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Species diversity structure analysis at two sites in the tropical rain forest of Sumatra

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ABSTRACT. Data from a hilly forest study site at Batang Ule, Sumatra, are organized into 30 100-m × 10-m subplots lying perpendicular to the line of maximal topographic gradient, from the valley to the plateau/ridge. The following methodological question is addressed: what species diversity measures are best used in order to reveal the ecologically distinct regions in the site. The main tool used to answer this question is the α-diversity curve (H_α). Graphical examination of tree and species densities, and α-diversity curves identifies an anomalous species diversity behaviour of the 'ridge above the slope' subplots which may have implications on land-facet class definitions. Factor analysis of the α-diversity curves indicates that the diversity space is two-dimensional: i.e. two diversity measures are sufficient to characterize the site; the species density (H_0), and the Berger-Parker index (H_∞). In the two-dimensional diversity-space three distinct species diversity groups are found which relate to the topographic gradient at the Batang Ule site. The results are compared with those for a flat homogeneous site at Pasirmayang, Sumatra. The implications of the results on land-classifications in species-diversity mapping and conservation strategy are discussed.

KEY WORDS: α-diversity, diversity-structure, land-facets, species-diversity

INTRODUCTION

Rain forests in the tropics are rapidly undergoing clear-felling, and either being replanted with commercial monocultures or being converted to different land-uses. There is widespread concern that these ecosystems, with unique and valuable biodiversity resources, are being lost. One management conservation strategy involves leaving 'conservation areas' within the region being felled, so that they may act as repositories of biodiversity and possibly provide a source of natural regeneration. However, such an approach requires that the areas which will contribute most to biodiversity conservation be known prior to the felling operation. A widespread method is the use of biodiversity inventories prior to forest management operations to determine the nature and distribution of the biodiversity resources of the forested regions being managed. Such biodiversity inventories are best integrated with timber resource inventories in order that forest management operations can be planned in such a way that conservation regions are included in the management plan.

Extensive vegetation analyses have been done on a number of tropical forest sites. In particular, for the 50-ha Pasoh site in Malaysia (Manokaran & Frankie 1990), Appanah & Weinland (1993) have examined the relationship between the spatial distribution of species and the topography, with Baillie *et al.* (1987) extending this analysis to the effects of other site characteristics. Ashton (1969, 1976) have addressed in the Pasoh site the theory of community structure and speciation, and its variation. Similar analyses has been conducted on a 50-ha site on Barro Colorado Island, in the Panama Canal (Hubbell & Foster 1983), and on a 50-ha site in Costa Rica (Hubbell 1979, Lieberman *et al.* 1996), with the non-equilibrium hypothesis of tropical forest structure being one of the theoretical offshoots (Hubbell 1979, Terborgh *et al.* 1996). Other recent studies of species diversity in the tropical rain forest include Valencia *et al.* (1994) and Turner *et al.*(1997). The characterizations of biodiversity resulting from these studies can be useful in the planning of operations which aim to conserve biodiversity (Belbin 1995; Faith & Walker 1996a, b; Vanclay 1998).

This study has been conducted as part of an integrated forest-timber and forest-biodiversity inventory that has been under development in Indonesia for the last 3 y (Forest Inventory and Monitoring Project (FIMP)). It has the biodiversity conservation aims and approaches mentioned above.

Tree species diversity is an important aspect of forest ecosystem diversity, and in this paper only the issue of tree species diversity is considered. A necessary prerequisite of any analysis of biodiversity inventory data is that there be a clear definition of tree species diversity, and that it is estimable from the data collected in the inventory. However, species diversity analysis has a long history in ecology and there is no clearly agreed view of what species diversity measures are the best to use. There is a wide range of indices for the definition and assessment of tree species diversity, and the related concept of evenness (Fisher *et al.* 1943, Hill 1973, Magurran 1988, May 1975, Orloci 1991, Pielou 1975, Renyi 1961, Smith & Wilson 1996, Thothmeresz 1995, Wolda 1981). The recommendations of ecological theorists differ, and it has been found in empirical studies that different diversity measures, or combinations of measures have been best at characterizing a region (Magurran 1988). When the objective has been to best distinguish between different ecological habitats, different studies have resulted in the choice of different diversity measures (Taylor 1978, Kempton 1979, Kempton & Wedderburn 1978, Magurran 1988). The studies concerned with obtaining best ecological discriminatory power have usually aimed to select a single diversity index. The methods used for selecting the 'best-discriminating' index may be described as 'enumerative', in that all the well-known indices were evaluated and compared (Magurran 1988). There are also sampling and estimation problems associated with species diversity measures (Magurran 1988, Pielou 1975).

These limitations and difficulties with the use of species diversity measures have led some to call for the abandonment of the diversity concept (Hurlbert 1971), or its careful evaluation before use (Peet 1975). We adopt the latter course.

In this paper a generalized definition of a diversity index is adopted (Hill 1973, Orloci 1991, Renyi 1961). This generalized diversity index depends on a parameter (α) which may take a wide range of values, and may be represented by an α-diversity curve. For particular values of α the generalized diversity index reduces to well known forms, such as species abundance, the Shannon–Weaver index, Simpson's index and the Berger–Parker index.

STUDY SITES AND DATA SETS

General environment of the sites

The Pasirmayang plot (1°04′80″S; 101°47′27″) lies in the eastern lowlands of Jambi, Sumatra which has elevation varying between 50 and 150 m; the Pasirmayang plot is at *c*. 100 m asl. The physiography is flat to undulating with slopes ranging from 2 to 10%. A piedmont zone of *c*. 40 km in width separates the mountain range from the eastern plains (elevation ranging from 100 to 200 m). The Batang Ule plot (1°36′80″S; 101°47′30″) is located in this piedmont zone at an elevation of *c*. 150 m asl. The relief is undulating to hilly, criss-crossed by river tributaries and valleys for which a twin-terrace pattern is often observed. The forests in both study sites are typical of the 'mixed dipterocarp rain forests' found in the region (Laumonier 1997, Trichon 1996). The mean annual rainfall in Pasirmayang is between 2500 and 3000 mm y^{-1}. Monthly rainfall can fall below 60 mm for 1 mo per year at the most, and the yearly average of rainy days varies from 120 to 150. The Batang Ule piedmont site is slightly more humid receiving over 3000 mm y^{-1} with on average 180 to 220 rainy days per year, the least humid season being very short.

