

INTRODUCTION

The páramos of the South American Andes host the richest tropical mountain flora in the world (Smith & Cleef, 1988). The recently compiled species list of páramos, ranging from Costa Rica to northern Peru, includes 1298 and 3399 species of non-vascular and vascular plants, respectively (Luteyn, 1999). In the past there have been periods of páramo expansion and contraction due to climatic cycles (van der Hammen & Cleef, 1986; Bosman *et al.*, 1994; Hooghiemstra & Cleef, 1995), accompanied by associated speciation and radiation events (Simpson, 1975; Cuatrecasas, 1986; Reig, 1986). These climatic changes have promoted the evolution of endemic species in numerous plant genera, such as *Espeletia*, *Gentianella* and *Jamesonia* (Cuatrecasas, 1979; Pringle, 1995). Relations

between individual páramo floras are complex (Cuatrecasas, 1979; van der Hammen & Cleef, 1986; Ricardi *et al.*, 1997; Sklenár & Jørgensen, 1999), and comparisons of mountains may offer key insights into the processes responsible for observed patterns.

Previous studies divided the páramos in several zones related to altitude (Cuatrecasas, 1934, 1958; Harling, 1979; Cleef, 1981; Acosta-Solís, 1984; Ramsay, 1992; Jørgensen & Ulloa, 1994). Typically, the trees of the upper forest line are replaced by tussock grasses of the grass páramo (Fig. 1); sometimes a transition zone between the two, the shrubby subpáramo, is present but this has been lost in most areas as a result of human disturbance (Ramsay, 1992; Luteyn, 1999). In Ecuador, the tussocks of the grass páramo (typically belonging to *Calamagrostis*, *Festuca* and *Stipa*)



Fig. 1 Grassy páramo at 3800 m in Cajas National Park, southern Ecuador. The cattle were grazing in an area that had been burned approximately 3 years earlier. The sheltered woodland in the distance is one of many in the Ecuadorian páramos dominated by trees of the genus *Polylepis* (photo Paul M. Ramsay, 12 September 1987).

decline in abundance by around 4000–4100 m, although in drier páramos it may be 100–200 m higher, and are replaced by cushion plants (Ramsay, 1992; Sklenár, 2000). Ramsay (1999) describes the dynamic relationship between tussocks and cushions in the transition zone. The dominance of cushions, especially *Plantago rigida* Kunth, *Xenophyllum* and *Azorella*, over tussocks is particularly pronounced in the more humid páramos. Above this, at about 4200–4300 m, a narrow belt of the shrubby lower superpáramo can usually be found, where dwarf shrubs of *Loricaria*, *Pentacalia*, *Diplostegium* and *Chuquiraga* occur alongside the cushion plants and tussock grasses (Fig. 2). Higher still, towards the upper limits of plant life, scattered plants grow in a zone sometimes referred to as desert páramo (Fig. 3) (Jørgensen & Ulloa, 1994; Jørgensen & León-Yanez, 1999). All of the zones above the upper limit of more or less continuous tussock grass cover are known as superpáramo (Cleef, 1981; Sklenár, 2000).

Páramo diversity at regional and landscape scales is poorly understood. Factors such as climate, geological history, habitat diversity and also human influence determine the diversity of biota in the páramos (Simpson, 1974; Vuilleumier & Monasterio, 1986; Luteyn, 1992). Local climatic

gradients further complicate within-mountain diversity patterns, with spatial community changes often occurring over short distances (Cleef, 1981; Ramsay, 1992; Sklenár, 2000). Topographic variations at this scale result in azonal habitats such as cushion mires, and even finer scale differences within these habitats (Bosman *et al.*, 1993). *Polylepis* woodlands, probable remnants of more extensive upper Andean forest in the past (Fjeldsá, 1992; Lægaard, 1992), also contribute to the mosaic of the páramo habitats (Fig. 1).

The vegetation of the páramo zone is influenced strongly by burning, particularly by agricultural fires set to improve grassland productivity (Lægaard, 1992; Verweij & Budde, 1992; Ramsay & Oxley, 1996; Luteyn, 1999; Ramsay, 2001). A mosaic landscape results from this burning, creating temporal and spatial heterogeneity within the altitudinal gradient (Ramsay, 1999).

