

SECTION 2: RAPID VEGETATION SURVEY

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2.1 Introduction:

Evidence for the need to conserve biodiversity is well established in the literature and is reflected in the international Convention on Biological Diversity that has addressed a series of issues for attention by its signatories (CBD 1994). Despite the agreed urgency to develop a framework for biodiversity conservation, there is, as yet, no operational definition for biodiversity. According to Weitzman (1995), the implementation of any plan to preserve biodiversity is hampered by the lack of an operational framework or an objective function, and “*We need a more-or-less consistent and useable measure of the value of biodiversity that can tell us how to trade off one form of diversity against another*”. Miller and Lanou, (1995) also maintain “*The value of biodiversity is determined largely by the interaction between human society and biodiversity*”. This implies that among other things, there should be a dynamic link between biodiversity and productivity for human needs. The World Bank (1995) asserts it is necessary to integrate biodiversity concerns into national decision making, but the mechanisms for this remain elusive. In Indonesia, the Government recognises a lack of scientific and management expertise in biodiversity conservation (Government of Indonesia, 1993), that is further hampered by the current regime of property rights on public lands and waters, and the failure to use much of the financial returns from exploiting the country’s living resources to support biodiversity conservation (Barber *et al.* 1995).

These pressures highlight both the need for a working definition of biodiversity and a cost-efficient, generic tool for its assessment that can be used in turn to inform policy planners and managers. While the species remains the sole currency unit for biodiversity assessment (Heywood and Baste 1995) there will be little progress (*cf.* Wulff 1943). Species richness and abundance used alone and without other attributes of behaviour and performance can seriously misinform and impede biodiversity assessment. Parity in richness does not guarantee equivalence in either genetic composition or response to environment. Partly for this reason, an emerging school of thought now considers assessment should include functional features or types as well as species. (Box 1981, Gillison 1981, 1988, Nix and Gillison 1985, Cowling *et al.* 1994a,b, Huston, 1994, Collins, S.L. and Benning, T. 1996, Martinez 1996, Woodward *et al.* 1996). Varying definitions of functional types are so far most commonly associated with guilds (Bahr 1981, Gillison 1981, Huston 1994, Gitay and Noble 1996, Mooney 1996, Shugart 1996, Smith, 1996, Smith *et al.*, 1996, Gillison and Carpenter 1997), but as Martinez (1996) asserts “..the functional aspects of biodiversity are a broad and vague concept that needs substantial added specification in order to become scientifically more useful.” Cramer (1996) also feels the task of screening all the world’s species for functional types is impossible and that for a global model, a breakdown of the world’s vegetation can only be done based on major physiognomic or otherwise recognisable features. Recent global ecoregional studies (Gillison and Thomas, unpublished) suggest that, to the contrary, broad physiognomic and structural features can mask important functional and taxonomic differences in biodiversity. Gillison and Carpenter (1997) and Gillison (1997) and Gillison and Alegre (1999, unpubl.) have also shown it is possible to use generic functional or adaptive morphological attributes to characterise and quantify vegetation response to environmental change such as land use, climate and soil.

A new quantitative method has been developed for characterising vascular plants according to a set of 35 Plant Functional Attributes that describe a plant as a three component ‘coherent’ (*sensu* Vogel 1991) or functional model. This consists of the photosynthetic envelope, modified Raunkiaerean life form (Raunkiaer 1934) and above-ground root system. The method uses a semantic rule set and grammar (Gillison and Carpenter, 1997) to generate a theoretically finite set of unique PFA combinations for the world’s vascular plants. Any one combination is termed a functional *modus*. Using this rule set, about 7.2 million combinations or *modi* are possible, although it is thought that in reality the number is closer to 4,000. There is no *a priori* interdependence between *modi* and species; as the mapping is many-to-many, i.e. more than one *modus* can occur within a species and *vice versa*. The advantage of functional over solely species-based methods is that the former can be universally applied by observers with limited botanical and ecological experience. It can be used to compare functional characteristics of individuals and sets of individuals independently of species, e.g. where taxa may be geographically disjunct but may possess similar adaptations to environment. In a comparative study of methods of characterising site productivity and growth patterns in North Queensland rain forests, Vanclay *et al.* 1996 showed the PFA method outperformed traditional methods of site characterisation. The method is now undergoing further tests by the Forestry Department, Qld DPI (Keenan, Woldring pers. com.). Gillison *et al.*, (1996) has shown consistently high correlations between total numbers of species and total numbers of unique *modi* recorded from 40 x 5m plots across a wide range of environments (Annex II and *cf.* Baskin 1994). The implications from this are that in surveys where botanical expertise is lacking, *modi* can be used to predict species richness with a high degree of confidence. This may also benefit rapid assessment of plant biodiversity and improve correlations between plant and animal biodiversity (*cf.* Gillison *et al.* 1996). A field proforma specifically designed for rapid survey (see section 2.4) can now be used by observers with minimal training to characterise site physical features, vegetation structure, species composition and *modi* to rapidly describe a specific habitat for a taxon or set of taxa.

