Phylogenetic diversity of forest trees in the Usambara mountains of Tanzania: correlations with altitude

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The relationship between diversity of large trees and altitude was investigated in a Tanzanian tropical rain forest. In total, 231 samples of 20 trees of ≥ 20 cm d.b.h. from the East and West Usambara mountains, covering an elevation range from 280 m to 2180 m a.s.l., were analysed. An ordination demonstrated a constant turnover of species, genera, family and orders with elevation. There were no obvious zones or discontinuities. There was no decline in plot richness with respect to altitude for species, genera or orders. Family richness was shown to increase with altitude. A measure of genetic diversity, the avalanche index, was calculated for each plot to investigate the effect of incorporating phylogenetic relatedness of individuals into the diversity measure. Distances between taxa were extracted from a recent molecular phylogeny of the angiosperms. Incorporation of phylogenetic diversity at family level enhanced the positive correlation between plot diversity and altitude. © 2005 The Linnean Society of London, Botanical Journal of the Linnean Society, 2005, 149, 217–228.


INTRODUCTION

Diversity in plant communities is commonly measured as species richness. However, use of species alone can obscure some interesting patterns. For example, on a continental scale in sub-Saharan Africa, there are marked differences in taxon richness when different taxonomic levels are used. The southern African Cape and, to a lesser extent, the forests of Cameroon have floras whose richness is enhanced by certain genera containing many species (La Ferla et al., 2002). Although it is often shrubby or herbaceous genera that are very speciose, the pattern can also be seen in tropical trees. For example, in Indo-Malaysian forests the family Dipterocarpaceae and the genera Eugenia and Ficus are species rich (Whitmore, 1984), and in the Amazon, 12 species of Eschweilera were found in a single one hectare plot (Prance, 1987). Co-occurrence of closely related taxa can lead to interesting phytogeographical and ecological speculation. For example, the southern Cape flora appears to have resulted from a burst of speciation in the Pliocene (Richardson et al., 2001), and the Amazon pattern is thought to be due to allopatric speciation during dry periods followed by coalescence in more humid conditions (Prance, 1987). By using phylogenetic measures of diversity it may be possible to understand better the way that plant communities evolve and develop. In this study we investigate phylogenetic diversity at a local scale along an ecological gradient.

Many studies have revealed marked changes in diversity over ecological gradients. In particular, decline in species diversity with increasing elevation has been observed in a wide variety of groups, such as tropical birds (Hawkins, 1999), Australian ants (Brühl, Mohamed & Lisenmair, 1999), reptiles in Israel (Nathan & Werner, 1999), bats in Peru (Patterson et al., 1998), understory herbs in Mexico (Vazquez & Givnish, 1998) and woody plants in gen-
eral in Costa Rica (Lieberman et al., 1996). This decline in diversity has been associated with lowering of productivity at higher elevations (Rosenzweig & Abramsky, 1993) and a smaller land area near the tops of mountains (Rahbek, 1997). There are exceptions to this pattern. Species diversity of large-tree plots in the Eastern Arc forests of Tanzania does not decline with elevation (Lovett, 1996, 1999). However, a simple measure of diversity using species may mask a more complex relationship that might be revealed by analysing phylogenetic relatedness. Here, we analyse large-tree plot data from eastern Tanzania to investigate changes in diversity with elevation at different taxonomic levels, and use an index of phylogenetic diversity, the avalanche index (Ganeshaiah, Chandrashekar & Kumar, 1997; Ganeshaiah, 2000), to determine whether degree of genetic relatedness in the plots changes with elevation.

MATERIAL AND METHODS

Tree plot data were available from three studies in the Eastern Arc mountains of Tanzania, north-eastern Africa. These studies were in the East Usambara mountains (EUS) (Hamilton et al., 1989), West Usambara mountains (WUS) (Lovett, 1996) and Mazumbai University Forest Reserve (MAZ) in the West Usambara (Hall, 1991). The EUS and WUS tree plots were assessed in many different forest areas on each mountain, whereas the MAZ plots were concentrated at Mazumbai. Sampling was carried out using the variable area technique described in Hall (1991). Twenty large trees (≥ 20 cm d.b.h.) nearest to a random point, or grid point in the case of Mazumbai, were identified to species level where possible. In total, 231 plots were assessed (EUS = 70, WUS = 88, MAZ = 73) at altitudes ranging from 280 to 2180 m a.s.l. Not all trees were classified to species level so for the purposes of analysis, only plots in which all trees were identified down to the relevant taxonomic level were included. For example, analyses based on families excluded all plots in which trees were identified only to order level.

