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Body size and abundance relationship: an index of diversity for herbivores

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Abstract. It is evident to any biologist that small-bodied species within a given higher taxon (order, class, phylum, etc.) tend to be represented by more individuals. Hence small-bodied species are generally more abundant than large-bodied species. We analyzed large herbivore species data collected in Kenyan rangelands. An index of biological diversity derived from the negative relation between animal species body size and its local abundance is proposed. We compared the new index with species abundances at landscape scale (10 × 10 km) in individual districts, as well as in the combined regional data. The results show a consistently strong positive relation between the new diversity index and species abundances. The proposed diversity index has the advantage of incorporating information on species abundances without the need for time-consuming surveys.

Key words: animal abundance, biodiversity indices, body size, large herbivores, species diversity

Introduction

Biodiversity is the sum total of all biotic variation from the level of genes to ecosystems. The challenge comes in measuring such a broad concept in ways that are useful. The most commonly considered facet of biodiversity is species richness – the number of species in a site or habitat. Hence, species are an obvious choice of unit when trying to measure diversity (Purvis and Hector 2000). Many diversity indices have been developed to convey the extent to which individuals are distributed evenly among species. Species diversity indices usually combine two distinct statistical components, species richness and the distribution of individuals among the species (Huston 1994). The best known of these composite statistics are the Shannon–Wiener (H') and Simpson's indices (D) (McIntosh 1967; Peet 1974; Pielou 1975; Magurran 1988).

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

$$D = 1/\sum p_i^2 \tag{2}$$

where p_i is the proportion of the total sample (i.e. of the total number of individuals) composed of species i. Communities with the same species richness may differ in diversity depending upon the distribution of the individuals among the species.

Although as a heterogeneity measure H' takes into account the evenness of the abundance of species, Peet (1974) proposed an additional measure of evenness. Since the maximum diversity ($H_{\max}$) results if individuals are distributed equally among species, the ratio of observed diversity (H') to maximum diversity can be taken as a measure of evenness (E) (Peet 1974; Pielou 1975; Magurran 1988).

$$E = H'/H_{\max} \tag{3}$$

In mammal assemblages, the relationship between body size and population abundance is characteristically negative, that is, larger species have a lower abundance (Damuth 1981; Fa and Purvis 1997). Indeed, across a variety of habitats from different continents, large-bodied mammal species occur at lower densities than small-bodied species, with regression slopes of approximately −0.75 on logarithmically transformed scales (Damuth 1981; Peters and Raelson 1984).

Now assume the number of individuals in each species of a mammal assemblage is sampled. Plotting one point for each species on a graph of abundance against size yields an approximate universal form (Damuth 1981):

$$A = kW^{-0.75} \tag{4}$$

where A is the abundance of a species, W is the average body mass of the species, and different guilds have different values of k, even if they all share a common slope. Furthermore, it has been noted that the species diversity of any group of taxa generally increases as the abundance of the taxa increases (Diamond 1988). A new diversity index (B) is therefore proposed where species diversity is estimated using body mass (Equation (5)).

$$B = \sum_{i=1}^{n} W_i^{-0.75} \tag{5}$$

The performance of the proposed biodiversity index was tested by correlating it with species abundances from ecological communities. This comparison indicates whether the use of body size as a surrogate for diversity is adequate. Moreover, the proposed index was correlated with species richness, evenness, Shannon–Wiener and Simpson indices to assess which component of diversity it measures (Magurran 1988). The proposed diversity index was tested at a landscape scale because most management decisions concerning the conservation of species are made at this scale (Bohning-Gaese 1997).

Methods

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 districts, namely, Kajiado, Laikipia, Narok, Samburu and Taita Taveta (Figure 1). The major national parks and reserves are situated in four of these districts such as Tsavo National Park (Taita Taveta), Amboseli National Park (Kajiado), Masai Mara National Reserve (Narok) and Samburu National Reserve (Samburu). Although Laikipia district does not have game reserves, most ranches carry abundant wild herbivore species (Mizutani 1999).