The geology of the eastern lowlands of Sumatra consists of vast tertiary deposition basins mainly formed in sedimentary rock. These geological formations consist of layers several kilometres thick and mainly include sandstones, calcareous sandstone and marls. Folded to various degrees in the piedmont zone, they give way sometimes to alternating granite, metamorphic or volcanic massifs. Batang Ule itself corresponds to a granitic outcrop. The soil types encountered in both forest plots are oxisols/ultisols (red-yellow podzolic) on the acidic sediments which cover most of the peneplain. The litter layer is mostly very thin and covers a humus horizon 2–3 cm thick. The physical properties of these soils are good and large roots reaching down to a depth of 1 m are frequently observed. The A-horizon, located at a depth of 2–8 cm, contains superficial fine roots and its low organic content is a characteristic feature (C/N ranging from 8 to 15). Clay content increases with depth (A–B located between 10 and 40 cm), at least until the centre of the profile. Kaolinite *sensu stricto* accounts for at least 80% of the clay fraction and the low loam-over-clay ratio is characteristic. In the brown or yellow-brown B horizon, soil acidity remains relatively constant (pH between 4 and 5). The cation exchange capacity is very low at less than 15 meq (100 g)$^{-1}$ of clay. Calcium is the main cation and the absorbing complex is very desaturated with an $SiO_2/AlSiO_2O_3$ ratio < 2. These soils rank amongst the least rich in nutrients and are extremely fragile once forest has been cleared; erosion on slopes, compacting by heavy vehicles, insolation and rapid loss of surface minerals can occur.

Batang Ule

This site is very heterogeneous, including a valley region, steep slopes and narrow ridges. The plot is 3 ha in area, with dimensions of 300-m × 100-m, the longer dimension being oriented along the line of (approximate) maximal topographic gradient. For the species diversity analysis the plot was divided into 30 contiguous 100-m × 10-m subplots which were oriented orthogonally to the line of maximal topographic gradient. The objective was to cover as many distinct ecological subregions as possible. The topography was determined by detailed ground survey (Figure 1). Subplot 1 was the first strip along the bottom of the valley; subplots 1–8 lay essentially in the valley; subplots 9–14 were on the slope from the valley to the plateau/ridge; subplots 15–16 were on the top-of-slope/ridge; subplots 17–30 covered the 'plateau' region of the site, which consisted of a web of ridges with local valleys and slopes between them. Within subplots there was still considerable heterogeneity in terms of slope and aspect. It was of interest to see whether the 100-m × 10-m plots would display the ecological zoning which the choice of the site orientation was chosen to maximize (in spite of their internal heterogeneity). Smaller subplots, of size 10-m × 10-m for example, were considered too small for an analysis of tree species diversity since they only contained an average of 17 trees per subplot. A detailed report on the effect of topography on various aspects of tropical forest structure at Batang Ule may be found in Rennolls (1997a, b).

At Batang Ule 1885 trees with DBH ≥ 10 cm were recorded representing 504 species, including an 'unidentified' class. For the purposes of the analysis this class is treated as a single species. Methods have been developed which take into account this lack of species identification, and are reported elsewhere (Rennolls 1997b, Rennolls & Laumonier 1999b). The ten most frequent species are given in Table 1(a). The numbers of species with only one, two or three tree observations in the 3-ha plot were 221, 94 and 50 respectively (accounting for 30% of the observed trees).

Pasirmayang

The tree data-set available from Pasirmayang is relatively rich. A 6-ha plot was measured down to 10 cm DBH, and a 3-ha subplot was measured to 3 cm

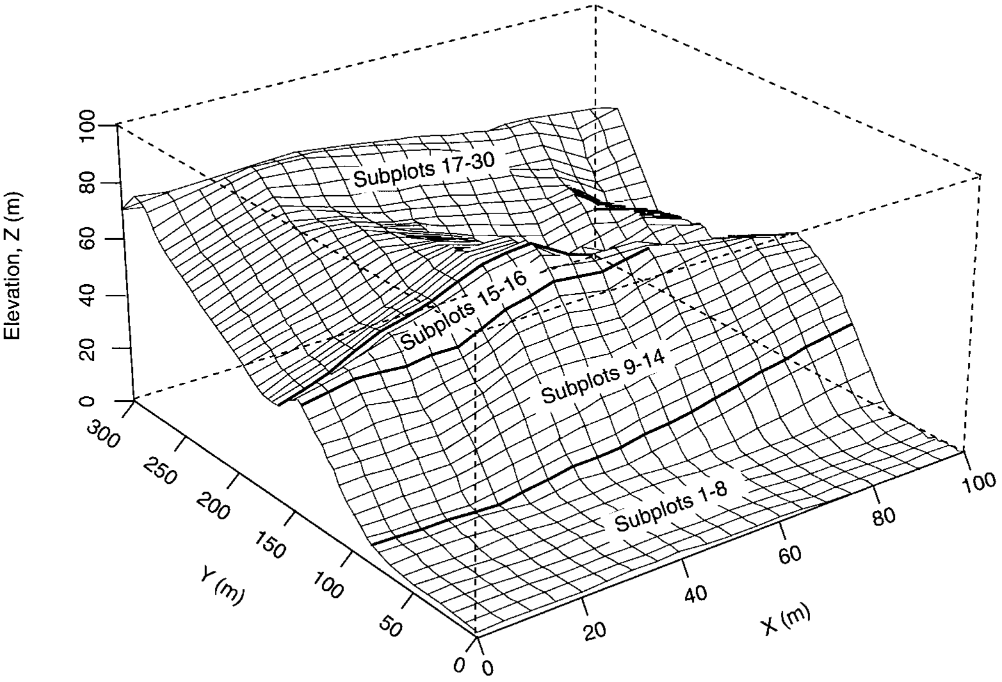

Figure 1. Topography of the Batang Ule site, Sumatra. Units are in metres. Subplots 1–8, valley; 9–14, slope; 15–16, ridge; 17–30, plateau. (Note: scales for axes have been chosen separately for illustrative purposes.)

