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# Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania

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## Abstract

This study describes changes in woody vegetation in the Mwanihana forest, Udzungwa Mountains National Park, Tanzania, over an altitude range of 470–1700 m. Two methods, fixed- and variable-area plots, are compared to elucidate altitudinal variation in tropical forest structure, diversity and community composition. Six 25 m × 100 m fixed area plots recorded a total of 2143 woody stems of ≥3 cm d.b.h. from 204 species. The 78 variable-area plots recorded the nearest twenty trees of ≥20 cm d.b.h. to an objectively chosen point, giving a total of 1560 stems in 9.1 ha from 156 species. A linear trend of increasing stem density with altitude was seen for variable-area plots. Species diversity is highest at high elevations. There was no clear zonation of elevational vegetation types. Restricted range taxa occur at all altitudes sampled. The study also revealed some methodological considerations. Bias in sample size and plot area can be tested by employing two sampling methods. Of the two methods used, fixed area plots are preferred as variable area plots are impractical in tangled understorey. Plot size must be controlled for in order to make reliable observations of diversity. Sampling along a continuous or near-continuous altitudinal gradient with sufficient replication is also important.

*Key words:* diversity, Eastern Arc, elevation, Tanzania, tropical forest, Udzungwa Mountains National Park

## Résumé

Cette étude décrit les changements de la végétation ligneuse de la forêt de Mwanihana, dans le Parc National d'Udzungwa Mountains, en Tanzanie, avec l'altitude, comprise entre 470 et 1700 mètres. Deux méthodes, des par-

celles de surface fixe/variable, sont comparées pour bien comprendre la variation altitudinale de la structure de la forêt tropicale, de sa diversité et de sa composition. Dans six parcelles fixes de 25 m × 100 m, on a relevé un total de 2143 pousses ligneuses de ≥3 cm de diamètre dbh appartenant à 204 espèces. Dans les 78 parcelles variables, on relevait les 20 arbres de ≥3 cm dbh les plus proches d'un point choisi objectivement, ce qui a donné un total de 1560 tiges de 156 espèces sur 9,1 ha. On a observé une tendance linéaire de densité croissante avec l'altitude dans les parcelles de surface variable. La diversité des espèces est plus élevée en altitude. Il n'y avait pas de zonage clair des types de végétation avec l'altitude. À toutes les altitudes échantillonnées, il existe des taxons à la répartition restreinte. Cette étude a aussi suscité quelques considérations méthodologiques. On peut tester les biais introduits dans la taille de l'échantillon et la surface des parcelles en employant deux méthodes d'échantillonnage. Des deux méthodes utilisées, celle des parcelles fixes est préférable parce que celle des parcelles variables n'est pas pratique dans les sous-bois enchevêtrés. Il faut contrôler la taille des plots pour faire des observations fiables de la diversité. Il est aussi important de faire des prélèvements en suivant un gradient altitudinal continu ou quasi continu, avec suffisamment de répétitions.

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## Introduction

Variation in species diversity along environmental gradients is a major topic of ecological investigation and has been explained by reference to climate, productivity, biotic interactions, habitat heterogeneity and history (Givnish, 1999; Willig, Kaufman & Stevens, 2003; Currie & Francis, 2004; González-Espinosa *et al.*, 2004; Qian & Ricklefs, 2004). A null-model has also been proposed which

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predicts species diversity to peak at intermediate parts of gradients because of overlapping ranges of species distributions which are bounded by the ends of the gradient (Colwell & Hurtt, 1994; Rahbek, 1995, 1997; Colwell & Lees, 2000; Kessler, 2001; Lomolino, 2001; Rahbek, 2005), a suggestion which has led to considerable debate (Colwell, Rahbek & Gotelli, 2005; Hawkins, Diniz-Filho & Weis, 2005; Zapata, Gaston & Chown, 2005).

The traditional view of the relationship between diversity and elevation in tropical forests is that diversity declines with increasing altitude (Richards, 1979; Lieberman *et al.*, 1996; Givnish, 1999). This fits with standard ecological theory on diversity and environmental gradients in that temperature declines with elevation leading to a lowering of productivity and biotic interaction. However, the pattern is not uniform. Remarkably, quantitative surveys of forest trees in the Eastern Arc mountains of Tanzania revealed that the number of species in plots of twenty trees remained constant with altitude (Lovett, 1996, 1999). It is possible that this observation is a function of methodology, as selection of appropriate sampling methods is key to interpreting diversity. Previous studies have missed trends because of sampling biases (Lomolino, 2001; Rahbek, 2005). Inadequate sample sizes may overlook patterns, whereas overly high sample sizes may be vulnerable to increased noise (Rahbek, 2005). It is also important to select appropriate analytical methods, particularly for assessing species compositional gradients and zones (e.g. Hamilton, 1975, 1989; Lieberman *et al.*, 1996; Tallents *et al.*, 2005).

This study aims to describe trends in woody vegetation with altitude in the Mwanihana forest of the Udzungwa Mountains National Park, Tanzania, with a particular focus on structure, diversity and community composition. A second aim is to compare trends shown by two different sampling methods and to draw conclusions on how best to measure altitudinal changes in tropical forest.

## Materials and methods

### *Study area*

The Eastern Arc is a disjunct chain of crystalline mountains stretching from southern Kenya to southern Tanzania (Lovett, 1990). This range contains relict forest fragments, which are thought to have persisted through a period of long-term climatic stability (Lovett & Wasser, 1993; Lovett & Friis, 1996; Fjelds  & Lovett, 1997). The forests have a high number of restricted range plant species in a relatively

small area and are considered to be a biodiversity 'hotspot' (Myers *et al.*, 2000).

The biological importance of the southern part of the Eastern Arc was recognized following discovery of a new primate species in the Udzungwa mountains and a proposal put forward for establishment of a national park (Rodgers & Homewood, 1982). The Udzungwa Mountains National Park was created in 1992 and covers much of the north-eastern part of the Udzungwa mountains. The forested east-facing Mwanihana escarpment lies within the eastern side of the national park and is recognized as a key site for conservation of the Udzungwa red colobus and Sanje mangabey (Dinesen *et al.*, 2001). Botanical collecting in the Mwanihana forests confirmed the biological importance of the area, with the discovery of many new species of plants (Lovett & Thomas, 1986; Lovett, Bridson & Thomas, 1988).