A rank abundance model was fitted to the data in two stages. Graphs of the logarithm of abundance against species rank were examined to determine whether they matched known patterns, and then the fit of the log series abundance model was tested. Fisher's alpha from the log-series model was calculated by iteration (Magurran, 1988) and this value was used to calculate the expected number of species in each abundance class. A chi-squared test was performed to assess whether the data differed significantly from the constructed log-series distribution. The above test was repeated for each site separately to check that it was valid to combine data from all three sites.

The data were explored using DECORANA (DEtrended COResponsondence ANALysis) (Mark Hill, Institute of Terrestrial Ecology, UK). The first axis was tested for a correlation with altitude to ascertain whether this variable had any effect on species composition of plots. The analysis was repeated using genera, families and orders as input variables. The raw data, with plots as row headings, species as column headings and numbers of individuals in the cells, were converted to the correct input format using the programs supplied with DECORANA: Tabldidy.exe and Tabcorn.exe.

Species richness was defined as the number of species in each variable-area plot of 20 individuals, and likewise for genus, family and order richness. These characteristics were analysed for changes with altitude. In addition, standard diversity indices were calculated for comparison with elevation to assess whether inclusion of evenness or dominance affected the pattern. The indices calculated were Shannon, Simpson-Yule, McIntosh D (dominance), McIntosh E (evenness), Berger-Parker (dominance) and Margalef (see Magurran, 1988 for formulae).

One weakness in standard measures of biological diversity is that they fail to incorporate information on the range of ecological traits or genetic diversity represented in the sample, instead assuming that all species contribute equally to diversity regardless of their functional uniqueness or genetic isolation (Cousins, 1991). The inclusion of such data would result in more of the true diversity of a sample being captured, thus enhancing our understanding of the relationship between diversity and other ecological attributes of a sample. The avalanche index (Ganeshaiah et al., 1997) is a generalization of the phylogenetic diversity index first proposed by Faith (1992), broadening the distance component to allow for any biologically informative, quantitative data (not just phylogeny) to represent the proximity of each pair of species. It is calculated using the following formula:

\[
AI = \sum_{i=1}^{c} \sum_{j=1}^{c} (P_i \cdot d_{ij})
\]

where \(P_i\) is the frequency of the ith species, \(P_j\) is the frequency of the jth species, and \(d_{ij}\) is a measure of the distance between them, calculated as:

\[
d_{ij} = \left( \sum_{k=1}^{c} (X_{ik} - X_{jk})^2 \right)^{1/2}
\]

where \(X_{ik}\) is the value of the ith species for the kth character. This formula incorporates the usual concepts of richness and evenness, but has a unique component, \(d_{ij}\), which embodies the distance between taxa. The component \(d_{ij}\) was calculated using a number of different methods, depending on the characteristics of
the data available. A program was written in C to calculate the avalanche index value for each plot, given the matrix of distances between taxa and the frequency data from the plots.

Two methods were used to analyse phylogenetic diversity. In the first method, four levels were used to compute the simplest phylogenetic distance between two species: Level 1 – species in the same genus; Level 2 – species in the same family; Level 3 – species in the same order; and Level 4 – species in different orders. Most applications of the avalanche index have utilized a similar approach (for example, soil dwelling dipteran communities, De Bruyn et al., 2001), although some have included a wider array of morphological and functional differences (for example, dung beetles, Kumar, Chandrahekara & Ganeshaiah, 2001). However, the former system does not adequately represent the relatedness of different taxa beyond the level of orders. Species in closely related orders (for example, Lauraceae in the Lamiales, and Myristicaceae in the Magnoliales) are assigned the same distance as species in distantly related orders (Lauraceae and Ulmaceae in the Rosales).

