Body size and measurement of species diversity in large grazing mammals

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Abstract

Species are by definition different from each other. This fact favours ranking rather than additive indices. However, ecologists have measured species diversity in terms of species richness, or by combining species richness with the relative abundance of species within an area. Both methods raise problems: species richness treats all species equally, while relative abundance is not a fixed property of species but varies widely temporally and spatially, and requires a massive sampling effort. The functional aspect of species diversity measurement may be strengthened by incorporating differences between species such as body size as a component of diversity. An index of diversity derived from a measure of variation in body size among species is proposed for large grazing mammals. The proposed diversity index related positively to species abundance, indicating that the use of body size as a surrogate for diversity is adequate. Because the proposed index is based on presence or absence data, the expensive and time consuming counting of individuals per species in each sampling unit is not necessary.

Key words: biodiversity index, body size, grazers, mammals

Résumé

Par définition, les espèces diffèrent les unes des autres. Ce fait favorise plutôt la classification que des indices supplémentaires. Pourtant, des écologistes ont mesuré la diversité des espèces en termes de richesse des espèces ou en combinant la richesse des espèces avec l'abondance relative des espèce dans un endroit donné. Les deux méthodes engendrent des problèmes : la richesse des espèces traite toutes les espèces de la même façon tandis que l'abondance relative n'est pas une propriété fixe d'une espèce mais varie considérablement dans le temps et dans l'espace, et exige des efforts d'échantillonnage importants. On peut renforcer l'aspect fonctionnel de la mesure de la diversité des espèces en intégrant des différences entre les espèces telles que la taille corporelle comme étant des composantes de la diversité. On propose pour les grands mammifères herbivores un index de diversité dérivé d'une mesure de la variation de la taille corporelle parmi les espèces. L'index de diversité proposé était lié positivement à l'abondance des espèces, ce qui montre que l'utilisation de la taille corporelle en remplacement de la diversité est opportune. Comme l'index proposé se base sur des données de présence ou d'absence, il n'est pas nécessaire de procéder dans chaque unité au comptage des individus de chaque espèce, si coûteux et si long.

Introduction

To prioritize conservation efforts, differences in biodiversity across an area often need to be assessed (Groombridge, 1992). There has been controversy over the meaning of biological diversity, over methods for measuring and assessing diversity as well as the ecological interpretation of different levels of diversity. In the ensuing confusion, Hurlbert (1971) despaired, declaring diversity to be a nonconcept. However, his despair proved premature, and when carefully defined according to an appropriate notation, diversity can be as unequivocal as any other ecological parameter (Hill, 1973). The controversy was largely the result of an unreasonable expectation that a single statistic should contain all the information about the assembly of objects that it represents (Huston,

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1994). Unfortunately, when we look for a suitable numerical definition, we find that no particular formula has pre-eminent advantage, and that different authors have plausibly proposed different indices (Hill, 1973; Magurran, 1988). Because no single statistic can ever be an adequate description of the diversity of a collection, several statistics should always be provided to represent the collection more completely (Huston, 1994). Regardless of the statistics that are chosen to describe diversity, it is critical that the sample be collected using a statistical design that will allow a reliable estimate of the properties of the community that are relevant to the diversity issue being studied (Magurran, 1988).

The concept of diversity has two statistical properties and two unavoidable value judgements. The statistical properties are the number of species in a given sample and the relative numbers (individuals) of each different type of species. The value judgements are whether the species are different enough to be considered distinct and whether the individuals are similar enough to be considered the same. The number of species in a sample (species richness) can provide a good definition of biological diversity. However, the great range of diversity indices and models, which go beyond species richness, is evidence of the importance of the relative abundance of species (Magurran, 1988). The relative number of individuals comprising each species is usually referred to as 'evenness', because the more even the number of individuals, the greater the perceived diversity (Huston, 1994). Thus, ecologists have devoted considerable effort to developing various indices of diversity that combine two distinct statistical components, species richness and their relative population densities, in a single number (Brown, 1988). The most frequently used are the Shannon–Wiener index (H′) and the Simpson index (D):