Richness in species and unique *modi* can be a useful complementary descriptor of habitat. But while these contribute to characterising biodiversity, they do not by themselves reflect evenness or dominance of individuals per species such as the frequently used diversity indices of Shannon-Wiener and Simpson (Magurran 1988). Many diversity indices have been developed, but the search goes on (Cousins 1991, Majer and Beeston 1996). The great majority are based on species abundance and at best are usually regarded simply as another species-based, stand attribute. A problem for survey in tropical forests is that to generate such indices requires time-consuming counts of individuals which is not cost-effective. To help circumvent this problem, Gillison *et al.* (Appendix 2.1) have developed a complementary measure of *functional diversity* based on the numbers of *modi* per species for each plot. This differs from approaches by others (e.g. Martinez 1996) and has the advantage that in rapid survey it is only species rather than numbers of individuals of species that are counted. A measure of *functional complexity* has also been developed by the same authors based on a computed functional ‘distance’ between *modal* assemblages derived from a table of weighted ‘transformation’ values between specific PFAs (Gillison and Carpenter 1997).

It is one of the tenets of RBA that for practical purposes there should be indicators or surrogates of more complex plant and animal assemblages. Whether this is a realistic assertion is a continuing source of debate (Cranston and Hillman 1992, Reid *et al.* 1993, Pearson 1995, Howard *et al.* 1996), and there is often questionable theoretical support for targeting so-called keystone species (Tanner *et al.* 1994). There is nonetheless an increasing need for reduced attribute sets that can be used to carry other information such as the status of key pollinators

and seed dispersers that may not be available at the time of survey (Miller *et al.* 1995). To demonstrate indicator efficiency requires calibration from very intensive baseline studies of taxa and functional types at a comprehensive range of spatial, temporal and environmental scales. Such baseline studies are almost non-existent in complex tropical environments. Ongoing studies within the context of ASB show varying correlative trends. In a baseline study of Sumatran rain forests, Gillison *et al.* (1996) showed that while plant biodiversity increased with elevation from 500 to 900m asl, the converse was true for insects and birds. While such confounding effects can be accommodated by appropriate regression models and multiple discriminant formulations, predictive models of biodiversity based on environmental correlates such as elevation clearly need to be carefully evaluated before being used by managers. It follows that environmental context and scale are important in designing field studies of biodiversity (see also He, *et al.*, 1994,).