Few studies have analysed patterns of vegetation diversity in tropical Andean mountains. Ramsay (1992) and Keating (1999) briefly examined diversity in the grass and shrubby páramo of Ecuador, and Baruch (1984) the diversity of *Espeletia* páramo in Venezuela. Wolf (1993) studied changes in diversity of epiphytic canopy cryptogams on a 3000-m-long altitudinal gradient reaching the páramos in



Fig. 2 Transition between grassy páramo and superpáramo at 4200 m on Volcán Cotacachi. Cushions of *Xenophyllum humile* (Kunth) V.A. Funk and *Plantago rigida* Kunth were codominant with *Loricaria* shrubs (photo Paul M. Ramsay, 11 October 1987).



Fig. 3 Superpáramo at 4600 m on Volcán Chimborazo. *Calamagrostis* tussocks and *Chuquiraga* shrubs were prominent but 10 other smaller species were also present (photo Paul M. Ramsay, 25 October 1987).

Colombia, while Balslev & de Vries (1982, 1991) and Bliemsrieder (1992) monitored temporal changes of páramo diversity in permanent plots in Ecuador.

This paper considers altitudinal patterns of diversity in zonal páramo vegetation in Ecuador. A number of questions will be addressed here. How does páramo species richness change from low to high altitudes? Is diversity more variable at higher altitudes? Are rates of species turnover

similar in different vegetation types across the altitudinal gradient?

METHODS

The vegetation of the grass páramo and superpáramo of Ecuador were surveyed in two independent studies — ‘Ramsay’ and ‘Sklenár’ — sampling 12 and 18 areas, respectively (Fig. 4). The Sklenár

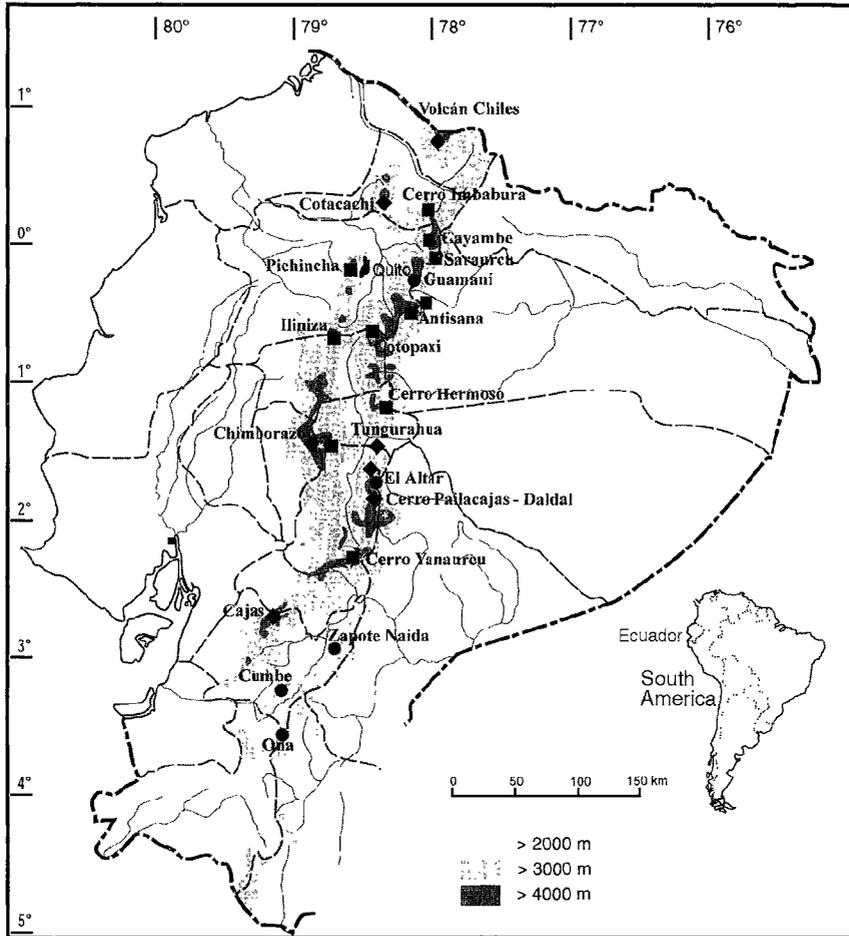


Fig. 4 Map of Ecuador indicating study areas. ● Ramsay study sites; ■ Sklenár study sites; ◆ both studies.

study focused on higher-altitude superpáramo, at 4000 m and above, while the Ramsay study included mainly grass páramo from altitudes below 4000 m. These areas were selected from high elevation regions of the country to provide a representative range of páramo types. The mountains visited included areas with different geological characteristics (igneous and metamorphic rocks) and volcanic history (tertiary vs. quaternary activity, relatively recent volcanic events).