DBH. However, for the analysis reported in this paper the data used have been restricted to the 3-ha subplot with the use of trees with DBH ≥10 cm, so that direct comparisons can be made with the Batang Ule plot. Effect of diameter cut-off on species abundance is considered in Rennolls & Laumonier (1999a). At Pasirmayang 2129 trees with dbh ≥10 cm were recorded representing > 340 species, including the 'unidentified' species class. The ten most frequent species are shown in Table 1(b). The numbers of species with only one, two or three tree observations were 88, 52 and 38 respectively (accounting for 12.6% of the observed trees).

The plot was divided into 30 100-m × 10-m subplots, with a similar arrangement to that described for Batang Ule, so that the two plots could be compared with respect to spatial or sequential changes in diversity. However, because of the uniformity of this site no significant ecological subzoning was expected.

METHODS

Measures of species diversity

Forest ecologists often restrict their consideration to the observed species count, and one other measure of species diversity, often either the Shannon–Weaver entropy measure, or Simpson's index. The Shannon–Weaver entropy

Table 1. Ten most frequent species at (a) Batang Ule, and (b) Pasirmayang, Sumatra (presence in 3-ha plot), ranked in declining order of frequency.

Species	Family[1]	Frequency
(a) Bantang Ule		
Shorea conica	DIPT	196
Paranephelium xestophyllum	SAPI	33
Palaquium oxleyanum	SAPO	33
Parashorea lucida	DIPT	32
Pouteria malaccensis	SAPO	29
Elateriospermum tapos	EUPH	27
Shorea parvifolia	DIPT	26
Pometia pinnata	SAPI	26
Pimelodendron griffithianum	EUPH	23
Hydnocarpus (sp.1)	FLAC	23
(b) Pasirmayang		
Palaquium oxleyanum	SAPO	49
Pimelodendron griffithianum	EUPH	42
Monocarpia marginalis	ANNO	41
Neoscortechinia kingii	EUPH	40
Ixonanthes icosandra	LINA	39
Gironniera hirta	ULMA	37
Eugenia (sp.5)	MYRT	36
Gymnacranthera bancana	MYRI	35
Shorea macroptera	DIPT	32
Santiria griffithii	BURS	30

1. Abbreviations to families: ANNO, Annonaceae; BURS, Burseraceae; DIPT, Dipterocarapaceae; EUPH, Euphorbiaceae; FLAC, Flacourtiaceae; LINA, Linaceae; MYRI, Myristicaceae; MYRT, Myrtaceae; SAPI, Sapindaceae; SAPO, Sapotaceae; ULMA, Ulmaceae.

measure may be derived theoretically from a maximum-likelihood estimation approach based on a multinomial model for the data (Rennolls 1997a), and has optimum properties with respect to consistency for hierarchical analysis of species diversity data (Pielou 1975). Simpson's index has the 'ecological' interpretation that it is equal to the probability that two new trees observed at random from amongst the trees of the forest will be of the same species (out of those species observed in the sample). Simpson's index is sometimes preferred by ecologists since it gives more weight to those species which occur more frequently (Magurran 1988).

The α-diversity ('functional' index of diversity), H_α, may be defined on data collected from a single plot, by

$$H_\alpha = \frac{\log(\sum_{i=1}^{s} \hat{p}_i^{\alpha})}{(1-\alpha)} \quad : \quad -\infty < \alpha < \infty \tag{1}$$

where $\hat{p}_i$ is the observed proportion of trees in the ith of s observed species. That H_α is a 'functional' index of diversity may be seen more clearly by writing it as $H(\alpha)$ where the argument α has the range given in (1). The functional nature of this index may be illustrated graphically by plotting a graph of $H(\alpha)$ over a suitable range of α to obtain an α-diversity curve. Hill (1973) considers the function $\exp(H_\alpha)$ and derives some of its properties. The properties of H_α include:

(i) the total species count on the plot, s = $\exp(H_0)$, (2)

(ii) the Shannon–Weaver index $H' \ (\equiv H_1) = -\sum_{i=1}^{s} \hat{p}_i \log \hat{p}_i$, (3)

(iii) Simpson's index of concentration, $\lambda = \sum_{i=1}^{s} \hat{p}_i^{\,2} = \exp(-H_2)$ (4)

(iv) H_α / H_0 is often used as a measure of species evenness (5)

(v) H_α plotted against α $(-\infty < \alpha < \infty)$ is a decreasing sigmoid curve with maximum value, $H_{max} = \log_e (1/p_{min})$ (as $\alpha \rightarrow -\infty$), and minimum value, $H_{min} = \log_e (1/p_{max})$ (as $\alpha \rightarrow \infty$), where p_{min} and p_{max} are respectively the minimum and maximum observed species proportions in the sample. The parameter p_{max} is the Berger–Parker measure of dominance, and was recommended by May (1975) as one of the most satisfactory diversity measures available. These α-diversity curves for $\infty \geq 0$ are illustrated later.