The second method employed phylogenetic distance data extracted from a recent molecular phylogeny of the angiosperms (Soltis, Soltis & Chase, 1999). This phylogeny was constructed using parsimony analysis of the DNA sequence of the plastid genes Pbel and atpB, and nuclear 18S rDNA from 560 species of angiosperm, using gymnosperms as an out-group. Very few of the genera in the present study were represented in the phylogeny. This meant that it only had any precision at family level, so information below this taxonomic level was lost. However, it did give a better representation of the phylogenetic relationships of families within a plot. Two distance matrices were constructed using the following methods.

(i) Mean branch length. The distance between two families was calculated as the mean branch length back to the node representing the most recent common ancestor of the two families. Starting at the branch tips, the branch lengths of the two sister taxa, 1 and 2, were summed \((a + b)\), and then divided by two (Fig. 1). The intervening branch length to the next node (c) was added, and the average between that value and the other branch (d) taken. This process was continued until the mean branch lengths had been calculated for every node in the phylogeny. This technique is similar to the averaging logarithm used in UPGMA, and was employed to reduce variability in branch lengths back to a specific node. In theory, all routes from the tips down to the same node should give identical branch lengths but in practice, substantial variability is observed. There are two causes of this: individual variation in the molecular sequences used to construct the phylogeny; and differences in the evolutionary rate between lineages. The avalanche index calculated using these distance values was called Meandist.

(ii) Maximum branch length. It was necessary to employ a second technique to calculate distances between families, as the first did not satisfactorily reflect phylogenetic relationships due to major differences in evolutionary rates between lineages. The second method therefore constrained branch lengths to increase with decreasing relatedness by taking the maximum summed branch length back to each node. For example, if \(a > b\), distance to node I equals \(a\), and if \(d > (a + c)\), distance to node II equals \(d\) (Fig. 1). This method retained the variation in branch length but gave a better picture of the evolutionary relationships captured in the angiosperm phylogeny. The avalanche index calculated using these distance values was named Longdist.

Calculations were performed on the entire phylogeny (Soltis et al., 1999), but the phylogeny pictured (Fig. 2) is the reduced version containing only those taxa found in the present study.

RESULTS

The total elevation range covered by the three sites, East Usambara (EUS), West Usambara (WUS) and Mazumbai (MAZ), was 280 m a.s.l. to 2180 m a.s.l. East Usambara covered the lower elevations, overlapping with West Usambara above 1000 m. The range of Mazumbai was completely contained within West Usambara (Table 1). MAZ was the poorest site in terms of the number of species, families and orders,
Figure 2. Phylogeny containing only those taxa found in the current study. Nomenclature from the Angiosperm Phylogeny Group (2003).

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but EUS had the fewest genera. Surprisingly, EUS had the highest species and family richness, although WUS was almost as rich, and these two sites had an equal number of orders. Given the likelihood of a turnover of taxa with rising elevation, these richness values were corrected for altitude range, giving the number of species per 100 m altitude band. This correction reversed the trend, with MAZ now being the richest site for all taxa except orders. However, this may be a result of the different sampling intensity between sites. Although MAZ covered a fairly narrow altitude band (450 m), it had an equivalent number of plots to the other two sites, making it the most intensively surveyed site, with an average of 16.22 plots per 100 m altitude band, compared with 7.45 and 7.46 for EUS and WUS, respectively. The effect of this increased sampling effort on recorded taxon richness is not a simple one. Species–area relationships are not monotonic but rather, the rate of species accumulation tends to decline with increasing area, eventually leading to an asymptote in richness. In this study, mean species richness did indeed rapidly decline as sampling effort increased; an average of eight species per plot with a sampling effort of three plots per 100 m fell to three species per plot when 15 plots per 100 m were surveyed. Therefore, it was not possible to obtain average values of taxon richness by dividing the richness per 100 m by the number of plots as MAZ is further up the accumulation curve than EUS or WUS, so the resultant values would not be comparable. However, modal species richness does remain relatively constant with sampling effort, ranging from seven to 11 species per plot within the range of seven to 20 plots per 100 m. Thus, total species richness in each 100 m altitude band is roughly comparable between sites: 32 species per 100 m in EUS and WUS, and 34 in MAZ.