Most practitioners now concede the landscape matrix is critical to supporting biodiversity (*cf.* Forman and Godron, 1986, Franklin 1993), and this has been central to survey design and data collection across all the ASB and CIFOR ecoregional benchmark sites. Because disturbance is a critical determinant of biodiversity (Petraitis *et al.*, 1989, van der Maarel 1993, Phillips *et al.* 1994), factors such as agriculture, shifting cultivation and forest fragmentation (Grime 1979, Bierregard *et al.*, 1992, Sayer and Wegge 1992, Margules and Gaston 1994, Brooker and Margules 1996) should be considered when designing a survey. For this reason, the ASB sites have been located specifically to sample a range of dynamic conditions, along successional gradients of land use from pristine rain forest, logged-over forest, plantations to degraded grasslands. Although the issue of plot size is a continuing source of debate in plant ecology, recent studies show that for plant diversity, useful information can be recorded from plots as small as 50 x 2m (Parker and Bailey 1992, Parker and Carr 1992, Parker *et al.* 1993) and 40 x 5m. (Gillison *et al.* 1996). The advantage of 'small and many' vs. 'few and large' is that the former is more cost-effective when sampling variation in biodiversity at landscape level (*cf.* Keel *et al.* 1992). Variation of this kind demands cost-effective survey techniques (*cf.* Margules and Haila 1996). Because the distribution of plants and animals is determined mainly by environmental gradients, gradient-based techniques using the gradsect approach offer one means of sampling such variation (Gillison and Brewer 1985). With gradsects, sites are located according to a hierarchical nesting of assumed physical environmental determinants such as climate, elevation, parent rock type, soil, vegetation type and land use. This approach has been shown to be more cost-efficient than purely random or purely systematic (e.g. grid-based) survey design (Gillison and Brewer 1985, Austin and Heyigers 1989). As gradients themselves are being sampled, this will enhance the efficiency of extrapolative spatial models.

Issues of biodiversity conservation inevitably raise important questions of site representativeness. For a programme involved in the selection of 'best-bet' options for biodiversity and productivity, a manager may need to choose between different locations to ensure optimal management. For this a range of sophisticated computer-based solutions already exists. These are based mostly on species occurrence but may include environmental features such as land classes (Nicholls and Margules 1993, Pressey *et al.* 1996, Csuti *et al.* 1997, Pressey *et al.* 1997). Other species-based approaches use additional levels of higher taxa (Prance 1995) or a measure of 'phylogenetic distance' to include taxic richness or genealogical relationships as embodied in taxonomic classifications, typically by a weighting of the relative number of species per genus, genera per family etc. (Vane-Wright *et al.* 1991, Williams *et al.* 1992, Faith 1992, 1993, 1995). A problem with species-dependent approaches of this kind is that for many tropical lowland forests, species identification is difficult and time-consuming. In addition, the majority of these algorithms require expertise that is frequently lacking in

developing countries. For this reason, and because functional types can be more easily identified than species, Gillison *et al.*, (unpublished 1998) developed an analogous concept of 'functional distance' based on *modi* (outlined in Annex I). The algorithm is being incorporated in a new data-entry software package PFAPRO designed to run on a PC as a Windows application (Carpenter and Gillison, unpublished 1998). When data from a series of plots containing functional *modi* have been entered, PFAPRO has the facility to generate a distance matrix on demand. By this method, managers can readily identify levels of similarity between plots or landscape units.

Data collected during this project will be used to generate and test spatial models of key sets of taxa and functional types and to couple these with productivity patterns based on land use. For this purpose a potential mapping software package DOMAIN (Carpenter *et al.* 1993) will be used. Unlike other packages such as BIOCLIM (Busby 1991) or CLIMEX (Sutherst and Maywald 1985) that are either climate-dependent or require detailed, process-based knowledge about the species in question, DOMAIN uses any georeferenced data that are considered important in influencing performance of an individual. This may include environmental data used to construct a gradsect-based survey. DOMAIN then accepts known distribution points for specific taxa or functional types and constructs an environmental envelope for these using environmental correlates and a distance measure based on the Gower metric. It then computes a grid-based distribution map of according to the similarity matching of each pixel or grid with the original environmental domain. DOMAIN has been used in previous baseline studies in Sumatra (Gillison *et al.* 1996) and has been modified by CIFOR to run as a user-friendly, Windows based package on a PC. The software is available *gratis* from the CIFOR home page on the internet. Since its installation in August 1997 CIFOR has recorded downloads from users in 35 countries. Because DEMs were constructed for each of the ASB benchmark sites in Phase II, it is anticipated DOMAIN will be used for generating and testing spatial models of biodiversity and related productivity. The effective extrapolation of data will depend to a large degree on the availability of georeferenced environmental data. These data have been compiled at CIFOR using mapping sources from within Indonesia (Laumonier *et al.* and other sources from within the GoI Ministry of Forestry). Remote sensing of tropical rain forest vegetation has been used elsewhere with some success (Tuomisto *et al.* 1994) and is expected to play a significant role in DOMAIN applications. Data for normalized difference vegetation index (NDVI) are available and can be used in DOMAIN. NDVI is commonly used with AVHRR (advanced very high resolution radiometer) data for which appropriate calibrations are necessary (Roderick *et al.*, 1996a,b).