(vi) H_α has value $\log_e$ s (= $\log_e (1/(1/s))$) when $\alpha = 0$, where s is the number of observed species. If all of the $\hat{p}_i$ (i = 1, . . . , s) have the same value (= 1/s) the graph of H_α is horizontal with value $\log_e s$. The slope of the curve when $\alpha = 0$ is $\log_e (\tilde{p} \,/\, 1 \,/\, s))$ where $\tilde{p}$ is the geometric mean of the observed species proportions. Hence, the slope of the α-diversity curve when $\alpha = 0$ is one measure of how far the distribution of observed species proportions deviates from evenness.

In general, the shape (e.g. the inflexion point) and the placement of the α-diversity curve depends on the proportions $\{ p_i \}$, $_{i} = 1, \ldots, s$. The distribution of proportions of the relatively rare species observed in the subplot, i.e. those with proportions less than $(1/s)$, mainly determine the form of the α-diversity curve for $\alpha < 0$, while the relatively abundant species mainly determine the shape of the α-diversity curve for $\alpha > 0$. However, in this paper we only use α-diversity curves for positive values of α, since as indicated below, H_α has an ecological interpretation for positive integer values of α.

We note that

$$\lambda_{(k)} = \sum_{i=1}^{s} \hat{p}_i^{\,k} = \exp(-(k-1)H_k) \qquad (6)$$

is the estimated probability that k trees observed at random will be of the same species, so that $\lambda_{(k)}$ for $k = 3, 4, \ldots$ etc. (and hence H_k) have similar ecological interpretations to Simpson's λ (= $\lambda_{(2)}$). The higher order indices $\lambda_{(k)}$ $(k>2)$, and hence the corresponding H_k, give even more weight to the more frequently occurring species than Simpson's index.

Orloci (1991) adopted H_α as a measure of the diversity/entropy of a system. The fact that it encompasses almost all of the standard measures of diversity/entropy makes it is a good candidate for use as a routine diversity assessment tool. We use the results from the data analysis of H_α to suggest the best choice of diversity indices.

Finally, it should be mentioned that any diversity index calculated from data collected from a sample plot of finite size will be an underestimate of the corresponding diversity measure defined on the population of trees from which the sample data is drawn. Pielou (1975) and Rennolls & Laumonier (1998) consider methods for eliminating this bias. This issue is side-stepped in this paper by considering the 'unit' under consideration to be a 100-m × 10-m subplot, as this is the subplot size used in the FIMP inventory. Within such a framework it would be reasonable to use spatial interpolation methods on a dispersed set of subplots to produce estimated maps of spatial diversity distribution.

Species diversity structure

The concept of diversity-structure. In many of the empirical studies of forest tree species diversity referred to in the Introduction more than one diversity index was used to characterize the diversity of the sampled forest region; usually the species abundance and either the Shannon–Weaver index or Simpson's index. It is generally regarded that both indices give appropriate measures of diversity, and provide different insights into the diversity of the forest. Each of the chosen indices will have its own and differing power to discriminate between the ecological subregions of the forest.

Therefore, tree species diversity is best not characterized by a single diversity index. It should be regarded as a multi-factorial feature of a forest. The number of such indices required, and their precise form, and the relationship between them, is called the 'diversity structure' of the region. The diversity structure of a particular forest may be simple, and a single index of tree species diversity may be an adequate characterization. However, a more extensively forested region, with varying topography, soil and geology may require the use of two or more diversity indices to adequately characterize the diversity structure of the region.

Determination of diversity structure and ordination of sample plots. Associated with the view of diversity as a multi-factorial measure is the question of how the component indices of this multi-factorial diversity measure should best be chosen, from amongst the large number of available indices. We consider this question in the context of the biodiversity inventory approach discussed earlier. We suppose that data on tree species have been collected on a number of sample plots which are distributed over the forest region being inventoried. For each subplot on a site we may construct an α-diversity curve.

Visual inspection of the α-diversity curves for a site can lead to a choice of diversity measures which best characterize the α-diversity curves for that site. For both Batang Ule and Pasirmayang it is shown below that H_0 (species abundance) and H_∞ (the Berger–Parker index) are adequate measures. These could be used as the basis for an ordination of the subplots on each site. Such an ordination does provide a segmentation of the Batang Ule site into three ecologically distinct regions which are ecologically interpretable. The results for this are not presented in detail in this paper, since an equivalent segmentation is provided by the use of factor analysis, and the results from this approach are presented below.

Factor analysis involves a model in which it is postulated that there are a limited number of underlying diversity factors (orthogonal or not) and that each of the separate diversity index scores for a sample plot can be expressed as linear combinations of the sample plot scores on the underlying diversity factors. The best factor model, in terms of the number of underlying factors, and their relationship to each other (orthogonal or not), and the separate diversity indices (the factor loadings) are determined from the raw-diversity-scores (indices) of the sample plots by a range of statistical and geometric methods, e.g. maximum-likelihood, minimization of error sums of squares (Lawley & Maxwell 1971). The choice of the best underlying diversity-factor structure depends on the use of rotation techniques with the naming and interpretation of the factors depending on ecological interpretation of the factors from their loadings on the original set of diversity indices. The scores of the sample plots on the underlying diversity factors may then be used (via ordination or clustering techniques) to allocate the sample plots into groups which may be considered to be ecologically distinct. Hence it is possible, in principle, to obtain an ecological classification of the sample plots, and hence possibly to obtain an ecological stratification of the forest region (using map interpolation techniques). Multivariate methods of analysis which require a training-set of sample plots for which the ecological classification is already available, are not appropriate for data from an inventory.