$$H' = -\Sigma p_i \ln p_i \qquad (1)$$

$$D = 1/\Sigma p_i^2 \qquad (2)$$

where p_i represents the fractional abundance of the *i*th species. The derivation, properties and uses of these indices are discussed thoroughly in the ecological literature (Peet, 1974; Pielou, 1975). The maximum diversity ($H_{\max}$) that could possibly occur is found where all species are equally abundant (Magurran, 1988). The ratio of observed diversity to maximum diversity can therefore be taken as a measure of evenness, *E* (Pielou, 1975):

$$E = H'/H_{\max} \qquad (3)$$

Shannon–Wiener and Simpson indices measure different aspects of the partition of abundance between species. Simpson's index, for example, is sensitive to the abundance of the most common species, while Shannon–Wiener index is sensitive to rare species in the sample (Magurran, 1988).

In constructing indices based on the proportion of species, the importance of every species is related to the count of individuals in each species. In other words, it is assumed that all species have an equal weight (e.g. an elephant [*Loxodonta africana*] is equivalent to warthog [*Phacochoerus aethiopicus*] in a count of species present). A commonly used diversity measure that treats species as equal only if their abundances are approximately equal is the rank abundance distribution (Cousins, 1991). Because an objective of the species abundance distribution may be to explain resource use, it is particularly relevant that species differ in their resource demands. Body size is an important species variable defining resource use (Cousins, 1991), and studies on the nutrition of herbivores species have established that large grazers are better suited to handling high biomass (low-quality forage) than smaller species (Prins & Olff, 1998). Thus, the use of the herb layer by large grazing species increases the availability of resources for smaller animals in some ungulate communities (Vesey-Fitzgerald, 1960; Bell, 1971; McNaughton, 1976; Gordon, 1988).

Facilitation has been frequently deduced in African grazing studies because different grazers have various capabilities for exploiting grasslands with different structural properties, species composition and productivity. Hence, relations among herbivores interacting through their food supplies are facilitative in some respects (Vesey-Fitzgerald, 1960; Bell, 1971; McNaughton, 1976). Vesey-Fitzgerald (1960) observed in Tanzania, elephants feeding and trampling the tall grass around the edges of Lake Rukwa thereby providing habitat for buffalo (*Syncerus caffer*), which in turn provide short grass patches that can be grazed by smaller antelopes such as topi (*Damaliscus korrigum*). Thus, the presence of elephants increases the number of grazing herbivores that can live in the Lake Rukwa ecosystem. Bell (1971) described grazing succession amongst large mammals of the Serengeti ecosystem. In certain areas when the dry season starts, zebra (*Equus burchelli*) eat the tough tall grass stems, thereby making basal leaves more available to wildebeest as well as topi, and these in turn prepare the grass sward for Thomson's gazelle (*Gazella thomsoni*). McNaughton (1976) suggested that migrating Thomson's gazelle prefer to feed in areas already grazed by wildebeest because these areas produce young green regrowth not found in ungrazed areas. Another good example of facilitation is provided in Ngorongoro Crater where cattle, donkeys and small stock were removed in 1974. Since that time, plains zebra, common wildebeest (*Connochaetes taurinus*), common eland (*Taurotragus oryx*), Hunter's hartebeest (*Damaliscus hunteri*) and Grant's gazelle (*Gazella granti*) all declined in numbers. However, buffalo sharply increased in numbers after livestock removal (Runyoro *et al.*, 1995). The interpretation might be that cattle and buffalo showed competitive exclusion while the other herbivores were favoured by facilitation (Prins & Olff, 1998). The evidence suggests that the presence of large grazers in ecosystems enhances the nutritive value of forage and facilitates for more selective smaller grazers. Thus when facilitation takes place, small species are prevented from going extinct and such areas are likely to have more species because both selective and unselective grazers coexist (Table 1). Consequently, species richness of grazers should be highest where such facilitation interactions are strongest (Prins & Olff, 1998). Hence, facilitation interactions may form a basis for developing a new diversity measure.

The main objective of this study was to develop a new diversity index for large grazing mammal species that incorporates body size as a component of diversity. The study was carried out at landscape scale (10 × 10 km) because it is at this scale where the consequences of human activities such as ecosystem modification and fragmentation are most dramatic (Halffter, 1998). Hence, most management decisions concerning the conservation of species diversity are made at landscape scale (Bohning-Gaese, 1997).