Most vegetation classification and survey methods incorporate a combination of broad structural variables coupled with seasonality (deciduousness) and a list of dominant species, e.g. 'Very tall evergreen Dipterocarp forest'. While this is useful for many geographic purposes it is insufficiently diagnostic for management purposes. In addition, structurally similar vegetation types are usually annotated by regionally different plant species. Within a region, vegetation described according to vegetation structure may be adequate for describing animal habitat but similar structure in separate global ecoregions are not necessarily ecologically equivalent. For ecologically sensitive classifications additional, response-based attributes such as adaptive features or plant functional attributes (PFAs) provide added value. As PFAs are generic and largely independent of species, they can be used to make ecological comparisons between geographically remote areas where environments and adaptive features may be similar but where species differ.

2.2 Methods:

The Plant Functional Attribute proforma (modified from Gillison, 1988 and updated by Gillison and Carpenter, 1997) was used to record site physical features [georeference by GPS in degrees, minutes and seconds; slope percent (clinometer); elevation (m) (digital aneroid altimeter); aspect in degrees (compass); parent rock type; soil type; vegetation structure, (mean canopy height (m), crown cover percent, basal area (m^2ha^{-1}); litter depth (cm); Domin scale cover-abundance estimates of wood plants <2m tall and Domin estimates of bryophytes; all vascular plant species and plant functional types (PFTs)]. As described by Gillison and Carpenter (1997), Plant Functional Types or PFTs or functional *modi* are combinations of essentially adaptive morphological or functional attributes (e.g. leaf size class, leaf inclination class, leaf form and type (distribution of chlorophyll tissue), coupled with a modified Raunkiaerean life form and type of above-ground rooting system. PFTs are derived according to a specific grammar or rule set from a minimum set of 35 functional attributes. An individual with microphyll-sized, vertically inclined, dorsiventral leaves supported by a phanerophyte life form would be a PFT expressed as MI-VE-DO-PH. Although they tend to be indicative of a species, they are independent of species in that more than one species can occur in one PFT and more than one PFT in a species. PFTs allow the recording of genetically determined, adaptive responses of plant individuals that can reveal infraspecific as well as interspecific response to environment (e.g. LUTs) in a way that is not usually contained in a species name. They have a major advantage in that, because they are generic, they can be used to record and compare data sets derived from geographically remote regions where, for example, adaptive responses and environments may be similar but where species differ. The data are recorded along a 40x5m strip transect located along the contour.

The data were compiled in a laptop computer using a recently developed software package, PFAPro (Gillison and Carpenter, unpublished). PFAPro facilitates compilation according to the rule set developed by Gillison and Carpenter (1997). It also facilitates the summary analysis of meta-data as well as producing graphs of relationships between different plant and vegetation variables. Using PFAPro, data logged for each 5x5m quadrat allow the generation of cumulative species and PFT totals per unit area and this allows the subjective inspection of asymptotic curves that can indicate whether or not a plot is an adequate sample of the vegetation or LUT (See Annex 1, Fig.1).

In addition to site physical data, simple totals of species, PFTs and vegetation structural variables, PFAPro can be used to generate a range of diversity indices for PFTs (Shannon-Weiner, Simpson and Fisher's alpha). The calculations are not trivial as, unlike diversity indices for species that are based on abundances of individuals per species, the PFT indices are derived on the number of species per PFT. Since the species to PFT relationship is many-to-many, this must be taken into account when calculating diversity. The method is described more fully in Appendix 2.1.

Four observers (ecologist and assistant, botanist (x2) and two laborers) collected plant voucher material later identified and curated at the *Herbarium Bogoriense*. A complete set of identified species and associated PFTs is listed in Annex III, Table 3. This method facilitated sampling even the most complex rain forest plot of 177 species in less than three hours. Photographic records were made of each plot. A sub-set of these has been scanned and will be cross-referenced with the data set.