The zonal páramo vegetation was sampled using a stratified random sampling method, with three replicate samples randomly placed at 100-m intervals of altitude. The number of altitudinal levels varied among the study sites as a result of

different mountain height. In a single case of a grass páramo in the southern Ecuador only one level was sampled, while longest gradients covered 11 levels when the Ramsay and Sklenár transects were pooled. The average gradient length was 5.4 altitudinal levels. In the Ramsay study all samples were 5 × 5 m, but in the Sklenár study, while most samples were 5 × 5 m, larger plots of 10 × 10 m were used usually at the highest elevations where vegetation was very patchy and the smaller plots would have sampled only a fraction of plant communities. Random samples falling within areas which had been burned within 2 years (evident from the altered state of the vegetation) were not used and the selection protocol repeated, locating

the sample elsewhere. Within each sample, percentage cover scores of all vascular plants were recorded [$< 5\%$, $6\text{--}25\%$ (in Sklenár data divided into $6\text{--}15\%$ and $16\text{--}25\%$), $26\text{--}50\%$, $51\text{--}75\%$, $> 75\%$], and later were converted to scores using their midpoint values to calculate diversity indices. Voucher specimens were collected for identification purposes and, in critical plant groups such as grasses and ferns, specimens were collected from most sampled altitudinal levels. In the Ramsay study, overall disturbance was recorded on an ordinal six-point scale (0 = no disturbance, 5 = highest disturbance). In each case, an assessment was made using visible evidence for burning (tussock condition, ash deposits, charred remains), grazing (cropping of vegetation, faeces of grazing animals) and trampling (microterracing of slopes, poaching, hoofprints, broken branches of shrubs). Although disturbance history may be considered as important in shaping plant communities as contemporary disturbance regimes, no attempt was made to estimate past disturbance histories because of the difficulties in assessing this accurately.

For each of the samples, species richness was calculated, along with two measures of within-community diversity and one measure of between-community diversity. Species richness, S , was the number of species encountered in each plot. Within-community diversity, or α -diversity, was calculated as a reciprocal of the Simpson's index for finite sample size:

$$D = \frac{1}{\sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)}$$

where n_i is the number of individuals (in this case cover value) of species i , and N is the total number of individuals (total sample cover). The index basically measures the probability of two randomly selected individuals being the same species, but in the reciprocal form the index value can be interpreted as the number of equally abundant species needed to produce the same heterogeneity as observed in the sample (Peet, 1974). Equitability, the other within-community diversity index concerning the evenness with which importance within the plant community is divided among species, was calculated as $E = D/S$. This index varies between 0 and 1: the higher the value, the more equitable the sample. Between-community diversity, β -diversity, was

measured using the index proposed by Wilson & Shmida (1984):

$$\beta_r = \frac{g(H) + l(H)}{2\bar{\alpha}}$$

where the $g(H)$ and $l(H)$ are numbers of species gained and lost, respectively, in the samples along the altitudinal gradient, and $\bar{\alpha}$ is the average species richness. The index, independent of α -diversity and sample size, has a direct meaning of degree of species turnover along the environmental gradient. The three sample plots from each altitude were pooled to calculate β . In Wilson & Shmida's (1984) original example, gaps in species distributions across and altitudinal gradient were filled — in other words, a species distribution was simplified as the range between its first and last occurrence. In the current analysis, such simplification of the dataset was not carried out. 'Temporary' gains and losses in species along the altitudinal gradient were considered important and retained.

To analyse the effect of disturbance on the community diversity, Kruskal–Wallis one-way analysis by ranks (Sokal & Rohlf, 1995) was employed using the STATGRAPHICS statistical package.