Methods

The study area and animal species data

Kenya is situated between latitudes 5°40′ north and 4°4′ south and between longitudes 33°50′ and 41°45′ east. The study area covered five rangeland districts, namely, Kajiado, Laikipia, Narok, Samburu and Taita Taveta. The natural vegetation types of these districts are as follows: Kajiado district consists of wooded grassland, open grassland, semidesert bushland and scrub.

Table 1 The average body mass of grazing mammals larger than 10 kg, occurring in Kenyan rangeland. Average body mass of each species is defined as the midpoints of quoted weight ranges and averaged male and female body weights. The grazer species may be categorized from selective to unselective grazers (Caughley & Sinclair, 1994). Small size (<50 kg) species are selective feeders on leaves of bushes and grass while medium species (>100 kg) select high-quality grass leaves. Mixed feeders change from grazing in rainy season to browsing in dry season. Unselective feeders prefer low-quality grass (i.e. high biomass). Body mass data were obtained from Haltenorth & Diller, 1980)

Common name	Scientific name	Body mass (kg)	Feeding method
Steinbok	*Raphicerus campestris*	11.1	Selective
Thomson's gazelle	*Gazella thomsoni*	24.9	Selective
Reedbuck	*Redunca redunca*	44.8	Selective
Impala	*Aepyceros melampus*	52.5	Mixed
Grant's gazelle	*Gazella granti*	55.0	Mixed
Warthog	*Phacochoerus aethiopicus*	73.5	Mixed
Topi	*Damaliscus korrigum*	119	Selective
Wildebeest	*Connochaetes taurinus*	132.3	Selective
Hunter's hartebeest	*Damaliscus hunteri*	134	Selective
Waterbuck	*Kobus ellipsiprymnus*	211	Selective
Grevy's zebra	*Equus grevyi*	408	Selective
Oryx	*Oryx gazella*	203	Unselective
Burchell's zebra	*Equus burchelli*	235	Unselective
Eland	*Taurotragus oryx*	471.3	Unselective
Buffalo	*Syncerus caffer*	631	Unselective
Hippopotamus	*Hippopotamus amphibius*	1900	Unselective
Elephant	*Loxodonta africana*	3550	Unselective

Wildlife is an important feature of the district and is found within Amboseli and Chyulu Game Conservation Area, as well as within defined dispersal areas that consist of group and individual ranchers (Republic of Kenya, 1990). Laikipia district has mainly dry forms of woodland and savanna with no game reserves but most ranches carry abundant wild herbivore species (Mizutani, 1999). Narok district carries variable vegetation cover, that is, moist woodland, bushland or savanna and has one of the world's famous wildlife sanctuaries, Maasai Mara National Reserve. Samburu and Taita Taveta districts are dominated by *Commiphora, Acacia* trees or woodland and perennial grasses such as *Cenchrus ciliaris* and *Chloris roxburghiana*. Samburu has three game reserves, Samburu, Shaba and Buffalo Springs, while Taita Taveta district covers a large portion of Tsavo National Park.

The source of large grazing mammal species (greater than 10 kg) data (1981–97) was the Department of Resource Surveys and Remote Sensing (DRSRS), Ministry of Environment and Natural Resources, Kenya. The systematic reconnaissance flight methodology used by DRSRS for aerial census of animals is fully described by Norton-Griffiths (1978). Statistical analyses to validate DRSRS survey methodology have proved the method to be efficient and the data to be reliable (De Leeuw *et al.*, 1998; Ottichilo & Khaemba, 2001). Topographic maps of scale 1 : 250,000 were used for flight planning and all transects conform to the Universal Transverse Mercator (UTM) coordinate system. The aerial surveys were carried out along transects orientated in an east–west direction and spaced at 5-km intervals. The standard flying height and aircraft speed were 120 m and 190 km h^{-1}, respectively. Two experienced and well-trained observers occupied the rear seats of a high wing aircraft (Cessna 185 or Partenevia) and counted animals that appeared between two rods attached to the wing struts. The field of vision between these rods was calibrated by flying repeatedly across ground markers of known spacing (Ottichilo & Sinange, 1985). The number of animals falling within the survey strips on either side of the aircraft along each 5 km transect segment were counted and recorded into tape recorders by the two rear seat observers. Groups of animals more than ten in number were also photographed. After every survey the tape-recorded observations were transcribed to data sheets, which together with processed photographs were interpreted for herbivore species using 10 × binocular microscopes and an overhead projector. Because our study was executed at landscape scale, the processed data at 5 × 5 km spatial resolution were converted to 10 × 10 km grid cells by averaging. The study focuses on large mammal species that have grass as an important component in their diet and are native in rangeland districts with at least 4 years of survey during the 16-year period (1981–97).