The Udzungwa Mountains are at the southern end of the Eastern Arc chain and occupy about 10 000 km<sup>2</sup> in south-central Tanzania between the altitudes of 200–2500 m. The focal area for this study is an area of forest on the steep east-facing escarpment of Mwanihana forest, now part of the Udzungwa Mountains National Park, lying above Sanje village on the far east of the Udzungwa range (400–1700 m altitude; 7°50' S, 36°55' E) in the catchment of the Sanje river. At altitudes below those sampled in this survey, the Udzungwa habitat consists of dry deciduous woodland, forest heavily altered by human activity and cultivation. At higher altitudes, forested slopes coexist with a mosaic of bamboo and *Hagenia abyssinica* J.F. Gmel. woodland. The forest is under the direct climatic influence of the Indian Ocean with rainfall for Sanje at 366 m altitude recorded as 1747 mm year<sup>-1</sup> occurring predominantly in a single wet season between November and May (Lovett, 1996). The mean daily temperature was 15.2°C at 500 m altitude, declining to 11.7°C at 1700 m. Soils were mostly sandy-loams or sandy-clay-loams. Soil pH at 15–25 cm depth declined from 5.1 at 500 m to 3.8 at 1700 m, but with a peak of 5.8 at 1250 m, although this may be a local anomaly. Further information on soil pH is given in Tattersfield *et al.* (2006). Study sites were positioned in areas of broadly similar slope and aspect without evidence of soil truncation, slumping or landslips.

### *Vegetation sampling*

Forest vegetation was sampled by Jon Lovett, Jeff Carr and students from Ruthin School and Huddersfield New

College, U.K. Fixed-area plots were sampled during July 1984 and July 1986 and consisted of 25 m × 100 m plots divided into four equal sections of 25 × 25 m. A total of six plots were enumerated at altitudes of 500, 750, 1000, 1250, 1500 and 1700 m. The diameter at breast height (d.b.h.) of all woody stems ≥ 3 cm d.b.h. was measured using a girthing tape and height was estimated in metres. Basal area was calculated using the equation for the area of a circle. For individuals with multiple stems, basal area was estimated as the sum of the circular area of each stem. In addition to the fixed-area plots, 78 variable-area plots were enumerated to sample large trees between October 1983 and October 1984 by Jon Lovett and Langson Kisoma (Lovett, 1996). Sample points were positioned at 100 m intervals along transects of variable length positioned to cover as much of the topographic variation at each locality as possible, from valley floors to ridge tops between 400 and 1670 m altitude. The diameters of the nearest 20 trees ≥ 20 cm d.b.h. from these points were measured in the same way as for fixed-area plots (Hall, 1991). Plot area was estimated using the distance from each sample point to the halfway distance between the 20th and 21st furthest trees as the radius. For fixed-area plots, results were analysed for all stems as well as for those ≥ 10 cm and ≥ 20 cm d.b.h. This was to determine the underlying trends of the parent community and also to allow a more complete comparison with data from the variable-area plots (trees ≥ 20 cm d.b.h. only).

Stems were identified in the field where possible. Where identification was uncertain, specimens were collected for verification at the Royal Botanic Gardens, Kew. Nomenclature follows Hubbard, Milne-Redhead & Polhill (1952–to date) and Exell & Launert (1970–to date) with updated name changes following more recent taxonomic revisions.

#### Data analysis

Species richness was calculated for all plots. Because of high variation in stem density between fixed-area plots, richness was adjusted by individual-based rarefaction using EcoSim 7.0 (Gotelli & Entsminger, 2001). Three additional measures of  $\alpha$ -diversity and 95% bootstrapped confidence intervals were calculated using SDR 3.0 (Pisces Conservation Ltd, 2002a). These included one measure of richness diversity (Shannon index) and two measures of dominance (Simpson and Berger–Parker). The Shannon Index was chosen for its widespread use and therefore can be compared with other studies. Despite some drawbacks

including sensitivity to sample size, the Shannon index remains one of the most commonly used indices for measuring richness diversity (Magurran, 2004). Simpson's index of dominance was chosen for its lack of sensitivity to sample size (Magurran, 2004). This was calculated using 1-C, where C can be calculated from

$$C = \sum p_i^2 \quad (1)$$

where

$$p_i = \frac{N_i(N_i - 1)}{N_T(N_T - 1)} \quad (2)$$

with  $N_i$  being the number of individuals in the  $i$ th species and  $N_T$  the total number of individuals in the sample. The 1-C format has been selected over  $1/C$  to avoid concavity and negative diversity results (Lande, 1996). The third measure of diversity used was the Berger–Parker index of dominance ( $d$ ), chosen for its simplicity and general usefulness for characterizing distributions (May, 1975; Magurran, 2004). The form  $1/d$  of the Berger–Parker index was preferred so that high values represent low dominance. For fixed-area plots, diversity was assessed for all stems, as well as for stems ≥ 10 cm d.b.h. and ≥ 20 cm d.b.h. Estimates of precision were made for all measures of diversity, using the standard error expressed as a percentage of the mean. Diversity measures were considered sufficiently precise if standard error was within 5% of the mean (after Hall, 1991).

Gamma diversity was assessed by pooling variable-area plot data into altitudinal bands and calculating sample-based rarefied species richness and 95% confidence limits using the Mao Tau function of EstimateS 7.5 (Colwell, 2005). An altitudinal band width of 140 m was chosen to maximize both the number of bands and the minimum number of sample plots per band.

To investigate community changes with altitude, detrended correspondence analysis (DCA; Hill, 1980) ordinations were calculated using CAP 2.1 (Pisces Conservation Ltd, 2002b). This ordination technique was chosen over classification techniques such as Cluster Analysis and TWINSpan, as it does not force sets of samples into groups and thus avoids erroneous classification of distinct vegetation communities. The influence of rare species was down-weighted for all DCA analyses so as to detect the major differences in community composition. For this, species rarer than the abundance of the commonest species divided by five, were down-weighted in proportion to their frequency (Pisces Conservation Ltd, 2002b). DCA ordinations were calculated using both stem number and basal area (after Lovett, 1996).

Simple hypothesis tests were employed using methods, assumptions and notation outlined by Dytham (1999). Linear trends were tested using simple (model I) linear regression. This method assumes that the two test variables can be defined as dependent ( $y$ ) and independent ( $x$ ), and that all values of  $y$  are normally distributed for each value of  $x$ . For cases where data were non-normal, and where the response and predictor variables were unclear, Spearman's rank correlation was used. Mann–Whitney  $U$ -tests were employed to test differences between pairs of non-normal datasets.