RESULTS

The zonal páramo vegetation was recorded in 192 and 243 sample plots for the Ramsay and Sklenár surveys, respectively (Table 1). Since it was not possible to verify all species determinations between the two studies, the total number of species cannot be provided yet. However, in the first study, located mainly in the grass páramo, 348 species were found, while in the Sklenár study, located mainly in the superpáramo, 284 species were present. The number of species for

Table 1 A summary table of the two independent surveys of the zonal páramo vegetation of Ecuador

	Ramsay	Sklenár
Number of study sites	12	18
Surveyed altitudinal range	3100–4600 m	4000–4800 m
Number of vegetation samples	192	243
Number of species	348	284

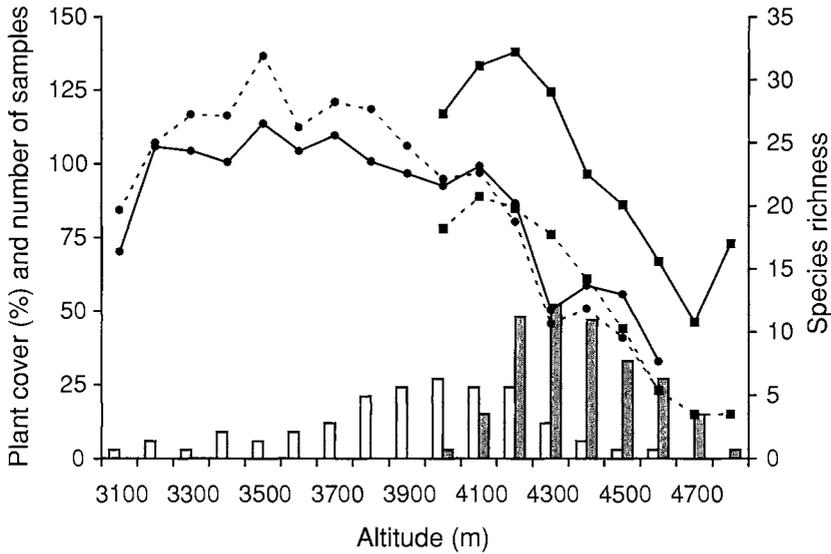


Fig. 5 Distribution of samples (bars), mean plant cover (dashed line), and mean species richness (solid line) along the altitudinal gradient (Ramsay study, open bars and ●; Sklenár study, shaded bars and ■).

individual mountain transects ranged from 117 in Cajas (grass páramo transect with seven levels) to 37 sampled on the western side of Volcán Chimborazo (seven levels), where the vegetation has been characterized as puna (Acosta-Solís, 1985; Cerón, 1994) or rain-shadow desert páramo (Ramsay, 1992). Although just 24 species were found in the páramo of Oña, only one altitudinal level was sampled in this region. The average numbers of species per transect was 73 ± 28.1 (mean ± 1 SD) in the Ramsay grass páramo study while it was 74 ± 17.9 in the Sklenár superpáramo survey. A maximum of 53 plant species was found in one sample plot from the El Altar volcano at 4200 m, while only one species was recorded from the plots at 4600 m on Volcán Cotopaxi.

The páramo communities between 3800 m and 4600 m were the best represented from the overall 1700 m-long altitudinal gradient with more than 20 sample plots at each 100-m level, while only three plots were recorded at the very ends of the gradient (Fig. 5). The multi-layered tussock structure of the grass páramo below 3800 m often exceeds 100% cover, and the total vegetation cover tends to be similar at those altitudinal levels (Fig. 5). From 3800 m the cover steadily decreases with increasing altitude, reaching a minimum of about 25% at 4600 m in the Ramsay data. This tendency is also

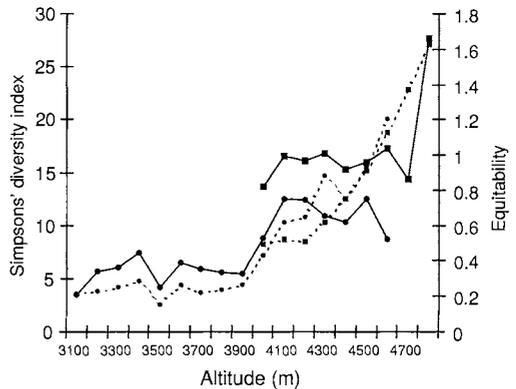


Fig. 6 Mean Simpson's diversity index (solid line) and mean equitability (dashed line) in zonal páramo communities. ● Ramsay study; ■ Sklenár study.

seen in the Sklenár superpáramo data above 4100 m. By 4700 m, the plant cover is well below 20%.