Explanation of the proposed diversity index

The proposed diversity index is based on the hypothesis that grazer species richness will be highest where large grazers are prevalent. From such a basis, high species richness should be expected where both small and large grazers coexist. Hence, a positive relationship between richness and any measure of variation in body size among species is expected. Therefore, two measures of variability, coefficient of variation (i.e. variation relative to the average body weight) and the ratio between the median average body weight and interquartile range were compared in order to identify which measure of variability correlates strongly with species richness and total average abundance.

Prior to calculation of coefficient of variation, average body weight (A) and standard deviation (S) were calculated as:

$$\mathrm{A} = \frac{1}{n}\sum xi \tag{4}$$

$$\mathrm{S} = \sqrt{\frac{1}{n-1}\sum (xi - x)^2} \tag{5}$$

where n is the number of individual average body weights and x_i is individual species average body weight within a sample unit. Therefore, coefficient of variation (CV) that gives the proposed diversity index is derived as:

$$\mathrm{CV} = \mathrm{S/A} \tag{6}$$

On the other hand, before calculating the ratio between the median average body weight and interquartile range, the median (M) was calculated as the midpoint in the ordered list of observations. Subsequently, the 25th percentile (first quartile) and 75th percentile (third quartile) were calculated as the median of the observations whose position in the ordered list is to the left and right, respectively, of the location of the overall median. The distance between the quartiles, interquartile range (IQR), is the measure of spread that gives the range covered by the middle half of the data. In this case, the ratio that gives the proposed diversity index is derived as:

$$\mathrm{IQM} = \mathrm{IQR}/\mathrm{M} \qquad (7)$$

Testing the proposed diversity index

The performance of the proposed diversity index on range of data sets was tested by two approaches (Magurran, 1988). First, because species diversity of any group of taxa generally increases as the total population of the group increases (Diamond, 1988), the proposed diversity index was correlated with total average abundance. The latter was calculated per grid cell (10 × 10 km) as the total number of all individuals observed divided by total number of survey years. Second, correlating the proposed diversity index with Shannon–Wiener and Simpson's indices, evenness and species richness tested the aspect of diversity that the proposed index is measuring as well as circumstances where the new diversity index is different from conventional indices. The number of grazer species was counted in 10 × 10 km sample units for districts, Kajiado, Laikipia, Narok, Samburu and Taita Taveta to give a value for total species richness. In addition, the total average abundance, Shannon–Wiener index, Shannon evenness and Simpson's index were calculated. Regression lines between the independent variable (proposed diversity index) and dependent variables (species richness, total average abundance, evenness, Shannon–Wiener index and Simpson's index) were calculated, as well as 95% confidence intervals.

Results

The two measures of variation in body size among species, coefficient of variation and the ratio between median and interquartile range correlated positively with species richness and total average abundance (Table 2). However, with exception of Samburu district, species richness and total average abundance correlated more strongly with coefficient of variation than with the ratio between median and interquartile range. Hence, coefficient of variation may be taken as a more appropriate measure of grazer diversity in the study districts than the ratio between median and interquartile range.

Although the proposed diversity index is not based on relative abundance of species, its correlation with total average abundance is moderately strong and comparable to conventional indices based on proportional abundance of species such as Shannon evenness, Shannon–Wiener and Simpson's indices (Table 3). Moreover, in Narok district with the highest species richness and abundance of individuals (Table 2) the new index yields stronger correlation with total average abundance than Shannon evenness, Shannon–Wiener and Simpson's indices (Table 3).