## Results

### Physical structure

A total of 3703 stems was recorded, with a combined basal area of 421 m<sup>2</sup>. Of these, 2143 stems (basal area 75 m<sup>2</sup>)  $\geq 3$  cm d.b.h. were recorded from the six fixed-area plots in a total sample area of 1.5 ha (2500 m<sup>2</sup> each). The 78 variable-area plots sampled an estimated area of 9.1 ha (mean plot size 1171 m<sup>2</sup>; maximum 3118 m<sup>2</sup>; minimum 284 m<sup>2</sup>) and contained 1560 stems  $\geq 20$  cm d.b.h., with a total basal area of 346 m<sup>2</sup>.

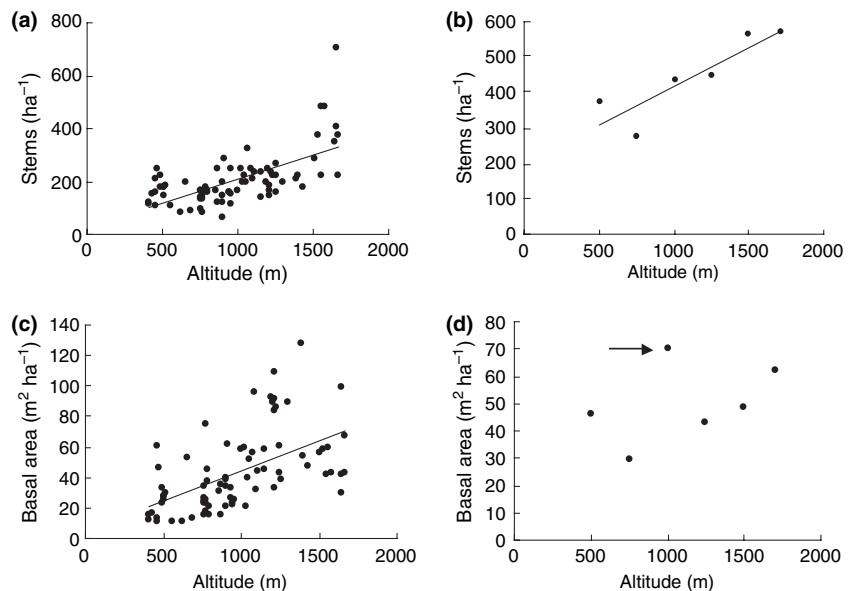
Stem density showed a significant increase with altitude for all stems in the variable-area plots and for stems  $\geq 10$  cm d.b.h. in the fixed-area plots (Fig. 1). In fixed-area plots, this trend was masked when stems  $< 10$  cm d.b.h.

were included (linear regression: d.f. = 5,  $r^2 = 0.30$ ,  $P = 0.258$ ). This was due to the superabundance of the understorey tree *Lasianthus kilimandscharicus* K. Schum. in the 1000 m plot, which comprised 237 of 492 individuals. There was also no significant relationship for stems  $\geq 20$  cm d.b.h. in the fixed-area plots (linear regression: d.f. = 5,  $r^2 = 0.14$ ,  $P = 0.470$ ).

Total basal area of variable-area plots also increased with altitude (Fig. 1). For fixed-area plots, basal area had a peak at 1000 m because of the presence of a few large individuals of the canopy tree *Parinari excelsa* Sabine, including the largest tree recorded in the study (250 cm d.b.h.). Otherwise the relationship between total basal area and altitude was positive, although not significant (Fig. 1d).

Other structural features of trees in the fixed-area plots showed less apparent trends. Maximum canopy height was greatest in the 1250 m plot (45 m), declining gradually below this altitude and more rapidly above. Mean d.b.h. and basal area for stems in both fixed-area and variable-area plots showed little variation between plots. The fixed- and variable-area methods showed no significant difference in mean d.b.h., stem number, basal area or species richness (Mann–Whitney  $U$ -test, d.f. = 83: mean d.b.h.  $U = 305.0$ ;  $P = 0.218$ ; stems per plot area  $U = 247.0$ ,  $P = 0.821$ ; basal area per plot area  $U = 269.0$ ,  $P = 0.543$ ; species richness per plot area  $U = 301.0$ ,  $P = 0.245$ ).

**Fig 1** Linear regression of stem density and basal area with altitude. (a) Stem density of stems  $\geq 20$  cm d.b.h. in variable-area plots, d.f. = 77,  $r^2 = 0.41$ ,  $P < 0.001$ ; (b) stem density of stems  $\geq 10$  cm d.b.h. in fixed-area plots, d.f. = 5,  $r^2 = 0.77$ ,  $P = 0.021$ ; (c) basal area of trees  $\geq 20$  cm d.b.h. in variable-area plots, linear regression d.f. = 77,  $r^2 = 0.30$ ,  $P < 0.001$ ; (d) basal area of stems  $\geq 3$  cm d.b.h. in fixed-area plots, d.f. = 5,  $r^2 = 0.16$ ,  $P = 0.429$ , arrow denotes plot influenced by large *P. excelsa* trees



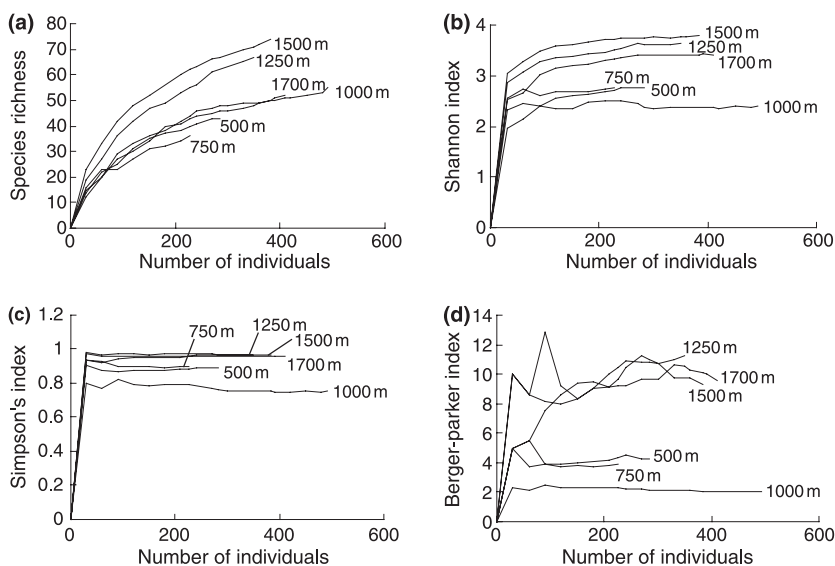
### Diversity

In the fixed-area plots, 204 different species  $\geq 3$  cm d.b.h. were recorded from 44 families. The variable-area plots, which sampled trees  $\geq 20$  cm d.b.h., recorded 156 species from 43 families. This compares to 81 species  $\geq 20$  cm d.b.h. from 30 families in fixed-area plots. Eighty-eight species were recorded in both fixed-area and variable-area plots, 71 of which were  $\geq 20$  cm in fixed-area plots. There were also 48 unidentified species in fixed-area plots and seventeen in variable-area plots.