Use of the factor analysis approach for diversity structure determination, and ecological classification faces a data-analytical problem. What raw diversity indices should be included in the initial analysis, from amongst the wide range of possible indices? Provided adequate computing facilities and software are available there is no reason that all of those indices defined in the diversity literature should not be evaluated and included in the subsequent diversity-structure analysis. In this paper we use the α-diversity values for a range of ∞ values. Of course, they are highly correlated because of their functional derivation. Also the multivariate normality assumption for maximum likelihood estimation and significance tests will not be satisfied. However this does not stop us using the factor analysis technique as an exploratory data-analytical tool to look at the multivariate structure of a set of α-diversity curves. It is in this spirit that the technique is used in this paper, and accordingly formal measures and criteria associated with the formal use of factor analysis are not presented. Once the diversity structure has been determined using factor analysis, the scores on the resulting factors may be used as a basis of an ordination of the α-diversity curves, and hence a segmentation of the sample plots.

RESULTS

Description of the diversity pattern

Batang Ule. The pattern of tree and species densities along the topographical gradient is illustrated in Figure 2. It shows that the stocking and the number of species were fairly low and steady in the valley subplots 1–7, increased together, and became more variable on the slope between valley and ridge (subplots 8–16). The densities were highest and most variable on the upper slope and ridge (subplots 12–16) and on the plateau (subplots 2–29). The upper slope and ridge subplots 12–16 have less species, relative to their tree counts, than the other subplots in the plot. The close relationship between the variations in tree and species densities (Figure 2) is an illustration of the species-count/sample-size relationship which is analogous to the species-area relationship (Rennolls & Laumonier 1999a).

In Figure 3, the pattern of species-diversity indices along the topographic gradient can be seen, the increasing trends reflecting partially the increase of tree and species densities with plot number. While H_1 (corresponding to the Shannon–Weaver index) does not really distinguish any anomalous behaviour, the higher-order α-diversity measures H_2 (corresponding to Simpson's index), H_3 and H_∞ (corresponding to the Berger–Parker index) clearly highlight an anomalous diversity behaviour on the upper part of the slope and the ridge (subplots 13–17).

Whilst the majority of the α-diversity curves shown in Figure 4 retain their relative ranking over the α-range, there are six plots which exhibit anomalously low diversity measures with increasing α. These anomalous α-diversity curves correspond to subplots 13 and 14 at the top of the slope, subplots 15 and 16 on

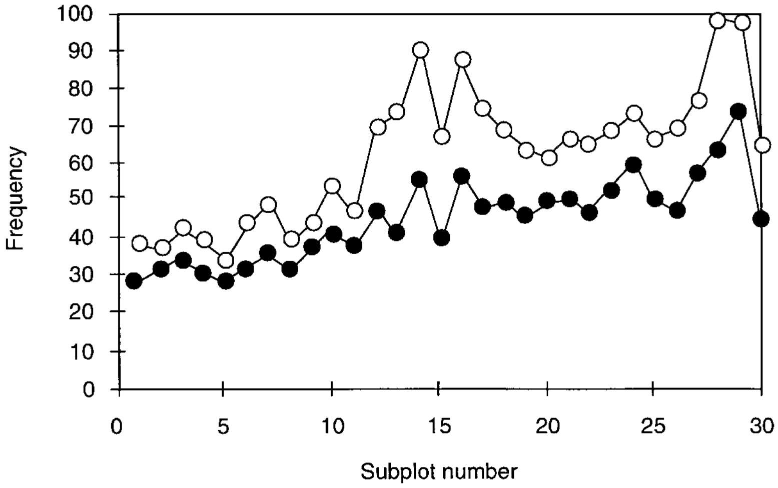

Figure 2. Changes in numbers of trees and species with subplot number across the plot at Bantang Ule, Sumatra from valley (1) to ridge-plateau (30).

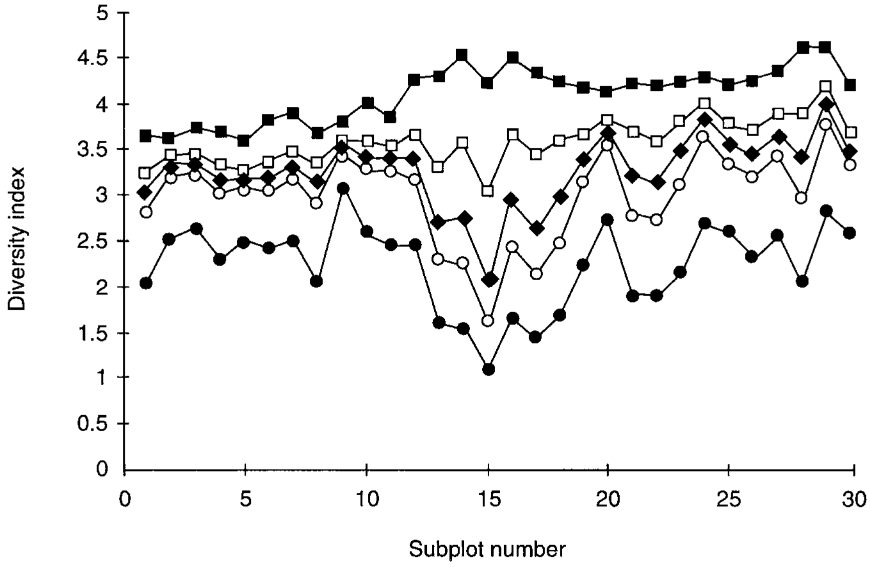

Figure 3. Changes of α-diversity measure with subplot across the plot at Bantang Ule, Sumatra: H_0, (■), H_1 (□), H_2 (◆), H_3 (○) and H_∞ (●).

the ridge over the slope to the valley, and subplots 17 and 18 which are the first two plots on the plateau. These plots are most clearly distinguished from the other plots in terms of the Berger–Parker index (corresponding to H_∞). The depression of the higher order α-diversity measures corresponds to increase of the higher order $\lambda_{(k)}$, as defined in (6). This means that the anomalous subplots are relatively more dominated by their most frequently occurring species than the other subplots in the site. Subplots 27 and 28, which have relatively high tree counts (Figure 2) do not display anomalous α-diversity behaviour in Figure 4.