Species richness follows a similar pattern to that observed for plant cover (Fig. 5). The number of species is high until 4100–4200 m, but above this altitude richness declines sharply in both datasets, so that 500–600 m higher the number of species is reduced by approximately two-thirds. The increase in species richness in the Sklenár data at 4800 m is very atypical, and it is due to three

samples located on top of a well-colonized glacial moraine on Volcán Chimborazo, which comprised an unusually high number of species at such altitudes.

The Simpson's diversity index is plotted in Fig. 6. In the Ramsay data the values oscillate around $D = 6$ at altitudes below 4000 m, then increase markedly by 4100 m, the diversity values roughly doubling, and then remain more or less constant for the rest of the gradient. The Sklenár superpáramo data also remain roughly constant between 4100 and 4700 m, at around $D = 16$, with an obvious exception at 4800 m, the reason for which has already been explained. Similar patterns are also shown by both datasets for the equitability index (Fig. 6). In the Ramsay data, equitability is low and more or less constant until 3900 m, then it increases to reach a maximum at the very end of the gradient. The Sklenár data rise steadily from 4200 m, again reaching the maximum at the highest altitude.

The data tend to be more variable at higher elevations (Fig. 7). The coefficients of variation calculated for cover values, species richness, Simpson's diversity and equitability indices generally increase above 3900 m in the Ramsay data. A similar increase in the variability of cover, species richness and Simpson's index can also be seen in the Sklenár data, although in this dataset the CV for equitability peaks at 4300 m and declines above this altitude.

Disturbance shows a clear relationship with altitude and the three measures of diversity (Table 2). Disturbance is highest at low altitudes associated with grass páramo, and its intensity decreases towards the superpáramo. The greatest

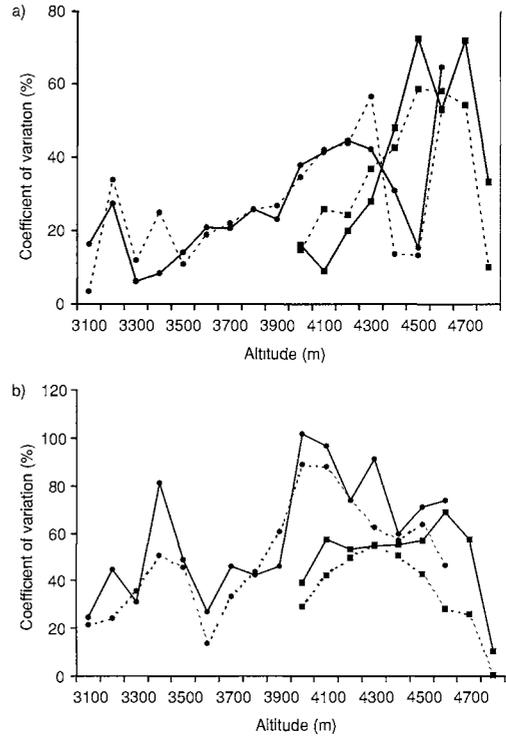


Fig. 7 Coefficients of variation for: (a) plant cover (solid line) and species richness (dashed line); (b) Simpson's diversity index (solid line) and equitability (dashed line). ● Ramsay study; ■ Sklenár study.

species richness was found with intermediate levels of disturbance, while severe and no or little disturbance resulted in far fewer species. By contrast, any level of disturbance caused a significant

Table 2 Mean altitude, species richness, Simpson's diversity index, and equitability in six disturbance classes (mean \pm SE). The last two rows indicate the results of the Kruskal–Wallis one-way analysis by ranks; 0 = no disturbance, 5 = maximum disturbance