The large herbivore species were observed from 1981 to 1997 across the five districts in Kenya. The data were obtained from Department of Resource Surveys and Remote Sensing (DRSRS), Ministry of Environment, Kenya. The systematic reconnaissance flight methodology used by DRSRS for aerial census of animals is well documented (Norton-Griffiths 1978). Topographic maps of scale 1:250 000 were used for flight planning and all transects conform to the UTM coordinate system. The aerial surveys were carried out along transects oriented in east–west direction and spaced at 5 km intervals. The standard flying height and aircraft speed were 120 m and 190 km h^{-1},

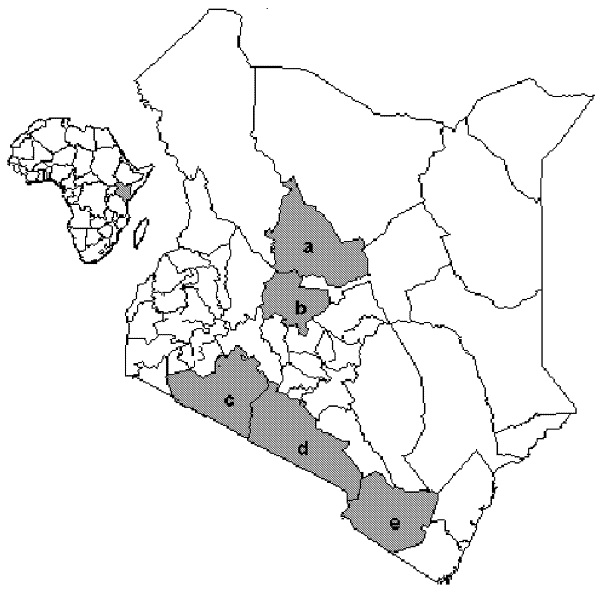

Figure 1. The location of Kenya and the study districts, Samburu (a), Laikipia (b), Narok (c), Kajiado (d) and Taita Taveta (e).

respectively. Two experienced and well-trained observers (Dirschl et al. 1981) 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 and 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 onto tape recorders by the two rear seat observers. Groups of animals more than 10 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 animal species using $10\times$ binocular microscope and overhead projector. Since our study was executed at landscape scale, the processed data at 5×5 km spatial resolution were converted to 10×10 km grid cells.

The study focuses on a group of species exploiting the same class of environmental resource in a similar way – such a group has been termed a guild (Begon et al. 1990). Examples of such classes of environmental resources for herbivores are fruits, seeds, tree leaves, herbs and grasses (Prins and Olff 1998). We have limited our investigation to herbivores heavier than 10 kg and native to Kenya. The average body mass of each species is defined as the mid-points of quoted weight ranges and averaged male and female body weights (Prins and Olff 1998). Body mass data were obtained from Haltenorth and Diller (1980).

Analysis

The sum of the species abundances was calculated in every quadrat (10×10) across the five districts, Kajiado, Laikipia, Narok, Samburu and Taita Taveta. The number of herbivore species present was also counted to give a value for total species richness. In addition, in every quadrat the Shannon–Wiener and Simpson's indices as well as Shannon evenness were calculated (Equations (1–3)). The expected abundance (A) of every species was calculated from their average body mass (W) as:

$$A = W^{-0.75} \tag{6}$$

The abundance (A) is higher in smaller species (e.g. steinbok (*Raphicerus campestris*) 11.1 kg ($A = 0.164$) than larger species (e.g. elephant (*Loxodonta africana*) 3550 kg ($A = 0.002$). Since the estimated species abundance values are fractions, calculating the total (Equation (5)) in every quadrat gives a single value (the new diversity index) which lies between 0 and 1. For smaller species with body mass <1 kg, the diversity index will have values >1, for example, by including shrews (2 g) – the diversity index will range from 0 to $\sim$106. The highest values occur in ecosystems with numerous species of small body mass; large body mass species contribute relatively less to the proposed biodiversity index (Equation (5)). The Pearson Product-moment correlations between the new diversity index and species abundance as well as species richness, Shannon evenness, Shannon–Wiener and Simpson's indices were then calculated at 95% CI.

Results

The response of the proposed diversity index to species abundance is quite good. Table 1 shows that the new index is strongly related to the abundance of individuals compared to diversity measures based on proportional abundances of species such as Shannon evenness, Shannon–Wiener and Simpson's indices.

A comparison of diversity indices (i.e. for two districts known to be rich in large herbivore species, Narok and Laikipia) reveals that biodiversity indices are highly correlated (Table 2). The proposed diversity index yields a stronger correlation with measures of richness (i.e. species richness and Shannon–Wiener index) than with a measure of dominance (Simpson's index) or evenness.