The clear way in which subplots 13–18, which also have high and variable responses in Figures 2 and 3, are picked out is striking. Examination of the α-diversity curves also suggests the most appropriate diversity indices for the characterization of the set of α-diversity curves, (for Batang Ule, the species-abundance and the Berger–Parker index).

Pasirmayang. Pasirmayang is a flat site, and it might be expected that the diversity properties of each of the subplots will be similar. This has been confirmed to be the case, with the α-diversity curves approximately being straight lines with about the same slopes. The curves are not presented here since they are not informative.

Factor-analysis and ordination of the α-diversity curves

Batang Ule. The 40 α-diversity measures, α = 0.1, 0.2, . . . ,4.0, for each subplot were taken as raw data for a principal components analysis/factor analysis using

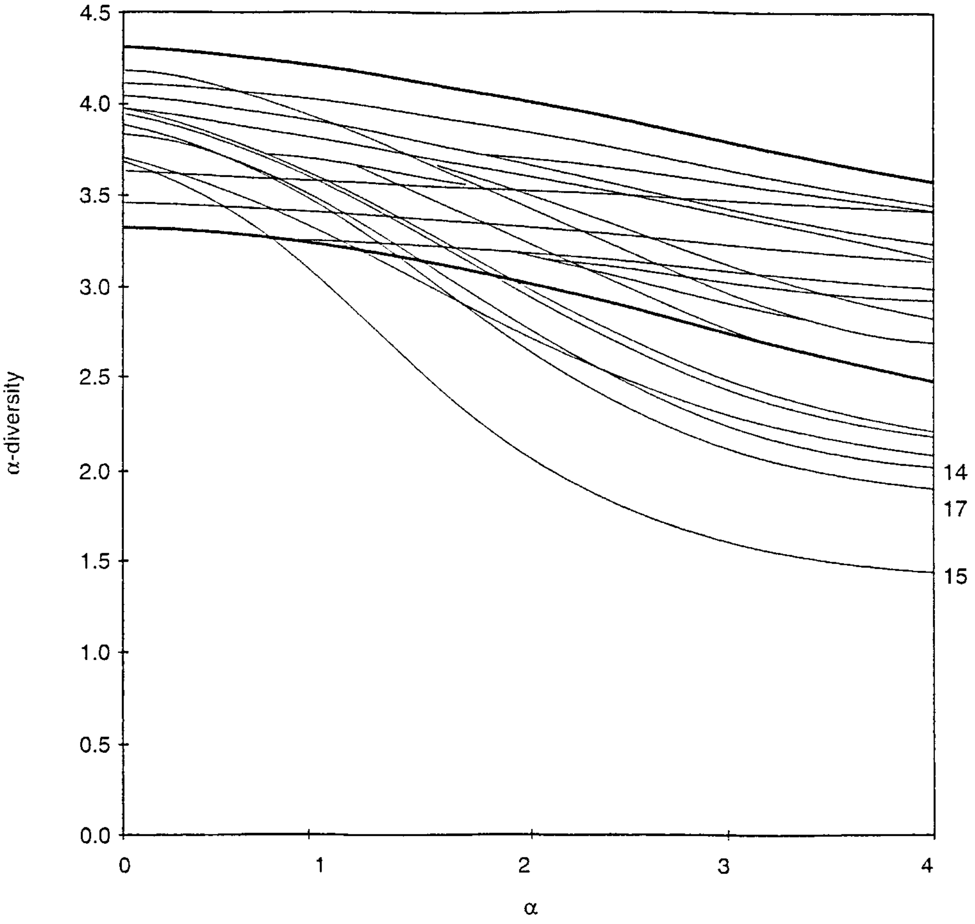

Figure 4. Curves of α-diversity for the 30 subplots in the 3-ha plot at Batang Ule, Sumatra, for trees DBH ≥10 cm. These curves for the subplots at the top of the slope and the start of the plateau have been plotted separately. Subplots 15, 17 and 14 have been indicated on the right-hand side. The curves with more solid lines enclose the remaining subplots.

SPSS (1994). Correlations between α-diversities with close values of α are very high, not surprisingly. However there is relatively little correlation between the α-diversities of widely differing order. For example, the correlations between $H_{0.1}$ (essentially the species-abundance) and H_1, H_2 and H_3 were 0.85, 0.34 and 0.12 respectively; the correlations between H_1 and H_2, H_3 were 0.78 and 0.61.

The results of an initial PCA (on standardized α-diversities) are clear. Two components (factors) adequately characterize the α-diversity curves, the first two eigenvalues being 31.3 and 8.5. Varimax rotation of a two-factor model produces a first factor which is loaded most heavily on the high order α-diversities, whereas factor 2 is most heavily weighted on the low order α-diversities (Figure 5). We name these factors the 'BU-dominance factor' and the 'BU-abundance factor' because of their patterns of weights and because they are specific to Batang Ule site.

