Predicting Mammal Species Richness and Abundance Using Multi-Temporal NDVI

Boniface O. Oindo

Abstract
There is need to map indicators of biodiversity such as species richness and abundance of individuals in order to predict where species loss is occurring. Species richness and abundance have been hypothesized to increase with ecosystem productivity. Moreover, productivity of ecosystems varies in space and time, and this heterogeneity is also hypothesized to influence species richness and abundance of individuals. Ecosystem productivity may be estimated using remotely sensed data, and researchers have specifically proposed the Advanced Very High Resolution Radiometer-Normalized Difference Vegetation Index (AVHRR-NDVI). Interannual average NDVI and its variability (standard deviation) were correlated with large mammal species richness and abundance of individuals at a landscape scale in Kenya. The biodiversity indicators associated negatively with interannual average NDVI and positively with variability of NDVI. Understanding these relationships can help in estimating changes in mammalian species richness and abundance in response to global climate change.

Introduction
Biodiversity, the totality of genes, species, and ecosystems in a region (Stoms and Estes, 1993), is distributed heterogeneously across the Earth. Some regions teem with more biological variation (for example, moist tropical forests and coral reefs) (Morin, 2000), others support lesser assemblages of biological species (for example, some deserts and polar regions), and most fall somewhere in between (Gaston, 2000). Patterns of species richness have been of inherent interest to biogeographers and ecologists (Brown, 1988). Hence, many studies have attempted to explain the geographical variation in the numbers of species that inhabit the Earth (Owen, 1990; Currie, 1991). Today, scientific interests in patterns of species richness are twofold. First, it reflects increased opportunity provided by improvements in available data and analytical tools (Gaston, 2000), and the use of remote sensing technology (to measure vegetation and other environmental variables) (Walker et al., 1992; Stoms and Estes, 1993; Gaston, 2000). Second, it reflects concern over the future of biodiversity, and the resultant need to determine its current status, in order to predict its likely response to global environmental change (Walker et al., 1992; Gaston, 2000).

Species diversity is an emergent property that results from the interaction of the biotic and abiotic elements in the landscape. Consequently, species diversity co-varies with the biotic and abiotic factors that regulate the distribution and abundance of species (Sankaran and McNaughton, 1999).

A key factor is “ecosystem productivity,” defined as the amount of energy captured and transformed into living matter per unit area (Morin, 2000). Because the abundance of individuals increases with ecosystem productivity, species diversity may also increase with productivity (Diamond, 1988). However, this does not always follow logically because there could simply be lots of individuals of a few species (Legendre and Legendre, 1998). In regional biodiversity studies, productivity is usually calculated from weather station records collected at scattered (and often biased) sampling points—these points are extrapolated in order to characterize productivity over a large region (Owen, 1990; Currie, 1991). Such climate-based models assume that the vegetation cover is “natural,” and ipso facto is under the control of climate (Box et al., 1989). However, at a landscape scale, vegetation productivity is also influenced by non-climatic factors including soil nutrient and structure, topography, disturbance, and land use. In view of the fact that satellite remote sensing provides synoptic coverage with more intensive sampling, the maximum normalized difference vegetation index (NDVI) derived from satellite data should provide a more accurate index of actual or current ecosystem productivity compared with climate-based models (Box et al., 1989).

The heterogeneity of an area is strongly (positively) correlated with the number of species that are found in that particular area (Huston, 1994). Factors contributing to the environmental heterogeneity are the spatial or temporal variation in the physical, chemical, or biological features of the environment that create different conditions (or niches) that species can preferentially exploit (Morin, 2000). Hence, species diversity increases with niche or resource diversity because each species must occupy a distinct niche (Stoms and Estes, 1993). Because species diversity of any given group of taxa generally increases with the group’s total population size (Diamond, 1988), it follows that abundance of individuals also increases with niche or resource diversity. It has been proposed that the within-region variability of NDVI values, as defined by the standard deviation of NDVI, may be used to estimate the heterogeneity of ecosystem productivity (Walker et al., 1992).

Seasonal variations in climate are responsible for differences in plant species growth and establishment patterns, leading to changes in species composition and distributions (Hobbs, 1990). Thus, yearly variations in vegetation can take the form of changes in the spatial distribution of plant growth (Tucker et al., 1986). The interannual variation of the maximum NDVI (per month, per season) can be used to assess whether vegetation cover over the years is seasonally changing or is constant. For example, calculating the standard deviation for a number of years may describe the seasonal variation of vegetation cover for an Advanced Very High Resolution Radiome-
ter (AVHRR) NDVI image pixel. Hence, image pixels with a high standard deviation within a geographic area would likely contain high temporal niche differentiation (Begon et al., 1990), and should therefore have a positive relationship with species richness and number of individuals. Therefore, this paper aims to examine the relationships between interannual maximum NDVI variables (average and standard deviation) and species richness of large mammals as well as abundance of individuals in Kenya. The study was executed at landscape scale (10 by 10 km)—a scale appropriate for management decisions concerning the conservation of species diversity (Bohnig-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 (Figure 1). The study area encompasses five rangeland districts of Kenya with diverse landforms ranging from highland moors to savanna grasslands to coastal plains, and the analyses were carried out on individual district data, as well as on the combined regional data.