The relations between diversity indices were compared in two districts with different levels of species richness and total average abundance (Table 4), that is, Narok district with the highest species richness and abundance of individuals, and Samburu district with the lowest species richness and abundance of individuals (Table 2). The results (Table 4) reveal that the proposed diversity index is more strongly associated with conventional indices in the district (Narok) with the highest species

Table 2 The coefficient of correlation (r) between measures of variation in body size among species and species richness as well as abundance of individuals: species richness (S) versus (vs) coefficient of variation (CV); species richness versus the ratio between median and interquartile range (IQM); log-total average abundance (I) versus coefficient of variation; log-total average abundance versus the ratio between median and interquartile range across five range land districts. *Logab* and *rich* represent the maximum log-total average abundance and maximum species richness in 10 × 10 km while n stands for number of sample points. Significant at $P < 0.001$ is represented by ** while* represents significant at $P < 0.05$, ns = not significant at $P < 0.05$

District	S vs CV	S vs IQM	I vs CV	I vs IQM	*Logab*	*Rich*	*n*
Kajiado	0.525^{**}	ns	0.384^{**}	ns	6.0	11	204
Laikipia	0.649^{**}	0.486^{**}	0.471^{**}	0.280^{*}	5.3	12	81
Narok	0.749^{**}	0.429^{**}	0.637^{**}	0.299^{**}	8.0	13	122
Samburu	0.332^{**}	0.524^{**}	ns	0.460^{**}	4.3	7	87
Taita Taveta	0.566^{**}	0.328^{**}	0.519^{**}	0.318^{**}	5.0	11	161
Pooled data	0.508^{**}	0.363^{**}	0.361^{**}	0.268^{**}	8.0	13	655

Table 3 Coefficient of correlation (*r*) between log-total average species abundance and diversity indices, species richness (S), Shannon–Wiener index (H′), Simpson's index (D), evenness (E), proposed diversity index (CV) across five rangeland districts in Kenya. With exception of ns, which represents not significant at $P < 0.05$, all other correlations are significant at $P < 0.001$, n = number of sample points

District	S	H′	D	E	CV	*n*
Kajiado	0.650	0.505	0.374	0.486	0.384	204
Laikipia	0.779	0.676	0.495	0.657	0.471	81
Narok	0.820	0.586	0.443	0.585	0.637	122
Samburu	0.714	0.548	0.429	0.489	ns	87
Taita Taveta	0.747	0.567	0.403	0.561	0.519	161
Pooled data	0.805	0.637	0.517	0.572	0.361	655

Table 4 Coefficient of correlation (*r*) between diversity measures. The diversity of grazer species in two districts were correlated for five diversity indices, species richness (S), Shannon–Wiener index (H′), evenness (E), Simpson's index (D) and proposed diversity index (CV). Significant at $P < 0.05$ is represented by* while ns stands for not significant at $P < 0.05$, and other correlations are significant at $P < 0.001$. Na and Sa represent Narok and Samburu districts, respectively

	I	H′	D	E	CV		I	H′	D	E	CV
S	0.820	0.761	0.644	0.760	0.749	S	0.714	0.863	0.717	0.713	0.332
	I	0.581	0.443	0.585	0.637		I	0.548	0.429	0.488	ns
		H′	0.899	1	0.436			H′	0.951	0.842	0.240*
			D	0.898	0.368				D	0.803	ns
				E	0.435					E	0.240*
Na					CV	Sa					CV