Disturbance score	Number of samples	Altitude (m)	Species richness	Simpson's diversity index	Equitability
0	33	4218 \pm 30.9	19.0 \pm 1.16	16.33 \pm 1.80	0.93 \pm 0.10
1	33	4161 \pm 46.6	11.8 \pm 1.33	9.49 \pm 1.85	0.74 \pm 0.08
2	27	3926 \pm 51.1	25 \pm 1.18	7.69 \pm 1.03	0.30 \pm 0.03
3	38	3755 \pm 59.6	24.4 \pm 0.98	5.86 \pm 0.53	0.25 \pm 0.03
4	55	3738 \pm 23.6	25 \pm 0.72	5.69 \pm 0.31	0.22 \pm 0.01
5	6	3650 \pm 22.4	18.7 \pm 1.17	4.39 \pm 0.48	0.23 \pm 0.02
Kruskal–Wallis statistics		101.8	65.6	37.3	91.9
Probability		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$

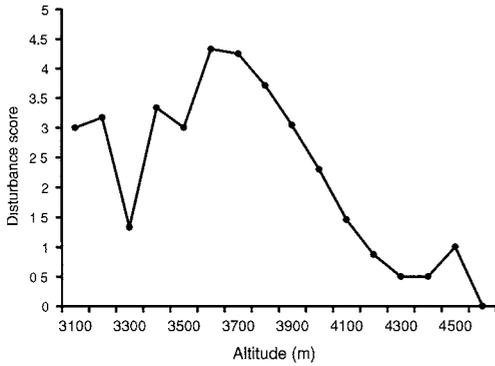


Fig. 8 Changes in mean disturbance scores with altitude (solid line).

decrease in the Simpson's diversity and equitability indices. The Kruskal-Wallis non-parametric analysis showed highly significant relationships between disturbance regime and altitude, plant cover, Simpson's diversity and equitability. When disturbance is plotted against altitude, a pattern similar to that seen in plant cover and species richness can be observed (Fig. 8). Disturbance scores are high below 4000 m, and gradually decrease through 4000–4100 m to reach very low levels at the highest altitudes.

Figure 9 shows the turnover of species, β -diversity, along the altitudinal gradient. The Ramsay data show higher turnover at lower altitudes (3300–4000 m) than at higher altitudes (4200 m +). The Sklenár data demonstrate a roughly consistent, low turnover of species in the superpáramo (4000–4800 m).

DISCUSSION

The diversity data examined here support the distinction of the páramo belt in two altitudinal zones, the grass páramo and the superpáramo. Clear differences between the two zones were demonstrated by changes in plant cover, species richness, α -diversity and β -diversity. The results indicate that the transition begins at around 4000 m in Ecuador. However, the presence of altitudinal subdivisions of the superpáramo into the lower and upper zone (Cleef, 1981) was not evident from these analyses, although it was detected when a single mountain was treated (Sklenár, 2001).

Species richness in the sample plots was higher in the grass páramo compared with the superpáramo. The number of species in the Ramsay samples was more or less consistent (20–30) throughout the grass páramo, and then declined steadily above around 4100 m to less than 10 at

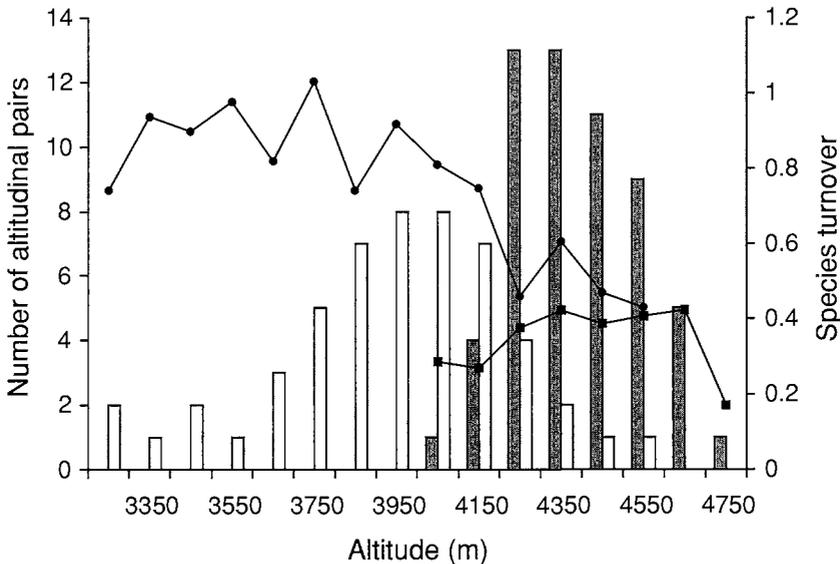


Fig. 9 Rate of species turnover along the altitudinal gradient (solid lines; ● Ramsay study; ■ Sklenár study). The bars indicate the number of compared altitudinal pairs.