Figure 2 shows the negative relation of herbivores abundance to body size – abundance declines with body mass according to the -0.75 power law. The least-squares fit for the relations between body mass and species abundance accounts for 51% of the variance. The proposed diversity index shows a very strong correlation with species

Table 1. The coefficient of correlation (r^2) between log-species abundances and diversity indices, species richness (S), Shannon–Wiener index (H'), Simpson's index (D), Evenness (E) and proposed diversity index (B) across five districts in Kenya. n stands for number of sample points.

	S	H'	D	E	B	n
Kajiado	0.473	0.273	0.180	0.224	0.392	215
Laikipia	0.586	0.396	0.219	0.410	0.552	81
Narok	0.720	0.152	0.021	0.130	0.703	129
Samburu	0.493	0.283	0.193	0.218	0.336	83
Taita Taveta	0.562	0.313	0.153	0.306	0.400	157
Lumped	0.677	0.374	0.210	0.279	0.633	665

Table 2. Coefficient of correlation (r^2) between diversity measures. The diversity of large herbivore species in two districts were correlated for five diversity indices, species richness (S), Shannon–Wiener index (H'), Simpson's index (D), Evenness (E) and proposed diversity index (B). La and Na stand for Laikipia and Narok districts, respectively.

	H'	D	E	B		H'	D	E	B
S	0.443	0.198	0.403	0.892	S	0.817	0.596	0.816	0.767
	H'	0.842	1.000	0.523		H'	0.851	1.000	0.592
		D	0.796	0.264			D	0.849	0.382
			E	0.483				E	0.565
Na				B	La				B

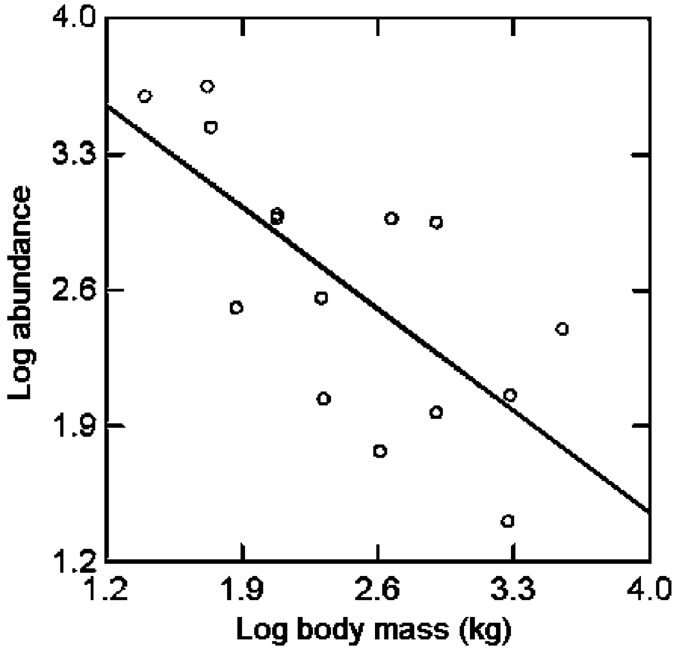

Figure 2. Species abundance ($\log A$) compared with the mean body mass ($\log W$) for 16 large herbivores; each point represents one species. The line represents the least-squares regression line, $\log A = -0.75\ (\log W) + 4.46$; $r = -0.711$, in five districts (Kajiado, Laikipia, Narok, Samburu and Taita Taveta) lumped.

abundance. The straight-line (Figure 3) relationships between species abundance and the proposed diversity index accounts for 63% of the variance.

Discussion

The usual measure of biological diversity using species richness gives equal weight to all taxa, whether there is a single individual or many individuals in a sample. Hence, ecologists have devised diversity indices that weigh the contributions of species according to their abundance, usually discounting rare species to some degree (Hurlbert 1971). Because the abundance of species within samples tend to exhibit regular patterns of distribution, the sample size, species richness and various indices of species diversity are generally interrelated (Schluter and Ricklefs 1993).