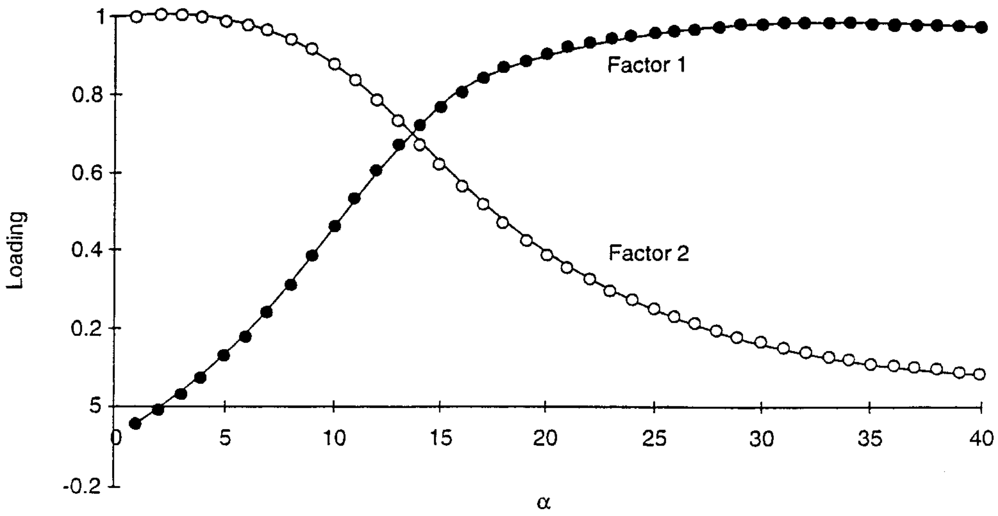

Figure 5. Relationships between the loadings of the two-factor model and α-diversity for the plot at Batang Ule.

The two-dimensional ordination of the subplot factor scores presented in Figure 6 shows a very clear picture. This ordination groups the valley subplots (1–8), the subplots at the top of the slope and the start of the ridge/plateau (13–18), and the plateau subplots (19–30). The lower slope subplots (9–12) lie between but overlap the valley and plateau parts of the diversity ordination-space. Factor-1 (the 'dominance-factor') is discriminating the top-of-slope plots from other plots. Factor-2 (an 'abundance-factor') is discriminating between valley and plateau plots, which is in accordance with the interpretation given for Figure 2.

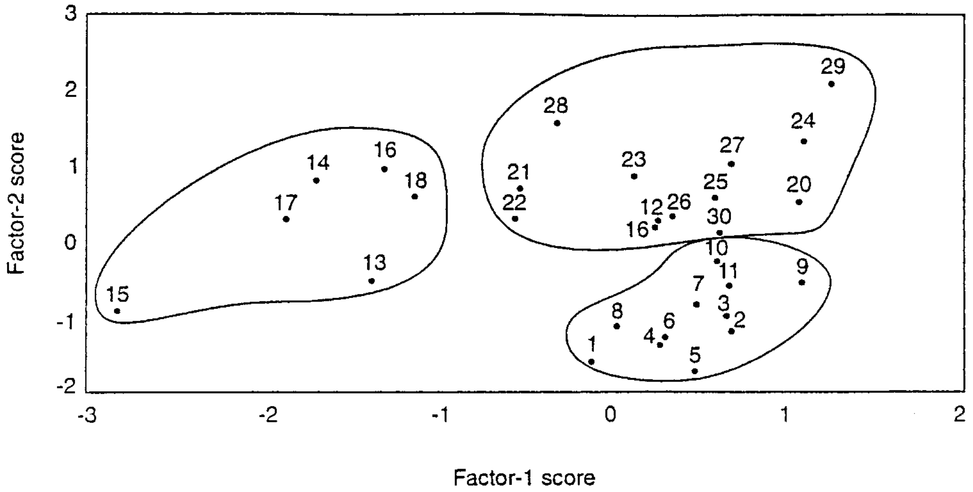

Figure 6. Ordination of the subplots at Batang Ule based on α-diversity values.

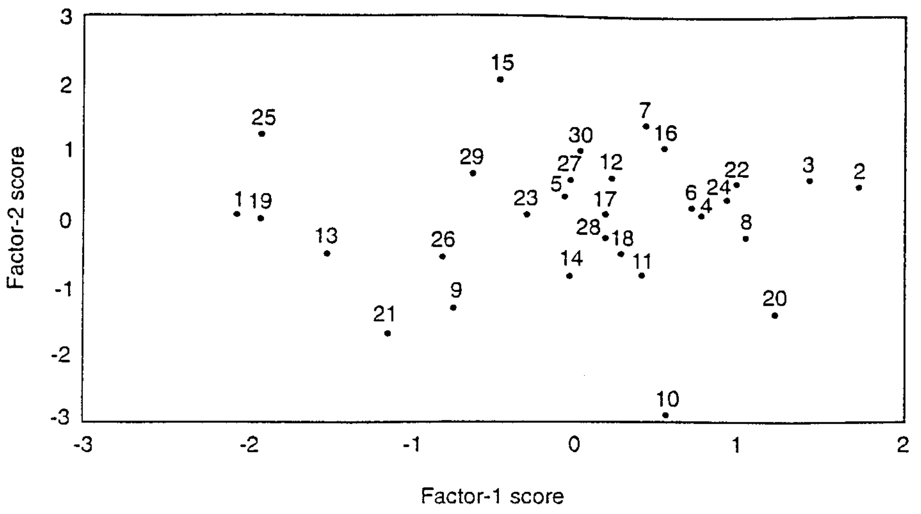

Figure 7. Ordination of the subplots at Pasirmayang, Sumatra, based on α-diversity values.

Pasirmayang. Factor analysis (with varimax rotation) extracted two main α-diversity factors selected with the same general form as those obtained for Batang Ule. That is, factor-1 (eigenvalue 37.6) is dominated by high weightings on high-order α-diversities, and factor-2 (eigenvalue 2.4) is dominated by high weightings on low-order α-entropies. A scatter plot of the subplot scores on the two factors is shown in Figure 7. The contiguous subplots 2–8 have relatively high factor-1 scores; subplots 9–18 as a group have somewhat lower factor-1 scores. While formal significance tests of these suggested groupings has not been done, there is not strong evidence of an underlying spatio-environmental pattern which is generating a diversity distribution grouping.