2.2 Results:

The data were analysed according to the methods described above and in Part B. The most useful interpretations came from multidimensional scaling in which a two vector solution was extracted from plot data (Part B, Annex I, Fig. 7). This graph shows a zone of maximum biodiversity richness that is associated with jungle rubber. The peak in richness can be explained in part by the greater variety of available ecological niches in this agroforestry system compared with pristine rainforest. The analyses are based on a minimum data set of mean canopy height, basal area, species richness, PFT richness and a ratio of species numbers to numbers of PFTs or *modi*. Cumulative species, modi and species/modi richness area curves per 40x5m plot are indicative of vegetation type per LUT (Part B, Annex I, Fig.1 (1-7)). More detailed results from analyses of combined sets of taxa and functional types are described in the synthesis (Section 11). Other analyses dealing with variations on compositional structure of species, PFTs and vegetation structure and their relation to LUT will be dealt with in a later report. Plant taxa and functional types for each LUT are listed in Annex III Table 3. Summary data are listed in Table 2.1 and estimates of green biomass are given in Table 2.2 below. Relationships between vegetation and LUTs are described briefly in Section 3 below.

Table 2.1.
Summary of Taxa and Plant Functional Types (*Modi*) per LUT

No.	Site	Family	Genus	Species	Uniq Sp/Plot	Modi
1	BS1	44	82	103	102	37
2	BS2	43	81	104	100	36
3	BS3	32	48	50	50	20
4	BS4	45	83	111	108	39
5	BS5	43	82	117	112	38
6	BS6	26	35	42	42	27
7	BS7	25	43	48	46	33
8	BS8	37	60	68	65	37
9	BS9	31	52	58	54	30
10	BS10	53	97	115	111	47
11	BS11	49	89	100	97	41
12	BS12	6	10	11	11	10
13	BS13	6	7	7	7	5
14	BS14	7	12	15	15	12
15	BS15	8	19	19	19	13
16	BS16	22	40	43	42	34
	Total	477	840	1011	981	459
	Unique Total	91	320	—	557	216

Table 2.2.
Green biomass per Land Use Type*

Site.no	LUT	Av.kg/m2	stdev	coefvar	SEM	C-t/ha
BS01	NF	0.133	0.079	0.594	0.028	0.533
BS02	NF	0.000	0.000	*	0.000	0.000
BS03	LOF	0.000	0.000	*	0.000	0.000
BS04	LOF	0.045	0.083	1.854	0.029	0.179
BS05	LOF	0.007	0.020	2.828	0.007	0.028
BS06	HTI	0.247	0.159	0.642	0.056	0.987
BS07	HTI	0.092	0.131	1.424	0.046	0.368
BS08	RUB-P	0.107	0.126	1.178	0.044	0.426
BS09	RUB-P	0.083	0.093	1.121	0.032	0.331
BS10	J_RUB	0.033	0.400	1.194	0.014	0.133
BS11	J_RUB	0.018	0.035	1.913	0.012	0.073
BS12	IMP	0.227	0.057	0.252	0.033	0.908
BS13	IMP	0.180	0.008	0.045	0.004	0.719
BS14	CAS	0.207	0.028	0.136	0.016	0.829
BS15	CAS	0.288	0.089	0.308	0.051	1.150
BS16	CHROM	0.335	0.143	0.427	0.082	1.340

*Source M.Van Noordwijk and K.Hairiah

NOTE: Additional results from the vegetation survey are described in Section 11

2.3 References:

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Appendix 2.I

Unpublished measures of functional diversity and functional complexity used in this project

(extracted from Gillison, A.N. Carpenter, G. and Thomas, M., *Plant functional diversity and complexity: two complementary measures of species diversity*.)

Functional diversity

Concepts of functional diversity vary; according to Martinez (1997) (see also Steele, 1991 quoted by Martinez), functional diversity is defined as “..*the variety of interactions with ecological processes*” and can be quantified by determining the nature and extent to which functional groups are represented in an ecological system. Functional diversity can also refer to the number of such groups in a community each of which contains one or more species (Smith and Huston, 1989; Scott and Benning 1996). Whatever the nature of the functional groups it is generally accepted they will be fewer than the species under study, (Mooney 1997). In this sense functional ‘diversity’ is simply a measure of group richness rather than an estimate of evenness or dominance based on the abundance of individuals per group.