The most commonly used diversity measures based on proportional abundances of species are the Shannon–Wiener and Simpson indices. However, these indices are unsuitable for measuring herbivore species diversity over large areas because they require detailed and time-consuming measurement of relative numbers of different species. In addition, relative abundance of species is not a fixed property of species (Groombridge 1992) and hence more affected by quantitative variability (Pielou

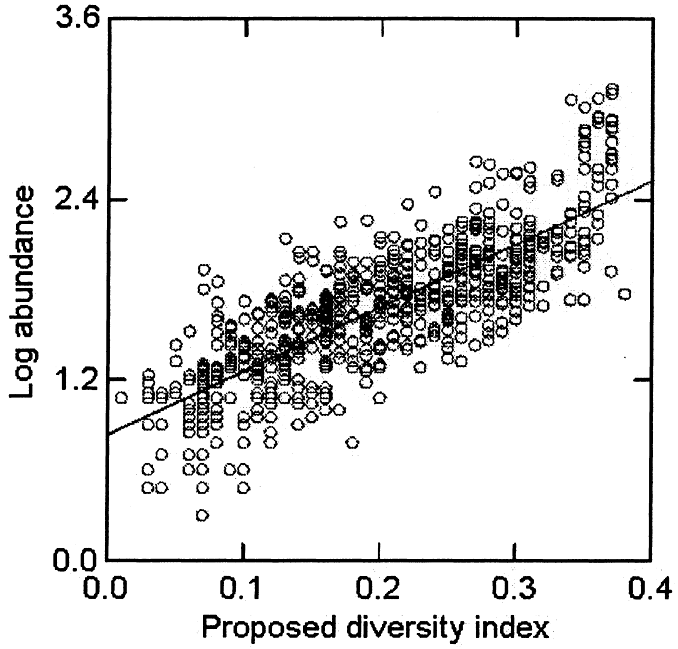

Figure 3. Scatterplots of relation between proposed diversity index (B) and species abundance ($\log A$), $\log A = 4.23B + 0.83$; $r^2 = 0.634$, $n = 665$, $P < 0.05$, in five districts (Kajiado, Laikipia, Narok, Samburu and Taita Taveta) lumped.

1995). Furthermore, biodiversity surveys already take a large proportion of conservation budgets and the demand for them is growing; cost-effectiveness is, therefore, becoming increasingly important (Burbidge 1991).

For rapid appraisals, suitable diversity indices should be based on presence or absence data. Such binary data must be easy to measure and capable of capturing the degree of difference between species. A potential animal species attribute that meets this condition is body size. Animal body size is easy to measure and it is related to many other species characteristics such as longevity, reproductive success, predation, competition and dispersal (Dunham et al. 1978; Siemann et al. 1996).

The proposed diversity index is based on a different kind of community pattern, that is, the inverse relationship between the body size of species and its local abundance (Figure 2). This pattern may be explained by the fact that within an assemblage of animals or a taxonomic group (e.g. birds, mammals, fish), larger-bodied species tend to be rarer (Diamond 1988). Since body size is positively correlated with generation time, large-bodied species will tend to have higher extinction rates resulting in lower speciation rates (Begon et al. 1990). In contrast, smaller-bodied species have lower extinction rates, probably due to high reproductive rates, hence the rate of speciation will be higher (Begon et al. 1990). Moreover, smaller species have a wider range of ecological niches at their disposal, to the extent that they can resolve the natural world at a finer scale.

The performance of the proposed diversity index on a range of data sets is promising (Table 1). The new index's strong relationship with species abundances (Figure 3) indicates that body size may be adequately used as a surrogate for diversity. Moreover, the results (Table 2) show that the proposed diversity index is correlated with other conventional indices. This is in agreement with the observation of Magurran (1988) that diversity indices are often correlated. However, the proposed diversity index is more strongly related to richness measures (species richness and Shannon–Wiener index) than to the dominance measure (Simpson's index). This gives strong evidence that the new diversity index is a species-richness measure. The highest values of the proposed diversity index are found mainly in the sampling units with numerous small-bodied species. Thus, diversity is maximized with species of small body size. A consequence is that a community of 10 steinbok would have a higher index of diversity than 9 steinbok and an elephant. Thus, even though the proposed diversity index has a bias towards small species, it performs well when tested with real ecological data (Table 1).

The main practical advantage of the proposed index over previous ones is that it incorporates information on species abundances without the need for time-consuming surveys. By estimating the abundance of every species from its body mass, differences between species are also incorporated in the proposed index. Moreover, the fact that the proposed diversity index is based on binary data (presence–absence) makes it ideal for rapid appraisal of diversity of herbivores over large areas (Pielou 1995). Since the true value of a diversity measure is determined by whether or not it is empirically useful (Magurran 1988), the significant positive correlation with other indices indicates that the proposed diversity index has the potential of being used in conservation management as well as environmental monitoring (McIntosh 1967).

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