The nonlinear pattern of log (abundance) versus species rank (Fig. 3) precluded application of the geometric model (Magurran, 1988), so the log series model was fitted to the data. The combined data set was not found to differ significantly from the log-series model, once the categories were amalgamated to give expected values of five or greater (EUS \( P = 0.59, N = 7 \); WUS \( P = 0.28, N = 10 \); MAZ \( P = 0.14, N = 9 \); total \( P = 0.14, N = 16 \)). Despite differences in sampling effort between sites, it was necessary to amalgamate them in order to provide the wide altitude range needed for this study.

Figure 3. Rank-abundance chart for species in all three sites combined (number of plots = 133).
Axis 1 of the ordination is strongly correlated with elevation (Fig. 4A–D). The correlation is tightest at species level, with elevation explaining less of the variability in plot composition with increasing taxonomic level. The smooth change in axis 1 scores with elevation indicates that composition of the plots changes steadily with altitude. There are no discontinuities, thus providing no evidence of vegetation zones at different elevations.

Species, genera and order richness did not show significant changes with elevation, but family richness is positively associated with increase in altitude (significant at the 0.05 level). However, this relationship is not obvious to the eye (Fig. 5), and the large variation in richness obscures any possible patterns. None of the species diversity indices are significantly correlated with altitude (Spearman’s rank correlations, N = 133: Shannon, 0.066, P = 0.45; Simpson-Yule, 0.044, P = 0.62; McIntosh D, 0.044, P = 0.62; McIntosh E, -0.003, P = 0.97; Berger-Parker, -0.026, P = 0.77; Margalef, 0.093, P = 0.29). This is not surprising as, for species diversity estimates, the 20 tree sampling unit is small. Further, the indices are all very closely correlated with richness (Table 2), indicating that little is added to the analysis by including the abundance data.

Figure 4. DECORANA Axis 1 scores for plots against altitude: A, species; B, genera; C, families; D, orders. Axis 1 eigenvalues: Species 0.80, Genera 0.74, Families 0.53, Orders 0.39. Spearman’s rank correlations of DECORANA Axis 1 plot scores against altitude: Species -0.92 (P < 0.0005, N = 133); Genera -0.93 (P < 0.0005, N = 218); Families 0.75 (P < 0.0005, N = 218); Orders 0.62 (P < 0.0005, N = 218).

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Figure 5. Number of taxa per plot against altitude: A, species; B, genera; C, families; D, orders. Spearman’s rank correlations of richness and altitude: Species 0.085 ($P = 0.33, N = 130$); Genera $-0.031$ ($P = 0.65, N = 215$); Families 0.14 ($P = 0.034, N = 218$); Orders 0.049 ($P = 0.47, N = 218$).

Table 2. Results of the Spearman’s rank correlations of diversity indices against richness ($P$-value/Correlation coefficient). Sample size is 133 plots in each case. Au correlations are significant throughout at $P < 0.0005$

<table>
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<th>Orders</th>
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</tr>
<tr>
<td>Margalef</td>
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Relationships between the phylogenetic diversity indices and elevation are presented in Figure 6. The first phylogenetic diversity index, using simply the taxonomic distinctness of each species relative to other species in the plot, does not show any correlation with elevation (Fig. 6A, Spearman’s rank correlation coefficient = −0.01, $P = 0.91$, $N = 133$). Most plots lie close to an upper bound (around 350), and the outlying points are not the same as those produced by Mean-dist or Longdist.

The first of the avalanche indices based on the phylogeny, Meandist, is positively correlated with altitude (Fig. 6B, Spearman’s rank correlation coefficient = 0.28, $P < 0.0005$, $N = 218$). However, the problem of different lineages having different evolutionary rates causes some anomalies in the distance matrix. There are points in the tree where progressing to the next node results in a decrease in distance, rather than an increase. A particularly marked anomaly of this kind occurs upon inclusion of Hamamelidaceae (Fig. 2),

![Graphs showing avalanche index against altitude](image)