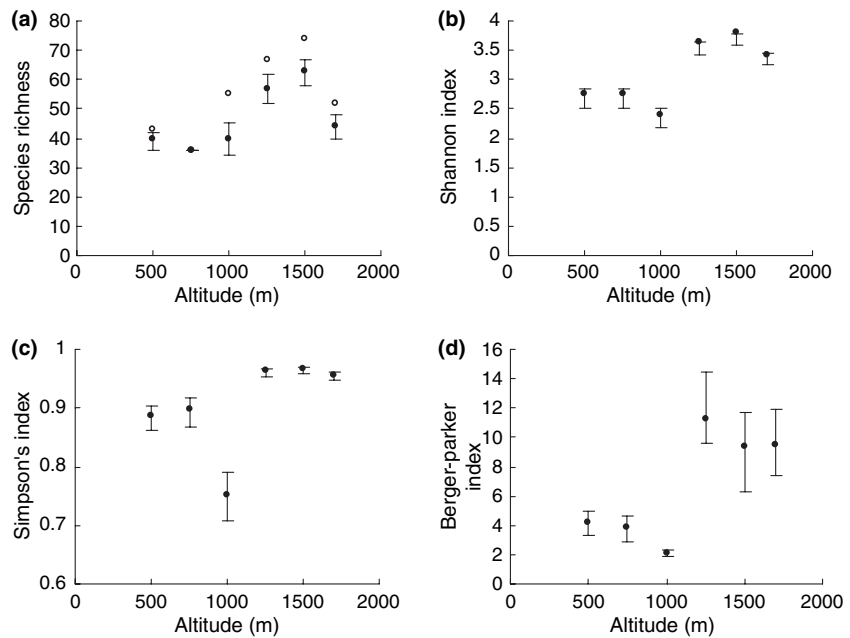
Accumulation curves in Fig. 2 show the effect of the high variation in the number of stems  $\geq 3$  cm d.b.h. on the calculation of diversity indices (range 227–492 stems per plot). From these, Shannon and Simpson's indices appear to have reached an asymptote by the stem number of the plot with the lowest stem density (750 m). Therefore, for these indices, sampling intensity is not likely to have affected the relative diversity of the plots. The Berger–Parker index has also levelled off for most altitudes, although the distinction between the three highest altitude plots is unclear. This however is unlikely to have altered the overall trend as these plots have similar diversity indices and remain more diverse than all other plots. Curves have not levelled off completely for species richness, therefore demonstrating the need for rarefaction. With the exception of Simpson's index, precision estimates for the four measures of diversity were also not within the desired 5% of the mean (mean for all plots: rarefied species richness = 9.50; Shannon index = 7.32; Simpson's index = 3.72; Berger–Parker index = 22.90).

The diversity of stems  $\geq 3$  cm d.b.h. in fixed-area plots did not show a significant linear relationship with altitude (linear regression: d.f. = 5, number of stems per plot: 500 m = 282, 750 m = 227, 1000 m = 492, 1250 m = 350, 1500 m = 383, 1700 m = 409; species richness  $r^2 = 0.44$ ,  $P = 0.151$ ; Shannon  $r^2 = 0.53$ ,  $P = 0.10$ ; Simpson's  $r^2 = 0.25$ ,  $P = 0.314$ ; Berger–Parker  $r^2 = 0.55$ ,  $P = 0.092$ ; Fig. 3). For all indices, there was a peak in diversity in either 1500 m or 1250 m plots. This was most marked for species richness and Shannon index, which both peak at 1500 m. Diversity was also relatively low in the 1000 m plot because of the high number of *L. kilimandscharicus* trees.

Shannon and Simpson's Indices showed a significant increase in diversity with altitude for stems  $\geq 10$  cm d.b.h. in fixed-area plots whereas rarefied species richness and Berger–Parker Index do not (d.f. = 5, number of stems per plot: 500 m = 93, 750 m = 68, 1000 m = 109, 1250 m = 111, 1500 m = 141, 1700 m = 143; Shannon  $r^2 = 0.74$ ,  $P = 0.028$ ; Simpson's  $r^2 = 0.67$ ,  $P = 0.047$ ; species richness  $r^2 = 0.57$ ,  $P = 0.083$ ; Berger–Parker  $r^2 = 0.51$ ,  $P = 0.111$ ). There were no significant linear relationships for trees  $\geq 20$  cm d.b.h. (linear regression: d.f. = 5, number of stems per plot: 500 m = 51, 750 m = 32, 1000 m = 52, 1250 m = 35, 1500 m = 38, 1700 m = 74; species richness  $r^2 = 0.28$ ,  $P = 0.277$ ; Shannon index  $r^2 = 0.52$ ,  $P = 0.108$ ; Simpson's index



**Fig 2** Accumulation curves of diversity with increasing sample size for fixed-area plots. Curves were plotted for randomly-ordered individuals in groups of 30. (a) Species richness; (b) Shannon index; (c) Simpson's index; (d) Berger–Parker index

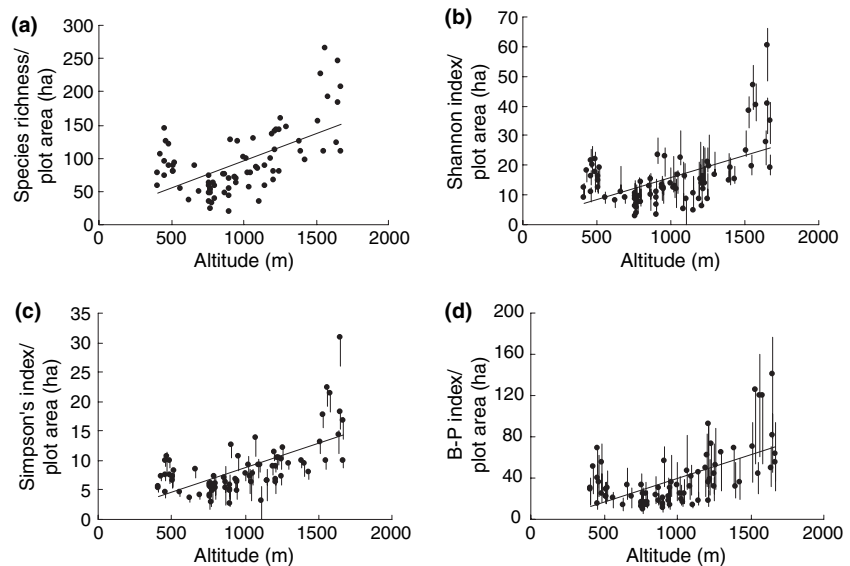


**Fig 3** Diversity indices and 95% confidence intervals plotted against altitude for stems  $\geq 3$  cm d.b.h. in fixed-area plots. (a) Species richness – open circles show the observed species richness, closed circles and bars show adjusted species richness calculated by rarefaction; (b) Shannon index; (c) Simpson's index; (d) Berger–Parker index