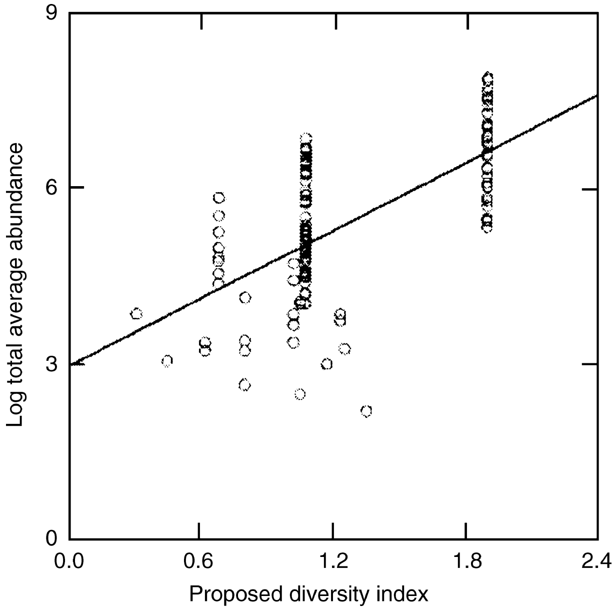

Fig 1 The relationship between proposed diversity index (CV) and log-total average abundance (I) in Narok district ($I = 2.803 + 2.056$ CV, $r^2 = 0.469$, $P < 0.001$)

richness and abundance than in the district (Samburu) with the lowest species richness and abundance. Moreover, the proposed diversity measure gives stronger correlation with measures of richness (species richness and Shannon–Wiener index) than with a measure of dominance (Simpson's index). This indicates that the new index is a species richness measure that takes variation in body size among species into account, as opposed to conventional indices. Fig. 1 shows that straight-line relationship between the proposed diversity index and total average abundance in Narok, which account for 47% of the variance.

Discussion

The proposed diversity index has values ranging between 0 and 3 across the five districts studied. The lowest values (Table 5) are found mainly in the sampling units with less variation in body size among species (i.e. low coefficient of variation). In essence, low values of the proposed diversity index reflect a community where grazer species are more or less similar in body mass. Consequently, resource

Table 5 An example of the grazers' species individual body weights observed in sample units in Narok district. The average body weight (A), median (M), standard deviation (S) and interquartile range (IQR) were calculated per sample unit (10 × 10 km). The proposed diversity index is calculated as average body weight divided by standard deviation, coefficient of variation (S/A) or interquartile range divided by median (IQR/M)

	Grazer species body weights													A	M	S	IQR	IQR/M	S/A
	45	51	53	55	73									55	53	10.5	10	0.19	0.19
25	45	51	53	55	73									50	52	15.6	10	0.19	0.31
	45	51	53	55	73			211	235					103	55	82.5	22	0.40	0.80
25	45	51	53	55	73	119	132	211	235					100	64	73	81	1.27	0.73
	45	51	53	55	73			211	235	471	631			203	73	214	184	2.52	1.05
25	45	51	53	55	73					471	631			176	54	236	28	0.52	1.34
	45	51	53	55	73	119	132	211	235	471	631			189	119	194	158	1.33	1.03
25	45	51	53	55	73	119	132	211	235	471	631			175	96	191	160	1.67	1.09
	45	51	53	55	73	119	132	211	235	471	631	1900	3550	579	132	1026	418	3.17	1.77
25	45	51	53	55	73	119	132	211	235	471	631	1900	3550	539	126	996	418	3.33	1.85

competition is expected to prevail over facilitation interactions leading to low species diversity (Prins & Olff, 1998). Conversely, high values of the proposed diversity index occur in sampling units with a high variation in body size among species (Table 5). This reflects a community where all species with different body weights are represented (i.e. small, medium and large species). In this case, grazing succession is expected to occur where large grazers, which are unselective feeders, remove the tough tall grass thereby making basal leaves available to medium grazers. The medium size grazers in turn prepare the grass sward for highly selective feeders (small species). However, in some cases the high values of the proposed diversity index cannot be attributed to facilitation. For instance, smaller species may join larger grazers to dilute individual predation risks and not to benefit from grazing facilitation. In addition, grazers are water-dependent so the proposed diversity index is expected to be high near water bodies, again independently of grazing facilitation. Furthermore, there tend to be more species of small-bodied species than of large-bodied species (Diamond, 1988) and hence the variations in body size among smaller species are lower than among larger species (Table 5). As a consequence, two large species will give a higher value of the proposed diversity index than two small species even though the richness is not different.