**Figure 6.** Phylogenetic diversity of plots against altitude: A, avalanche index values based on the simple measure of taxonomic distinctness, plotted against altitude ($N = 133$); B, avalanche index values calculated using mean branch lengths, plotted against altitude ($N = 218$). C, avalanche index values based on mean branch lengths for plots containing only families below Hamamelidaceae, plotted against altitude ($N = 14$). D, avalanche index values using distances calculated from the maximum branch lengths, plotted against altitude ($N = 218$).

with mean branch lengths declining from 163.8 to 102.8. This affects the rest of the tree above this node. The averaging process ensures that the influence of the hamamelid branch declines with progression towards the root, but it still severely distorts the evolutionary relationships between the euroids (Ochnaceae to Melianthaceae) and the other taxa on the tree. For example, the branch lengths give the impression that Oleaceae in the order Lamiales is no more closely related to Apocynaceae in the Gentianales (its sister order: distance = 140.8) than to Rhizophoraceae in the order Malpighiales (distance = 140.5), a rosist rather than an asterid. This skewing of the mean branch lengths by slow molecular evolution in the hamamelid lineage compromises the ability of Meandist to represent the true phylogenetic diversity of the plots.

An investigation of the outliers from Figure 6B reveals that the majority of the plots with high Meandist values contain gymnosperms (either Podocarpaceae or Cupressaceae). The relatively high distance between the gymnosperms and the other taxa (distance = 336) might be driving the pattern of increasing avalanche index with altitude. This was tested by excluding all plots containing gymnosperms from the analysis (N = 48). With this attenuated data set, a Spearman's rank correlation shows no significant correlation between Meandist and altitude (correlation coefficient = 0.123, P = 0.11, N = 170). A slight positive trend is still evident, though it is not statistically significant. Evidence that there is still a pattern of increasing phylogenetic diversity with altitude that is merely obscured by the effect of the hamamelids on distance comes from examining the 14 plots that only contained trees from the euroid lineage below the Hamamelidaceae influence (Fig. 6C, Spearman's rank correlation coefficient = 0.65, P = 0.011, N = 14). This correlation still remains, although weakened, when the extreme outlier in the bottom left of the graph is excluded (Spearman's rank correlation coefficient = 0.57, P = 0.044, N = 13). This prompted a re-examination of the branch lengths to improve their ability to reflect the evolutionary relationships between families. The resultant avalanche index values, Longdist, were less tightly clustered (Fig. 6C), and the gymnosperms still had a large influence on diversity (note the spike at 900 m a.s.l. caused by the occurrence of Podocarpus in the plots), but the index is now truly representative of phylogenetic relatedness of families. There was a highly significant positive correlation between Longdist and altitude (Spearman's rank correlation coefficient = -0.41, P < 0.0005, N = 218). This relationship appears to be curvilinear, with Longdist values increasing more rapidly at higher altitudes.

Families were found at characteristic elevations and often displayed a rather restricted altitudinal range (Fig. 7). For example, individuals of the family Hamamelidaceae were only found at very high altitudes (Fig. 7A). Even those families with wider altitudinal ranges tended to be biased towards lower or higher altitudes, e.g. Moraceae (Fig. 7B) and Myrtaceae (Fig. 7C), although a few families were truly ubiquitous (Euphorbiaceae; Fig. 7D). When large numbers of individuals have been recorded, this is more likely to represent a real pattern, rather than failing to detect a family because it is rare.

**DISCUSSION**

There are three clear findings from the analysis. First, axis one of the ordination is correlated with elevation at all the taxonomic levels. There do not appear to be any discontinuities or zones over the elevation range represented by the plots. Second, plot diversity remains constant with elevation over a range of taxonomic levels, the exception being family diversity, which increases with elevation. Third, phylogenetic diversity increases with elevation. This relationship does not appear to be linear, with a more rapid increase in phylogenetic diversity with altitude.