As with species diversity, it would seem reasonable to derive a parallel measure of functional diversity based on the abundance of individuals per functional type or *modus* but without species-weighting. While logically viable, this is likely to be limiting in practice as to record all individuals, (e.g. in an epiphyte-rich, rain forest) can be excessively time-consuming and counterproductive if the aim is rapid assessment, and if the functional types or groups are likely to be significantly fewer than the species. Depending on the scale and purpose of the investigation, the additional effort may not be worth the gain. For these reasons, we explore the possibility of using species instead of individuals to serve as a ‘higher-order’ measure of abundance by deriving a species-weighted, rather than a spatial or density-driven, measure of Functional Diversity based on abundances of individuals. A species-weighted form of Functional Diversity (SFD) can therefore be defined as: ***The diversity of functional types expressed as a function of the number of species per type***. While the definition can be compared with that of Huston (1994) for species diversity where “*The total species diversity of a community is described by the number of functional types multiplied by the average number of species per functional type*”, this approach is more sensitive to evenness and dominance. We achieve this in the same way that species abundance is used to calculate species diversity but with the important difference that counts of species per functional type are used instead of counts of individuals per species. For this we apply the Shannon-Wiener formula to estimate evenness and that of Simpson to estimate dominance. Another difference is that, unlike the ‘one-to-many’ species to individual relationship, the mapping between species and *modi* is’

many-to-many' (i.e. more than one species can exist in one *modus* and *vice versa*) (Fig. 1). Both formulae have been modified to accommodate these multiple relationships.

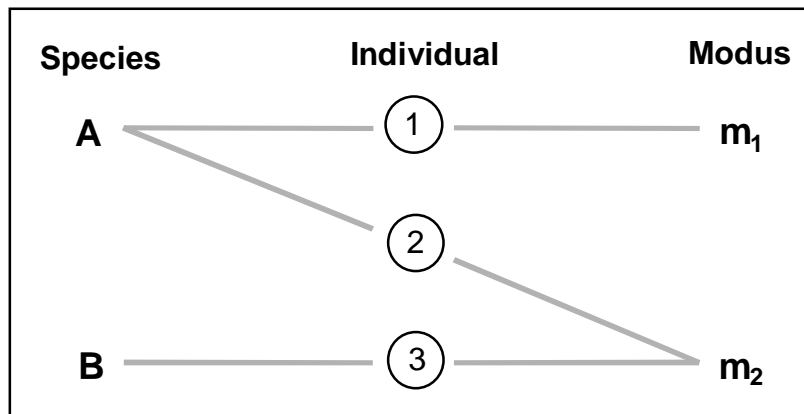


Fig. 1 An example of multiple linkages (many-to-many mapping) between Linnean species and functional types or *modi*. Species A occurs in *modi* m₁, m₂; species B in *modus* m₂, while m₁ occurs in species A, and m₂ in species A and B. An individual is recorded once if it satisfies any one of these relationships – duplicates are omitted.

Shannon Wiener Index

The Shannon-Wiener index is calculated from the equation (ref.):

$$H' = - \sum_{j=1}^{Nspp} p_i \ln p_i$$

where quantity p_i is the proportion of individuals found in the i th species, and is estimated using the maximum likelihood estimator:

$$p_i = \frac{n_i}{N}$$

Where n_i is the number of individuals in the i th species. For species/population data, each individual in the sample belongs to exactly one species. And N is the total number of species recorded. However with *modus*/species data, a species may be attributed to more than one *modus* if that species is present in multiple functional forms. To accommodate this difference, the maximum likelihood estimator is modified to divide the proportional count for a species evenly between the *modal* types in which that species is present. The equation for p_i , the proportion of species in the i th *modus* becomes:

$$p_i = \sum_{j=1}^{Nspp} \frac{n_{ji}}{n_j \cdot N}$$

Where $Nspp$ is the number of species,
 n_{ji} is the number of records for species j , *modus* i (either 0 or 1)
 n_j is the number of records for species j ,
and N is the total number of records.