The result (Fig. 1) shows that the proposed diversity index increases with increase in total average species abundance, which is consistent with the ecological rule that species diversity of any higher level taxon generally increases with the group's total population size (Diamond, 1988). This demonstrates that body size may be adequately used as a surrogate for diversity. The proposed diversity index seems to have better performance in the districts with high species richness and high numbers of individuals than in the districts with low species richness and low numbers of individuals. In Narok district with the highest grazer species richness and highest abundance of individuals, the new index yields a stronger correlation (Table 4) with total average abundance than Shannon evenness, Shannon–Wiener and Simpson's indices. Moreover, Table 4 reveals that the proposed diversity index is strongly correlated with conventional indices in the district with the highest numbers of species and individuals. This provides evidence that the proposed diversity index better reflects grazer diversity in areas where species richness and abundance of individuals are higher than in areas where species richness and abundance of individuals are lower. Generally, quantification of biodiversity using indices based on proportional abundance of species in areas with high species richness and high abundance of individuals requires expensive and time consuming counting of individuals per species in each sampling unit. In such areas the new diversity measure may be useful because it is derived from presence–absence data that require relatively less sampling efforts.

The significant positive correlation between the new index and conventional indices (Table 4) shows that the proposed diversity index has the potential to be used in environmental monitoring. For example, adverse effects of pollution will be reflected in a reduction in values of the proposed diversity index, because species with higher body weights are reduced in polluted communities (Magurran, 1988). Moreover, because the new index is based on a measure of variation in body size among species, the degree of difference between species is included in the index. This property has given the proposed diversity index an advantage over species richness and proportional abundances of species indices (Shannon–Wiener and Simpson's indices) that treat species as taxonomically equal. Furthermore, Shannon–Wiener and Simpson's indices combine species richness and relative abundance of species, which is more affected by quantitative variability (Pielou, 1995). Population sizes of grazer species fluctuate enormously from year to year in the study areas, therefore a diversity index based on body size that requires presence–absence data may provide a more effective estimate of biodiversity than diversity indices based on quantitative data that require massive sampling efforts.

Body size is one of the most studied attributes of animal species because it is related to many other species attributes such as longevity, reproductive success, predation, competition and dispersal (Dunham, Tinkle & Gibbons, 1978; Siemann, Tilman & Haarstad, 1996). In addition, body size is easy to measure, so it is a convenient surrogate for these other elusive variables. Hence, knowing the distribution of body size can thus give insights into how other variables might be distributed within taxa or assemblages. Body weights definitely differ between adults and youngsters, but possibly for some species between males and females as well. This is extremely difficult to spot when carrying out aerial survey on a small aircraft, although for elephants it may be possible, and may influence the quantification of biodiversity. However, it is assumed that taking average body weight of each species as the median of quoted weight ranges (young to adult) and averaged male and female body weights (Prins & Olff, 1998) are of sufficient precision for yielding a reliable biodiversity index.

Conclusion

In developing the new diversity index it has been assumed that larger grazer species facilitate for smaller species and hence species richness is expected to be higher in areas where both smaller and larger species coexist. From such a basis, an index derived from measures of variation in body size among species seems to be an appropriate measure of biodiversity because it correlates positively with species abundance from ecological communities (Table 2) as well as other conventional indices (Tables 3 and 4). The fact that the proposed diversity index is based on presence–absence data makes it ideal for rapid appraisal of diversity of herbivores over large areas (Pielou, 1995).

It is known for many groups of animal – birds, mammals and fish – that the distribution of body sizes is skewed, so there are more relatively small species than large ones (Brown, 1995; Nee & Lawton, 1996). In addition, this right skewness has been observed in five orders of insects where basic patterns link species richness, relative abundances and body size (Siemann *et al.*, 1996). Seemingly, the most abundant species among birds, mammals, fish and insects tend to be relatively small in size. Apparently, larger species have larger home ranges and lower densities (Peters, 1983) resulting in smaller local populations. Furthermore, smaller species take up less space than larger species and individuals of smaller species can live in very tiny places, filling ecological niches that would be unsuitable for larger species. Also, small individuals need only small amounts of food to reproduce quickly, and so large numbers can exist in restricted places. As a consequence, smaller species are generally more diverse than larger species (Diamond, 1988). However, for a given taxonomic group (e.g. birds, mammals, fish and insects) species richness should be expected to be high in areas where both small and large species coexist. In view of this, the proposed diversity index may be useful for quantification biodiversity for other taxonomic groups. However, more experiments need to be done to establish the possible merit of the proposed diversity index for other taxa.

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