The results of this study support the earlier finding of a continuous turnover of tree species with elevation in the Eastern Arc forests (Hamilton et al., 1989; Lovett, 1996, 1998). In contrast to the results observed here, different vegetation belts have been recognized at different altitudes in other studies. For example, Hsieh et al. (1998) identified four, dominance based forest types that succeeded each other up a mountain side in Taiwan, and Kappelle, Vanuweelen & Cleef (1995) classified the forest into eight zonal communities on the slopes of the Chirripo Massif in Costa Rica. However, continuous variation in forest composition with elevation does occur in other tropical forests, for example those studied by Hamilton (1975) in Uganda, Vazquez & Givnish (1998) in Mexico and Lieberman et al. (1996) in Costa Rica. The use of analytical techniques has an effect on the results of a study; a divisive technique such as TWINSPLAN will inevitably find groupings of plots based on species composition. Where composition varies with altitude, this will lead to the conclusion that elevational floriastic zones exist. DECORANA, on the other hand, does not attempt such groupings and so the likely conclusion is that such zones do not occur, unless there are obvious discontinuities in axis scores. Subjective observation in the field often indicates that there is substantial overlap between elevational forest types and therefore, the sampling regime will have a significant impact on the conclusions drawn. As Vazquez & Givnish (1998) point out, investigation of forest composition with respect to
altitude must include a large number of evenly spaced plots. Studies that use a few widely spaced samples, such as that of Pendry & Proctor (1997), will find discontinuities that may not be apparent if the vegetation is more intensively sampled. The data used here were from a large number of plots over a relatively wide altitude range. Although the plots were from three separate sites on the same mountain range, the graphs of DECORANA axis 1 against altitude do not provide any evidence for different forest zones at different altitudes at any of the taxonomic levels investigated.

In contrast to the results presented here, in several other studies, species richness has been found to decline with elevation. Both Waide, Zimmerman & Scatena (1998) and Kappelle et al. (1995) observed a decrease in vascular plant species richness with increasing altitude in the Luquillo mountains of Puerto Rico and Chirripo Massif in Costa Rica, respectively. In the former study, productivity was also found to decrease with altitude, supporting the hypothesis which links productivity with diversity (Rosenzweig & Abramsky, 1993). Working in the tropical Andes, Gentry (1988) found a sharp, approximately linear decline in diversity with increasing altitude, with no evidence of a mid elevational peak. Conversely, a peak in diversity at mid elevations has been observed in several studies (Rahbek, 2005). Tang & Ohsawa (1997) attribute this to the overlapping of forest zones with subsequent abundance of both evergreen and deciduous life forms at mid elevation on the slopes of Mt Emei in Sichuan, China. However, Lieberman et al. (1996) found no evidence for discrete floristic zones, so their observation of a mid elevational

Figure 7. Frequency distributions of individuals with respect to altitude for A, Hamamelidaceae; B, Moraceae; C, Myrtaceae and D, Euphorbiaceae.
peak in diversity cannot be attributed to such an overlap in forest types.

Although Vazquez & Givnish (1998) document a sharp decline in total vascular plant species (and higher taxa) going up the slopes of the Sierra de Manantlan, this was mainly due to a reduction in the number of herb species, with a lesser contribution from understory shrubs and vines. Considering trees alone, little change with elevation was observed. Lyon & Sagers (1998), working in Missouri, USA, also failed to find a significant correlation between elevation and woody species richness. Likewise, Hoftman (1998) did not observe any patterns in diversity with elevation, apart from a positive correlation between genera richness and elevation. This is similar to the observation presented here of an increase in family richness with elevation against a background of constant diversity by all other richness and evenness measures. However, Hoftman explains the pattern as a function of anthropogenic disturbance and distance from primary forest. In the Usambara mountains disturbance is spread throughout the elevational range of the forests, but the plots were sited in areas which were not heavily disturbed. In all, there are very few examples of increasing diversity with elevation. The general trend in most forests is either that of decreasing diversity with elevation, starting at low or mid elevations, or no obvious effect of elevation on diversity.

Given that species diversity generally decreases with elevation, or at least remains constant as in the case of the Eastern Arc mountains, it is remarkable that phylogenetic diversity actually increased. This is a consequence of the occurrence of particularly distinct lineages (notably gymnosperms) at high elevations, combined with the increase in family richness with altitude. The latter observation could result from adaptation to high altitudes being a trait that is displayed mainly at family level. Some evidence for this comes from the fact that many families occurred in a restricted altitude range. The difference in species diversity patterns also shows that the use of species diversity alone can obscure trends revealed using phylogenetic diversity.

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REFERENCES