DISCUSSION

Problems in the use of diversity indices

The use of tree species diversity indices does mean that sites with identical distributions of species proportions will have the same values of species diversity, even though the species involved may be entirely different. If species composition is of primary concern, then species diversity indices by themselves are not sufficient. Lande (1996) reviews the way in which the partitioning of Shannon–Weaver diversity measure, and other measures, can be used to test the difference in species compositions in different samples or communities. Kullback (1959) and Renyi (1961) give the information theoretic background for the Shannon–Weaver (-Weiner) measure. Rennolls (1997b) and Rennolls & Laumonier (1997c) adopt a similar approach to the analysis of the data presented in this paper, based on likelihood theory. They use a 'cross-entropy' measure of the difference (or distance) between species distributions and compositions which is a generalization of the Shannon–Weaver diversity index for a single plot. Multidimensional scaling is used as a method of ordination of the interplot distances, and produces results similar to those presented in this paper.

Species diversity indices and diversity structure

In Batang Ule the topography (Figure 1) has a strong effect on tree and species densities, though it may be a surrogate variable for other explanatory variables, such as soil, drainage or local canopy environment (forest dynamics). Use of simple graphical methods on the standard species-diversity indices is able to identify differences in species diversity between the valley subplots, the subplots at the top of the slope and the start of the plateau, and those on the plateau. However, it is not clear from such an approach which set of diversity indices is best for characterizing the diversity structure of the site. The diagram of α-diversity curves (Figure 4) clearly picks out the top of slope and start of plateau subplots as having distinctive diversity properties which are best characterized by the Berger–Parker dominance index (corresponding to H_∞). It is also fairly clear from this diagram that the species abundance is the other main index to characterize the diversity structure of the site. However, this approach to selection of the most appropriate diversity indices to characterize a site is also heuristic, and would be ineffective if the diversity structure were complex.

Use of PCA/FA on the α-diversity curves for both Batang Ule and Pasirmayang comes up with the very clear result that *two* diversity factors provide an adequate characterization of the diversity structure of the sites. For Batang Ule the resulting ordination of the subplots produces three subplot groups corresponding to the valley and lower slope, the top of slope and start of plateau, and the plateau. We may obtain a simple approximation to the Batang Ule diversity factors by considering only those α-diversities which weight most heavily on the diversity factors. The result is a high-order α-diversity measure, possibly H_4 or the Berger–Parker index (corresponding to H_∞) as an approximation for factor-1, and the species density (corresponding to H_0) as an approximation for the factor-2. This is the same result as is obtained from visual inspection of the α-diversity curves.

These substantive results will not be surprising to plant community ecologists because they merely reinforce the common practice of using the joint measures of species density and a concentration measure to characterize species diversity. However, the advantage to using the factor analysis approach to the analysis of diversity is that the number and form of the best diversity factors is produced from a routinely applicable data-analytical procedure, without a prior choice of measures having to be made. The process may be followed as an automatic data-analytic method which will provide a site-specific species-diversity characterization.

Other sites may be best characterized by other combinations of indices. Also, a two-dimensional α-diversity space is not expected to be the general outcome.

It is possible that in more complex situations, possibly involving plots over a more dispersed region, that more than two factors will be needed to represent the structure of diversity-space.

Characterization of biodiversity patterns and conservation issues

It is important to be able to make comparisons of biodiversity resources between regions, to be able to decide where biodiversity conservation efforts should be concentrated. Within-region species-diversity analysis on two or more separate regions would lead to a number of species-diversity structures. One conservation strategy that is considered in forest land management is to leave conservation areas untouched within the logging operation area. It is possible that this approach might replicate conservation of areas of similar species diversity and might fail to conserve areas of unique species-diversity structure. If the separate regions turned out to have diversity structures which were similar, an alternative conservation strategy might be to conserve only one area from all of the regions with a particular diversity signature. Such an approach could also fail to identify unique areas which need to be conserved. An analysis of diversity structure from the subplots from all of the regions would be necessary to identify the overall diversity structure, its dimensionality, and the number of distinct diversity groups in the set of regions. The conservation implication of the discovery of a higher dimensionality of diversity on such a combined analysis would be that conservation areas would need to span the regions and would need to be chosen in order to maintain this higher dimensional diversity, by including as conservation areas representatives of any groupings that may be observed in diversity space.

Diversity inventory, mapping and land-use planning

For forest land management in the tropics, including forest exploitation, replanting of plantations and/or conversion of the land-use, the information that is currently available usually includes course maps of geology, soil, and possibly a topographic map (Nohr & Jorgensen 1997). An additional information source that is now widely available is remotely sensed information. The main objective of biodiversity inventory is to map a region under management so as to highlight the subregions of high conservation value so that they may be included in a management plan which ensures biodiversity conservation.

If a topographic map is available then it is a simple task (using a geographic information system) to produce a land-facet map which classifies each pixel of the (raster) topographic map into a land-facet, where a land-facet is predefined by topographic properties such as elevation, aspect, slope, distance above a valley. The main problem in such regional classification/mapping based on topographic maps is to choose definitions of land-facets which are ecologically meaningful. Ecological relevance has been taken, in this paper, to be related to the species diversity structure. It has been shown that the analysis of species diversity structure, using α-diversity curves and factor analysis, is able to identify ecologically distinct subregions which are closely related to the topography of the region. The analysis of the species diversity structure of the sample plots collected in a region may therefore be used to guide the definition of meaningful land-facets. Hence, appropriately defined land-facet maps derived from topographic maps may potentially be used as a basis for land-use management which takes into account the underlying ecological/diversity structure of the region under management. The methods used, α-diversity curves in conjunction with factor analysis, are able to be performed automatically from the tree species data on the sample plots and would be equally applicable to a number of discontiguous 0.1-ha plots collected in the conduct of a forest inventory of a forested region. It is hoped that the 'automatic' methods of tree species diversity analysis and ordination used in this paper will provide a useful tool for ecological classification which may be used in the context of planning of timber extraction operations which are both efficient, and which attempt to conserve the rich store of tree species diversity which is found in the tropical rain forests.

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