the Andes and New Guinea. This might reflect the thorough botanical exploration of the afroalpine belt, especially in contrast to New Guinea. The most species-rich East African mountain, Mount Elgon, is, however, also distinctly older than any other site (van der Hammen & Clee, 1986; Hedberg, 1992; Schlüter, 1997; Hoorn et al., 2010). A longer time available for species accumulation, as also indicated by the highest number of local endemics (Hedberg, 1992), may have contributed to the high species richness of Mount Elgon.

The flora of Mount Meru, the smallest and most species poor in East Africa, is species rich compared with the flora of Andean and New Guinean sites several times smaller, such as Sumapaz and the Star Mountains. Simpson (1974) considered the páramo islands to be ‘oversaturated’ by plant species that immigrated via enlarged treeless areas during glacial periods. This scenario may hold true for the very small superpáramo of Sumapaz; although it is now surrounded by shrubby and grass páramo, it was directly connected to other (super)páramos of the Colombian Eastern Cordillera, such as Cocuy, during cold periods (van der Hammen & Clee, 1986; Hooghiemstra et al., 2006; van der Hammen et al., 2008). The relatively poor flora of Mount Meru was attributed to the mountain’s dry climate and young age (Hedberg, 1951, 1992), but relatively recent volcanic activity along with limited dispersal from nearby mountains may also be involved. For instance, the great majority of the 78 species held in common between Mount Meru and Kilimanjaro (the closest mountain with afroalpine vegetation) are widespread in the afroalpine region, whereas only three species are exclusively shared between the two mountains. In contrast, of the 68 species shared between Sumapaz and Cocuy, eight are confined only to those two mountains.

Floristic similarity thus decreases with distance at different rates, and nearby Andean sites are more similar than comparably distant sites in East Africa and New Guinea (Fig. 6). Although Kilimanjaro and Mount Meru are only about 70 km apart, their floras differ more than those of Sumapaz and Cocuy, which are separated by 370 km but with an almost direct grass páramo connection. The similarity between Chimborazo and Antisana in Ecuador, separated by 135 km across the inter-Andean valley, is more than three times higher than that between Mount Meru and Kilimanjaro. These patterns indirectly support Hedberg’s (1986, 1992) idea that plants have dispersed more effectively in the high Andes than among the East African mountains. Less effective dispersal may also be true for New Guinean mountains, which, especially in the eastern part of the island, are also more isolated than mountains in the Andes. As a result, two relatively well-explored New Guinean mountains, Mount Wilhelm and Mount Giluwe, appear to share fewer species than comparably distant Andean sites (see also Kalkman & Vink, 1970; Smith, 1975b).

The dispersal-limitation scenario outlined above for the East African mountains is contradicted by the distributions of a number of species, however. On average, 60% of the flora of an East African mountain is made up of widespread species that are present on five or more sites; moreover, almost 9% of afroalpine species are known from all seven sites, in contrast to less than 4% and 5% of such species in the Andes and in New Guinea, respectively (Fig. 4b). Dispersal does not appear to be a very rare event for many afroalpine species, such as Arabis alpina, for which evidence of multiple migrations within the eastern group of mountains was found (Assefa et al., 2007). Species with wide geographical distributions typically have wide elevational ranges (Hedberg, 1969, 1986; Smith, 1977; Sklenář & Jørgensen, 1999), which implies more abundant populations and broader ecological tolerances (Smith, 1977). Such species are most likely to disperse and colonize new habitats, such as deglaciated terrain, scree slopes, lava flows and ash deposits (Hedberg, 1986). This is shown indirectly by the floristic composition of the youngest East African mountain, Mount Meru, where the widespread species account for 75% of the species present. It remains to be determined, however, why the afroalpine flora contains a higher proportion of widespread species than the Andes and New Guinea.

Andean páramo is confirmed to be the most species-rich tropical alpine region; Andean genera tend to be richer in species than those in East Africa and New Guinea, and there is greater species turnover in the Andes. The flora of the East
African mountains appears to be more uniform than the flora of the Andes, due to the relatively large number of widespread species. Advances in understanding the processes that have determined the species diversity and composition of tropical alpine floras will require additional molecular phylogenetic studies. However, we believe that insightful and inspiring papers by Olov Hedberg and Thomas van der Hammen will remain starting points for students of the afro-alpine and páramo regions.

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Afroalpine species richness of the East African mountains.
**Appendix S2** Superpáramo species richness of the Andean mountains.
**Appendix S3** Alpine species richness of the New Guinean mountains.

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**BIOSKETCHES**

**Petr Sklenár** has studied the flora and vegetation of the equatorial high Andes since 1995 and his recent projects focus on functional ecology and phylogeny of páramo plants and human impact on diversity of páramo plant communities. He is co-author of the *Generic Flora of the Páramo*.

**Inga Hedberg** has been involved in biodiversity research of the East African high mountains since 1963. She co-authored the *Flora of Ethiopia and Eritrea* and is especially interested in biodiversity conservation in Africa. Presently she works on unpublished field records, her own and those by her late husband, Olov Hedberg, to make the data more widely available.

**Antoine M. Cleef** has studied Neotropical páramo vegetation since 1971 and published a number of papers on its flora, (palaeso)biogeography and vegetation communities. Presently he is focusing on digital documentation of past fieldwork and records with the help of GBIF-NL.

Author contributions: P.S. conceived the ideas, collected and analysed the data, and led the writing; I.H. and A.M.C. collected the data and participated in the writing.

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