4600 m. The Sklenár data showed the same decline, although species richness appears to have been somewhat higher in this survey (partly an artefact of the greater sample size used for some plots). There is a clear positive correlation between patterns in species richness and total vegetation cover. With increasing altitude, the climate becomes less hospitable and those plants which can survive are restricted to favourable microsites and the total vegetation cover decreases (Monasterio, 1981; Pérez, 1987; Pfitsch, 1988; Stern & Guerrero, 1997). A consequence of the limited availability of microsites is increased variation in the vegetation cover and plant community diversity, as can be observed in the superpáramo data (Fig. 7).

The superpáramos were more diverse than the lower-altitude grass páramos when equitability and Simpson's index are taken into account, consistent with the findings of Baruch (1984) for a Venezuelan páramo. The grass páramos were dominated by tussock grasses, whereas the superpáramos showed very little dominance. At the highest altitudes plants were mostly restricted to 'safe sites', the spatial and temporal availability of which are unpredictable (Fig. 3). Therefore, no single strategy is likely to be favoured in the superpáramo (Ramsay & Oxley, 1997), resulting in high equitability and high variability in α -diversity. The importance of favourable sites in the superpáramo is also evidenced by the three plots located at 4800 m. The glacial moraine upon which the vegetation was sampled provided numerous favourable habitats for plant establishment around small rocks and boulders so that the species richness increased markedly in comparison to the plots located on sandy soil on the slope lower down; this increased richness at such high altitudes on the Chimborazo volcano has already been noticed by Meyer (1907). This suggests that, rather than by the harsh climate itself, the upper limit of vegetation and plant occurrence is often controlled by habitat availability (Miehe, 1989; Stern & Guerrero, 1997).

In the grass páramo, tussock grasses are favoured by disturbance, particularly fire (Beck *et al.*, 1986; Ramsay & Oxley, 1996; Ramsay, 1999), which in turn results in concentrated disturbance in the form of grazing and trampling by livestock (Velázquez, 1992; Verweij & Budde, 1992; Hofstede, 1995). Thus burning represents the dominant component in determining overall

disturbance in grass páramo. Fires are most often set every 2–4 years by farmers to encourage the growth of nutritious new shoots (Lægaard, 1992; Ramsay & Oxley, 1996). Tussock grasses survive fires easily and regenerate within a few weeks or months after burning, while other species, especially shrubs and trees, may die (Williamson *et al.*, 1986; Lægaard, 1992; Ramsay, 1992; Horn, 1997). Subsequent grazing and trampling may also promote the abundance of certain species (Verweij & Budde, 1992; P. Sklenár, personal observation). The superpáramo is less susceptible to fire (and related disturbances) because there is not sufficient plant material to sustain fires and grazing is uncommon at such high altitudes, although cattle may occasionally roam as high as 4600 m.

Reinforcing tussock grass dominance through burning has several important consequences for species diversity in these areas. Our data suggest that more species are found in plots which are subjected to moderate burning frequencies and intensities while heavily burned samples contain fewer species, as do lightly burned or undisturbed plots. However, species diversity (as calculated in this study) is lower in burned plots, regardless of the intensity and frequency. This is undoubtedly related to the higher abundance of tussock grasses and its influence on equitability. The tussock/intertussock physiognomy imposes a well-defined and predictable structural basis for niche partitioning between plants while at the same time limiting the number of species and their abundances. The result is relatively low variability in plant cover and α -diversity across the altitudinal range of the grassy (burned) páramo. By contrast, the superpáramo — where the burning is absent and the physiognomic structure of the vegetation more varied — shows a steady decline of species richness with altitude.