$r^2 = 0.58$ ,  $P = 0.080$ ; Berger–Parker index  $r^2 = 0.50$ ,  $P = 0.118$ ). As seen above for stems  $\geq 3$  cm d.b.h., all indices showed a peak at 1250–1500 m for stems  $\geq 10$  cm d.b.h. and  $\geq 20$  cm d.b.h.. Precision estimates for these size classes were also similar to trees  $\geq 3$  cm d.b.h., with only Simpson's index showing a standard error within the desired 5% of the mean (trees  $\geq 10$  cm d.b.h.: rarified species richness = 7.37, Shannon index = 6.18, Simpson's index = 2.69, Berger–Parker index = 19.27; trees

$\geq 20$  cm d.b.h.: rarified species richness = 7.47, Shannon index = 4.31, Simpson's index = 9.59, Berger–Parker index = 20.48).

Variable-area plot data showed a similar increase in diversity with altitude (Fig. 4). Linear regression tests revealed a significant positive relationship for all four measures of diversity (d.f. = 77;  $P < 0.001$ ,  $r^2 > 0.27$ ). Figure 4 also shows that the lowest diversity was found at mid-altitudes. The highest diversity was found in one of the



**Fig 4** Diversity indices and 95% confidence intervals per unit area plotted against altitude for variable-area plots. (a) Species richness; (b) Shannon index; (c) Simpson's index; (d) Berger–Parker index. Linear regression tests showed a significant positive relationship between diversity and altitude (d.f. = 77, number of stems = 20 for all plots; Species richness  $r^2 = 0.34$ ,  $P < 0.001$ ; Shannon index  $r^2 = 0.27$ ,  $P < 0.001$ ; Simpson's index  $r^2 = 0.39$ ,  $P < 0.001$ ; Berger–Parker index  $r^2 = 0.33$ ,  $P < 0.001$ )

highest altitude plots, but there was high variation in plot diversity above 1500 m. For all diversity measures for variable-area plots, there was a high level of precision (mean precision of the four measures of diversity = 3.10%). Only the Berger–Parker index had a standard error >5% of the mean (5.08%). When no adjustment was made for differences in plot area of variable-area plots, the trend in increasing diversity with altitude was lost (Fig. 5a; linear regression: d.f. = 77; species richness  $P = 0.94$ ,  $r^2 < 0.001$ ; Shannon index  $P = 0.49$ ,  $r^2 = 0.01$ ; Simpson's index  $P = 0.40$ ,  $r^2 = 0.01$ ; Berger–Parker index  $P = 0.088$ ,  $r^2 = 0.04$ ). Gamma diversity also showed no clear relationship to elevation, with two peaks in species richness at 410–550 m and 1250–1390 m (Fig. 5b).

#### Species composition trends

For fixed-area subplots, species composition as defined by DCA axis 1 scores based on stem number, showed a discontinuous linear relationship with altitude (Fig. 6a). There was also a clear division between fixed-area plots at 750 and 1000 m (Fig. 6a). DCA axis 2 scores had a high level of overlap between different plots, but show no clear relationship with altitude (Fig. 6b). Following exclusion of stems <10 cm d.b.h., this discontinuity became less obvious (Fig. 6c). For stems  $\geq 20$  cm d.b.h., the lowest and highest plots had similar DCA axis 1 scores, indicating that species compositions of these plots had more similar species composition to one another than to the mid-altitude plots (Fig. 6d). This was primarily because of *Pouteria cerasifera* (Welw.) A. Meeuse stands that were found in both high and low altitude plots. DCA axis 1 scores for stems  $\geq 20$  cm d.b.h. weighted by basal area in fixed-area plots show a similar relationship with altitude to scores weighted by stem number (Fig. 6e). DCA axis 2 scores indicate a more

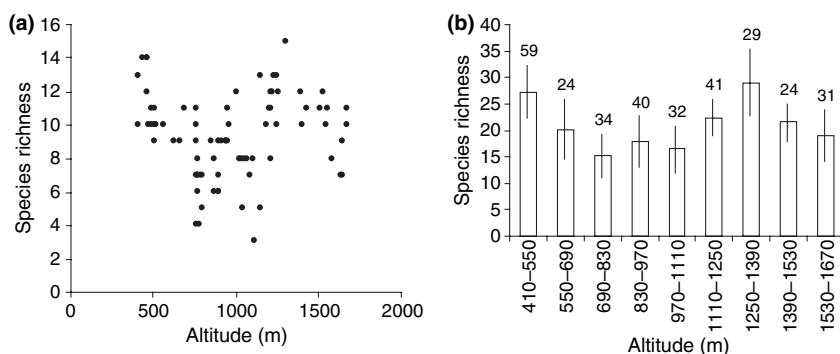
linear relationship with altitude (Fig. 6f). This suggests that altitude was having an effect on the species composition but was not the primary factor.

The DCA scores for variable-area plots weighted by stem number and basal area are shown in Fig. 7. Axis 1 scores weighted by stem number showed a continuous and highly significant relationship with altitude (Fig. 7a; linear regression: d.f. = 77,  $r^2 = 0.82$ ,  $P < 0.001$ ). Clear outlying plots from axis 2 scores may indicate a further influencing factor (Fig. 7b). These plots were characterized by *Brachystegia microphylla* Harms, a tree typically found in woodland habitats rather than closed forest and may thus represent variation with moisture. As seen for fixed-area plots, DCA axis 1 scores for variable-area plots weighted by basal area also show a characteristic pattern whereby the presence of large *P. cerasifera* trees at high altitudes have produced a curved pattern of species composition (Fig. 7c). Axis 2 scores weighted by basal area show that some plots are differentiated at high altitude (Fig. 7d).