Because the species to *modus* mapping is a many to many relationship N may be greater than both the number of species N_{spp} and the number of *modi* in the sample.

Simpson's Index

The same modified form of the maximum likelihood estimator is used in the calculation of the Simpson index which is usually formulated as:

$$D = \sum p_i^2$$

The Simpson index produces higher values for lower diversity, and is often expressed as $1 - D$.

Limits

Diversity values for the Shannon-Wiener index become progressively smaller with increasingly uneven distribution of species between *modi* where, for example, a small number of *modal* forms dominate the sample. Given the number of species and the number of *modi* in the sample, the absolute minimum index value possible can be found by computing the largest possible value for maximum likelihood estimator (P_0) for one *modus*, while minimizing the remaining $Nm-1$ estimators ($P_{i>0}$). The minimum estimator value occurs when only one species occurs in a *modus*, and that same species occurs in all other *modi*. The minimum is formulated as:

$$p_0 = 1 - \frac{Nm - 1}{Nm \cdot N_{spp}}$$

$$P_{i>0} = \frac{1}{Nm \cdot N_{spp}}$$

$$H'_{\min} = -[p_0 \ln(p_0) + (Nm - 1)P_{i>0} \ln(P_{i>0})]$$

The maximum value of the Shannon-Wiener index is generated when the species are evenly distributed between all *modi*, such that $P_i = 1/Nm$, yielding as a final form:

$$H'_{\max} = \ln(Nm)$$

The same proportion values determine the limits of the Simpson Index. This index returns smaller values for increasing diversity.

$$D_{\min} = \frac{1}{Nm}$$

$$D_{\max} = p_0^2 + (Nm - 1)p_{i>0}^2$$

Interpretation and Examples

When interpreting species-weighted functional diversity measures it is important recall that the measure describes the distribution of species between functional *modi*, not the distribution of individuals between functional types.

The values generated by of these species-weighted functional diversity measures, when applied over a broad range of sites, are typically higher than the equivalent measures from species/population data. This reflects the reduced likelihood of dominance of any particular functional type, and a similar degree of discriminatory resolution (or granularity) between functional types and species. The consistently high correlation between species counts and *modal* counts at the global level is explored elsewhere (Gillison, submitted for publication – see Annex II)

Functional complexity

Two approaches were adopted for the analysis of *modal* composition. The first was an exact mirror of the analysis of species composition. Instead of an analysis of species incidence, the incidence of each *modus* was used to generate a between-site Jaccard distance. This distance matrix was then input to the same multidimensional scaling procedure.

The second approach attempted to take account of the inherent similarity or dissimilarity between different *modi*. It was based on the syntactic distance between *modi* of Gillison and Carpenter (1997).

We consider sites *X* and *Y*, such that site *X* contains the set of *modi* $\{X_i, i = 1..m\}$ and site *Y* contains the set of *modi* $\{Y_i, i = 1..n\}$. Now let $f(a,b)$ be the distance between *modi* *a* and *b*. We define the dissimilarity between sites *X* and *Y* to be:

$$d_{X,Y} = \frac{\sum_i^m \min_j f(X_i, Y_j) + \sum_j^n \min_i f(X_j, Y_i)}{m+n}.$$

This index will be zero only if sites *X* and *Y* contain the same set of *modi*. In particular, it will be non-zero if *modi* at one site are a proper subset of *modi* at the other. It should also be noted that the dissimilarity index is not a metric.

The expected value of the dissimilarity index depends on the number of *modi* at each site. If the *modi* present at each site are generated by random sampling from a set of available *modi*, then the distance between two sites will decrease as the number of *modi* at each site increases. In the absence of any other aspect of pattern, we would expect sites with many *modi* to be very similar, whilst sites with few *modi* would be dissimilar - both to other sites with few *modi* and to sites with many *modi*. Ordination of such a dissimilarity matrix would result in a hyper-sphere - with *modi* rich sites at the centre, and *modi* poor sites at the periphery. Analyses of data from a range of global environments tend to confirm the utility of this procedure (Gillison and Thomas, unpublished).