Fires in the grass páramo promote a disturbance mosaic pattern, made up of patches of previously burned vegetation in various stages of recovery (Lægaard, 1992; Hofstede, 1995; Ramsay & Oxley, 1996; Ramsay, 1999). Plant survival of fires depends partly on plant growth form (tussocks and rosette plants do particularly well: Lægaard, 1992; Ramsay & Oxley, 1996), but also on chance factors such as fire intensity and the pattern of the burn (Ramsay, 2001). As the tussock grass structure rebuilds, recolonization of bare ground tends to be a largely random process (Ramsay & Oxley, 1996; Ramsay,

2001) with a slow turnover and accumulation of species with time, though the turnover rates may vary in various páramo life forms (Bliemsrieder, 1992). Eventually, the tussock canopy is fully formed and the burning cycle can begin again.

It seems likely that the high and varied β -diversity of the grass páramo documented in our data reflects this shifting mosaic more closely than an intrinsic species turnover related to the environmental gradient. Therefore, the use and interpretation of β -diversity values is meaningless when set in the context of the altitudinal gradient. There would be high species turnover between adjacent patches on the altitudinal gradient burned at various times while the mean α -diversity would not necessarily be much affected — this scenario is supported by the results of the two surveys. In the superpáramo, human-induced disturbance is generally absent and there was far less variation in β -diversity, which was also much lower.

On the evidence of the analyses presented here, it is suggested that the diversity of Ecuadorian zonal páramos is determined by three main factors, as follows.

Altitude

There is an apparent distinction between the grass páramo and the superpáramo. Grass páramo plots contained more species than superpáramo ones, but the dominance of tussock species resulted in lower diversity scores than the more equitable yet species-poor superpáramo samples. Although floristic data demonstrate a more detailed differentiation of community types over the altitudinal gradient, this is not evident from analyses of species richness and diversity.

Disturbance

Agricultural burning exerts a powerful influence on the diversity of grass páramo vegetation by encouraging uniformity in physiognomic structure and, to a lesser extent, species composition. Over a period of years, fires set at different times produce a patchwork of vegetation in different stages of recovery from variable intensity burns. Species richness is lower in plots subjected to little burning disturbance or where fires are frequent and/or intense. Any level of burning is associated with lower equitability of species once the vegetation has progressed beyond the initial recovery

stage. The turnover of species appears to be higher in the grass páramo with its fine-scale mosaic pattern than in the superpáramo where changes occur more gradually over the altitudinal gradient.

Availability of safe sites at high altitudes

In the upper reaches of superpáramo vegetation, plant cover, species richness and diversity are controlled mainly by the availability of suitable sites for colonization, survival and growth among a rocky substrate. Where such microsites are plentiful, species diversity is higher than where they are limited in abundance.

Teasing out the effects of each of these factors is difficult since they are so strongly interrelated. There is a strong correlation between disturbance and altitude in the surveys presented here, which reflects the change from the burned grass páramo to the unburned superpáramo. Clearly, the lower parts of the páramos are more productive (for both plants and livestock) and farmers' efforts tend to be concentrated in the grass páramo. The apparent environmental limits to the growth of continuous tussock cover above 4100 m or so, preclude the application of burning as a management tool in the superpáramo. As a result, the burns magnify the inherent altitudinal distinction between the two zones. To what extent is the altitudinal distribution of tussock grasses the result of human disturbance and how much is agricultural burning constrained by the presence of tussocks as the major fuel element, which is partially controlled by altitudinal factors? This is part of a larger debate involving the naturalness and distribution of forest and woodland communities at high altitudes in the Andes and other tropical alpine systems. There are currently a number of research efforts under way which may help to answer this difficult question.

ACKNOWLEDGMENTS

Paul M. Ramsay would like to thank Pete Merrow-Smith for his help in the field, Ralph Oxley for general support and the UK Overseas Development Administration, the Royal Geographical Society and the University of Wales for financial aid during the fieldwork. Petr Sklenár wishes to thank Veronika Sklenářová for field assistance and Pavel Kovář, Henrik Balslev and Renato

Valencia for general support. The Danish Research Academy (Forskerakademiet) and the Grant Agency of the Czech Republic (grant no. 206/97/0336) are acknowledged for financial help. Both authors are grateful to INEFAN for issuing research permits and to Peter M. Jørgensen, Dave Richardson, and two anonymous reviewers for valuable comments on the manuscript.

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