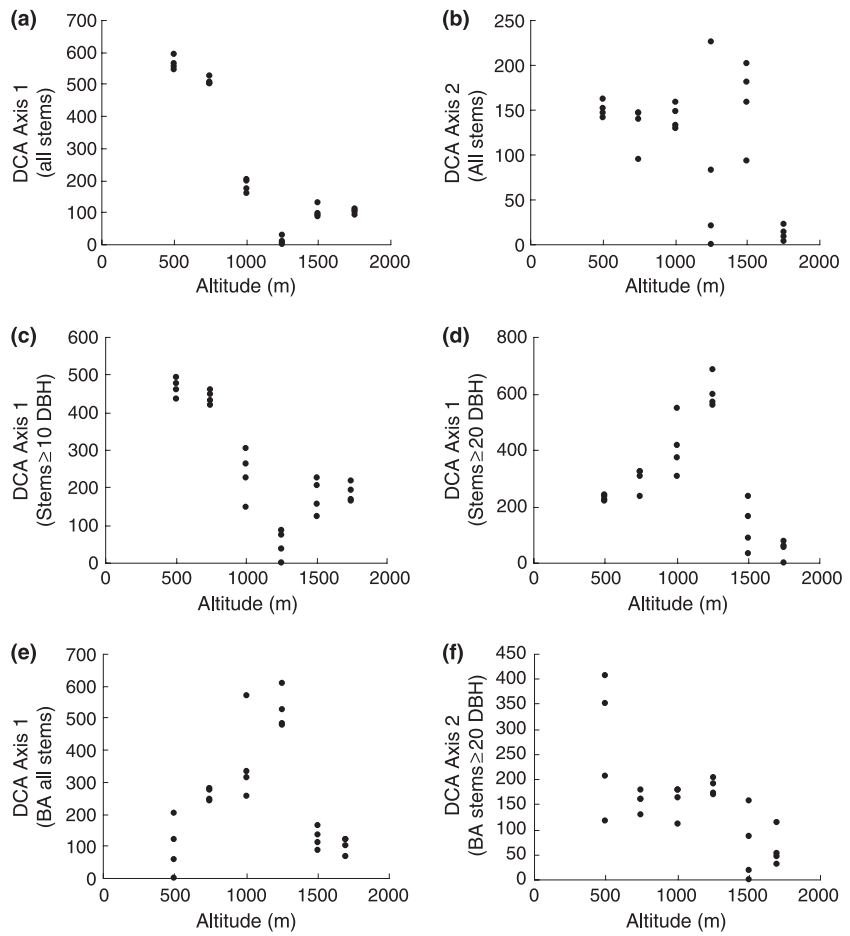
Tables of species composition and DCA ordination scores for 25 m  $\times$  25 m fixed-area subplots and variable-area plots are available from the corresponding author.

#### Endemism

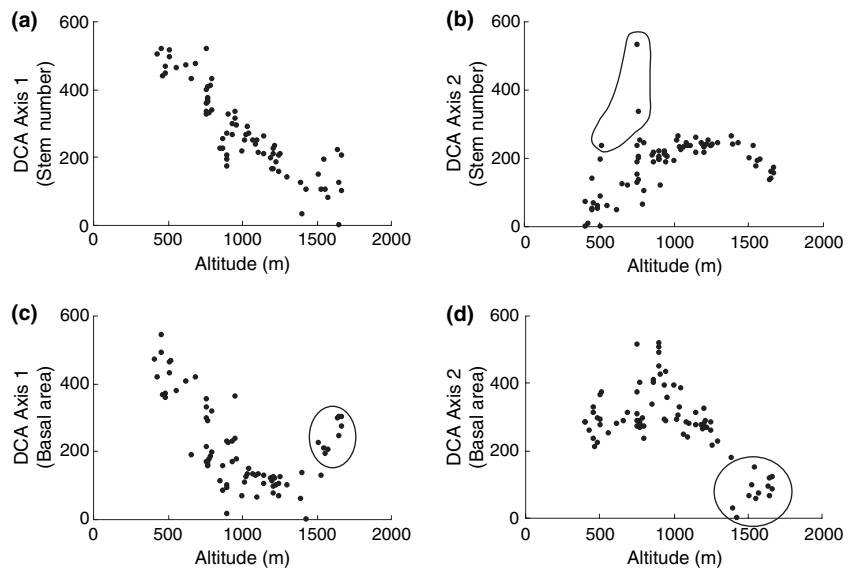
Endemic taxa are here regarded as those species which are found only in the Eastern Arc and Coastal Forest hotspot. Near-endemics also occur at a few locations outside the Eastern Arc, but are of very restricted distribution. For the analysis, restricted range species included both endemics and near-endemics. The number of restricted-range species found in the fixed area and variable area plots at different altitudes are shown in Fig. 8. The data for variable-area plots was corrected for sampling effort by including the same number of plots (thirteen) in each of the altitude



**Fig 5** Species richness of variable-area plots not divided by area, plotted against altitude. (a) Individual plots; (b) rarefied species richness for plots grouped into 140 m altitudinal bands (gamma diversity), from left to right the number of variable-area plots per band are 13, 4, 13, 13, 9, 11, 3, 4 and 8, and the figures above each bar show species richness without rarefaction

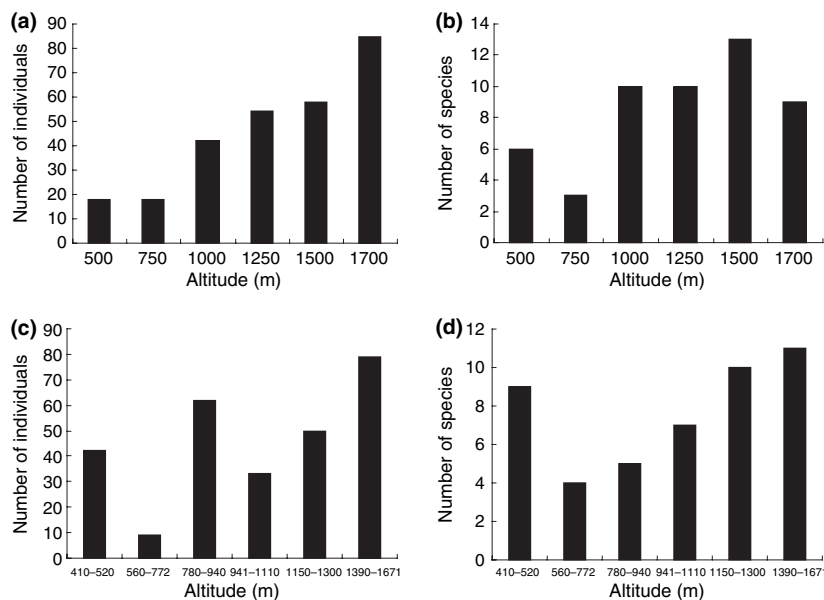


**Fig 6** DCA scores in relation to altitude for number of stems and basal area of each species in fixed-area plots. Points represent species composition of 25 m × 25 m sub-plots. (a) Altitude versus axis 1 for frequency of all stems; (b) altitude versus axis 2 for frequency of all stems; (c) altitude versus axis 1 for frequency of stems ≥10 cm d.b.h.; (d) altitude versus axis 1 for frequency of stems ≥20 cm d.b.h.; (e) altitude versus axis 1 for basal area of all stems (plots for stems ≥10 cm d.b.h. and ≥20 cm d.b.h. are similar to this and are not shown); (f) altitude versus axis 2 for basal area of stems ≥20 cm d.b.h.



**Fig 7** DCA scores in relation to altitude for variable-area plots. (a) Axis 1 scores weighted by stem number (linear regression: d.f. = 77,  $r^2 = 0.82$ ,  $P < 0.001$ ); (b) axis 2 scores weighted by stem number, ringed outliers were characterized by *Brachystegia microphylla*; (c) axis 1 scores weighted by basal area, ringed plots were similar to mid-altitude plots because of the presence of *Pouteria cerasifera*; (d) axis 2 scores weighted by basal area, ring indicates high altitude ridge top plots characterized by *Isoblerlinia scheffleri*, *Pouteria cerasifera* and *Syzygium guineense*





**Fig 8** Numbers of restricted range individuals and species recorded in fixed area (a and b, respectively) and variable area (c and d) plots. The data for variable area plots are corrected for sampling effort by including thirteen plots in each of the altitude classes

classes, resulting in uneven altitudinal bands. Restricted range taxa were found at all altitudes, but the fewest were found in the band 560–772 m and the most at higher altitudes. Different patterns resulted from the two methods. The fixed area plots showed a steady increase in the number of restricted range individuals in the plots with altitude (Fig. 8a), but a rather more even spread of number of restricted range species (Fig. 8b); whereas the variable area had relatively high numbers in the low altitude plots for both numbers of individuals and species (Fig. 8c,d). The numbers of restricted range individuals in the fixed area plots (Fig. 8a) are not correlated with stem density (Spearman's rank correlation  $r_s = 0.638$ ;  $P = 0.173$ ).

## Discussion

The results suggest that it is difficult to make generalizations about altitudinal trends in vegetation structure, diversity and community composition in tropical forests. Our results show a mixture of accordance and discordance to general theories. Stem density and basal area may increase with altitude in the Sanje area of Mwanihana forest, although the trend was unclear for one method. The trend in vegetation diversity with altitude is also unclear, however it does not decrease over the altitude range and is generally highest at the upper elevations in this study. Community composition is shown to change gradually with altitude and includes a higher number of species of conservation importance at high

altitude. These results are discussed below and placed in the context of other studies.

### Physical structure

The variable-area plots showed a significant increase in stem density and basal area with altitude (Fig. 1). This could be due either to natural factors, or human influence. Natural factors for the trend could be soil water and nutrient availability and increased light levels on ridge tops (references in Lovett, 1996), although we have no data to support this. Pressure of cutting for building poles can selectively remove certain species and size classes (Hall & Rodgers, 1986) and is likely to be greater at lower altitudes in the Mwanihana forest as the village of Sanje is adjacent to the base of the escarpment and close to the forest edge. Data from low altitude Tanzanian coastal forests indicates that stem densities can be in the range of 700–1000 stems  $\geq 10$  cm d.b.h. with basal areas as high as 50–70  $\text{m}^3 \text{ha}^{-1}$  (Lowe & Clarke, 2000). This suggests that altitude *per se* does not determine the stem densities or woody plant basal area. Basal area contribution is very dependent on the presence of large individual trees within the sampled area and, as with building pole collection, logging of larger trees for timber is likely to be more intense at lower altitudes because of the presence of a road along the base of the escarpment. With the exception of stems above 10 cm d.b.h., the relationship between stem density/basal area and altitude is less clear for fixed-area plots. However, this

may be because of low sample size as highlighted by the high influence of a single tree species *L. kilimandscharicus* in the 1000 m plot.

### Diversity

Our observation that diversity does not decline with altitude (Figs 3 and 4) is unusual for tropical forests. Comparable results for all four measures of diversity suggest that this observation applies to both rare and dominant species. The observation is consistent between both fixed- and variable-area plots. This is despite low precision of diversity measures for fixed-area plots, which may indicate under-sampling. Studies on large trees elsewhere in the Eastern Arc have also noted that tree diversity does not decline with altitude (Lovett, 1996, 1999; Tallents *et al.*, 2005). Molluscs surveyed in the same forest as the current study even show an increase in diversity with altitude, probably in relation to rainfall (Tattersfield *et al.*, 2006).

Observed decline of diversity with altitude in other forests has been explained by a variety of mechanisms. Island biogeography theory suggests that the isolated nature of montane forests prevents frequent migration and thus a lower equilibrium number of species is supported (MacArthur & Wilson, 1963; Lieberman *et al.*, 1996; Vazquez & Givnish, 1998). Similarly, the relatively limited area of land at high altitudes compared with low altitudes, may limit available space, thereby reducing diversity (e.g. Rahbek, 1997). Vazquez & Givnish (1998) also implicate altitudinal influences on the decline in plant growth and allocation of plant-herbivore defences.

However, it may be that our observations are not over a sufficiently long altitudinal transect to show general patterns. A mid-altitude humped relationship would fit with the mid-domain effect (Colwell & Hurtt, 1994; Rahbek, 1995, 1997; Colwell & Lees, 2000; Kessler, 2001; Lomolino, 2001). This kind of relationship may be a general pattern for species diversity along elevational gradients (Lomolino, 2001). If this is the case, then the general increase in diversity observed in this study may represent the upward slope of the hump. A similar prediction has been made for mollusc diversity in the same forest, which also increases with altitude to 1500 m (Tattersfield *et al.*, 2006). The fixed-area plots even suggest a humped relationship with a peak at 1250–1500 m (Fig. 3). The variable-area plots however suggest a more linear trend as two of the four diversity measures show a significant linear relationship with altitude (Fig. 4). Other studies have

shown a mid-altitude peak in diversity. Examples include pteridophytes in South and East Africa (1000–2500 m; Jacobsen & Jacobsen, 1989) plants in China (2700–2800 m; Wang *et al.*, 2002), trees in India (Swamy *et al.*, 2000) and epiphytes in the Ecuadorian Andes (1000–1500 m; Küper *et al.*, 2004). Human disturbance may also play a role. The lack of decline in diversity with altitude in the Udzungwa Mountains could be explained by the proximity of lower slopes to villages whose inhabitants may utilize the forest to obtain poles for tool handles and other natural resources, thereby decreasing woody plant diversity. Such an impact was observed along an altitudinal gradient in India, where there was monodominance in highly disturbed areas (Swamy *et al.*, 2000). Some evidence for a similar trend in the Udzungwa Mountains has been seen in the Kihansi Gorge forests at 600–700 m altitude, where monodominant stands of *Filicium decipiens* occur at low altitudes in formerly cultivated areas (Lovett *et al.*, 1997; Lovett, 1999). However, with the exception of the stand of *B. microphylla* trees in three of the variable area plots and the cluster of small diameter *L. kilimandscharicus* in the 1000 m fixed area plot, our Udzungwa data do not show monodominance.

Controlling for plot area can be important for recognizing broad trends in diversity (Fig. 4). In a simple situation where two plots have an identical number of trees and species composition, but one is of much smaller size, then it is logical to treat the smaller plot as being more diverse per unit area. Previous studies have not done this, possibly because such weighting is so highly influenced by the relationship between stem density and altitude. The resulting indices are highly correlated with stem density (Species richness/ha:  $r_s = 0.761$ ,  $P < 0.001$ ; Simpson/ha:  $r_s = 0.858$ ,  $P < 0.001$ ). So, although diversity increases with altitude in variable-area plots, this is primarily a density effect with more individuals leading to a greater number of species (Scheiner & Willig, 2005).

### Choice of sampling method

Our study does not show any major dissimilarity between sampling of stem size or density between the two different sampling methods and thus we consider both methods can be useful given sufficient repetition of plots. Variable-area plots are the simplest method to perform in habitats with open understorey. Furthermore, by selecting a predefined sample size, variable-area plots ensure there are equal numbers of stems for calculation of diversity, thus avoiding

the need for rarefaction. However, the results highlight some important weaknesses of the variable-area plot method. Firstly, because the plots are of varying size, there is variation in the scale of diversity being measured. Secondly, accumulation curves for fixed-area plots (Fig. 2) suggest that with the exception of Simpson's index, a sample size of just twenty individual stems may be insufficient for accurate calculation of diversity measures. Accordingly, bootstrapped confidence intervals generated for diversity indices of variable-area plots were often strongly skewed (Fig. 4). Increasing the number of stems used in such a method makes practical application of the method difficult, especially in areas of dense understorey (Marshall, pers. obs.). Spatial scale may also be important, although when variable-area plots were pooled into altitude bands, there was still no decline in diversity with altitude, only a possible bimodal distribution (Fig. 5b).

#### *Species composition trends*

The continuous and linear trend of DCA axis 1 scores for the variable-area plots (Fig. 7) suggests there is a steady replacement of species with altitude, supporting the individualistic hypothesis of plant community organization (Vazquez & Givnish, 1998). Such changes are likely to occur as a result of several environmental factors that may or may not vary with altitude. Examples of factors affecting community composition in other studies include rainfall, temperature, moisture, availability of minerals, pH, exposure, humidity and soil physical properties (Gentry, 1988; Givnish, 1999; references in Lieberman *et al.*, 1996; Tang & Ohsawa, 1997; Sollins, 1998; Eilu, Hafashimana & Kasenene, 2004).

Quantitative methods applied at a local scale facilitate statistical analyses of community compositional changes and avoid generalizations made in some methods of vegetation classification (e.g. Holdridge *et al.*, 1971; White, 1983). Ordination techniques have shown that variations between communities in tropical forests are often gradual (Hall & Swaine, 1976; Lieberman *et al.*, 1996; Lovett, 1996, 1998; Tallents *et al.*, 2005). Care must be taken, however, to ensure sufficient sampling along the altitude gradient to avoid erroneous classification of vegetation into discrete zones (e.g. Hamilton & Perrott, 1981). For example, discontinuous community changes suggested by the fixed-area method (Fig. 6a) are misleading because of incomplete sampling at intermediate altitudes. The low number of fixed-area plots at each altitude also means they

are strongly influenced by locally abundant species occurring in patchy distributions, as seen for *L. kilimandscharicus*, *P. excelsa* and *P. cerasifera*.

Further to the observed altitudinal trend, Fig. 7 suggests there is some influence of moisture as plots dominated by the woodland tree *B. microphylla* are outliers. Similar trends associated with moisture gradients have been observed elsewhere in the Eastern Arc (Lovett, 1996). For DCA scores weighted by basal area, axis 2 scores show a better relationship with altitude than axis 1 scores (Fig. 6f), indicating that factors other than altitude may be having an influence on the variation in species composition. This is also suggested by the nonlinear relationship shown for variable-area plots weighted by basal area in Fig. 7c. Basal area weighted trends can be indicative of forest dynamics as they are strongly affected by large trees. For example, there is a high altitude cluster of *P. cerasifera* trees along DCA axis 1, a species more commonly associated with lower altitudes. This result is also apparent from fixed-area plots (Fig. 6e,f). Altitudinal disjunctions of species ranges suggest individualist dynamics in which species can become established outside their normal altitude range when local conditions allow. In this case *P. cerasifera*, usually a low altitude tree, has become established at high altitudes. Dynamic patterns have also been observed in another Eastern Arc mountain, the West Usambara, where the montane tree *Ocotea usambarensis* occasionally occurs at lower altitudes, possibly following disturbance (Lovett, 1996). Axis 2 scores weighted by basal area also highlight a distinct community on high altitude ridgetops including *P. cerasifera*, *Isobertinia scheffleri* (Harms ex Engl.) Greenway and *Syzygium* sp. Gaertn. (Fig. 7d). This suggests that there are unmeasured variables associated with ridge tops that are influencing species composition.

#### *Endemism*

Conservation efforts tend to be focused on taxa of restricted distribution because local changes in habitat quality can result in global extinctions. Although numbers of restricted range individuals are greater at higher altitudes (Fig. 8), restricted range taxa occur at all altitudes in the Udzungwa Mountains National Park and are an important component of the diversity. From a management perspective, as Eastern Arc endemics and near-endemics tend to have narrow altitudinal ranges (Lovett *et al.*, 2001), the low altitude forests need to be conserved in order to protect the rare and endangered plant species occurring there.

This is an important consideration when national park management can include development of buffer zones adjacent to areas of human population.

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