The mammal species (herbivores with body weight greater than 4 kg) data collected from 1982 to 1993 were obtained from Department of Resource Surveys and Remote Sensing (DRSRS), Ministry of Environment and Natural Resources, Kenya. The aerial surveys were conducted twice a year—during the wet season and dry season—primarily to gather data on species abundance and distribution in different seasons. The systematic reconnaissance flight methodology used by DRSRS for aerial census of animals is fully described by Norton-Griffiths et al., 1990). Topographic maps at a scale of 1:250,000 (UTM) 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 oriented in an east-west direction and spaced at 5-km intervals. The standard flying height and aircraft speed were 120 m and 190 km/hr, 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 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 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 a 10× binocular microscope and overhead projector. Because our study was executed at landscape scale, the processed data at a 5- by 5-km spatial resolution were converted to 10- by 10-km grid cells by averaging. The study focused on large mammal species that are non-migratory in five rangeland districts (Figure 1) with at least four years of survey during the 11-year period (1982–1993). The number of large mammal species was counted in every grid cell (10 by 10 km) to give a value for total species richness. In addition, within the each grid cell of 10 by 10 km, the average number of individuals was estimated as the total number of individuals observed divided by total number of survey years.

NDVI Dekads Data

The AVHRR-NDVI data were derived from images collected by the National Oceanic and Atmospheric Administration (NOAA) satellites, and processed by the Global Inventory Monitoring and Modeling Studies (GIMMS) at the National Aeronautics and Space Administration (NASA). A complete record for Africa exists from August 1981 until the present at a 7.6-km resampled resolution (Los, 1996). NDVI is a measure derived by dividing the difference between near-infrared and red reflectance measurements by their sum (Sellers, 1980): i.e.,

\[ \text{NDVI} = \frac{\text{NIR} - \text{R}}{\text{NIR} + \text{R}} \]  

where NIR is the near-infrared measurements and R is the visible red measurements. High positive values of NDVI correspond to dense vegetation cover that is actively growing, whereas negative values are usually associated with bare soil, snow, clouds, or non-vegetated surfaces. Cloud contamination and other atmospheric effects, along with some effects of sensor geometry, attenuate the value of NDVI and contribute to a greater error in the signal. To minimize the effect of cloud and atmospheric contamination, dekad (10 days) temporal composites of NDVI are developed by choosing the maximum NDVI value for each individual pixel location (Holben, 1986). Additionally, differences of bare soil reflectance may cause large NDVI variations. However, differences in soil reflectance were presumed to cause less variation of NDVI values because time series data were analyzed for the same pixel area. Moreover, because Kenya experiences a bimodal rainfall distribution with peaks in April and November, it has two growing seasons. The interannual maximum NDVI used in this study generally represents NDVI at the height of the growing seasons (Lewis et al., 1998) when vegetation cover is present and adequate across the study area.

The interannual comparisons of AVHRR-NDVI data incorporating data for more than one year is desirable because of the substantial variations from year to year that occur in the extent and timing of photosynthetic activity (Townshend and Justice, 1986). Hence, the study aims at measuring ecological variations within pixels in such a way that regions affected by occasional droughts or erratic changes in the timing and strength of rains

Figure 1. Locations of study districts within Kenya. (a) Samburu. (b) Baringo. (c) Laikipia. (d) Narok. (e) Kwale.
could be separated from those where the impact of such anomalies is slight. Because the total species richness and abundance of a region may be constrained by distinct dry or cold seasons (Fjeldså et al., 1997), it is important to quantify the anomalous events such as droughts or interannual differences in the timing and strength of rains. This was done by aggregating dekads to their appropriate months, calculating the standard deviation of maximum NDVI for each month over the 11-year period, and then averaging the standard deviations for all 12 monthly NDVI values over the 11-year period (same for average NDVI). Thus, the variability over an 11-year period (1982 to 1993) of monthly NDVI values represents temporal variation of productivity.

The historical image products of Kenya (ADDS, 2000) comprising 396 dekads of maximum NDVI were downloaded from website (http://edcsnw4.cr.sgs.gov/bin/staform/a=ndvi/b=ke) 24 February 2000). These historical NDVI products are statistical summaries (i.e., average or maximum NDVI) for the historical time period (1982–1993), and, hence, there is no significant influence from cloud contamination. Because dekads span from the 1st to the 10th, the 11th to the 20th, and the 21st to month end, a year has 36 dekads (i.e., three dekads multiplied by 12 months). Hence, 396 dekads (i.e., 36 dekads multiplied by 11 years) correspond to an 11-year time period. This implies that each month over an 11-year period has 33 dekads (i.e., three dekads multiplied by 11 years). By using the Windisp 3.5 time series data processor (Pfirman et al., 1999), monthly average NDVI \( v_{im} \) was computed for each of the 12 months over the 11-year period as

\[
v_{im} = \frac{1}{n} \sum_{n=1}^{33} p_n
\]  

where \( p \) is the individual pixel values (i.e., for all 33 dekads maximum NDVI images) and \( n \) is the number of dekads. Calculating the average NDVI for all 12 monthly values produced the interannual average NDVI image (Figure 2a). The monthly standard deviation of NDVI \( \text{SD}_m \) was also calculated for each of the 12 months over the 11-year period as

\[
\text{SD}_m = \sqrt{\frac{1}{n-1} \sum (x_i - v_i)^2}
\]

where \( n \) is the number of observations (i.e., 33 dekads), \( x_i \) is the observe value for pixel \( i \), and \( v_i \) is the average NDVI for individual pixels. Calculating the average standard deviation for all 12 monthly, NDVI values produced the standard deviation of the NDVI image (Figure 2b).

The coordinates of the sample units containing species were then geometrically conformed to the same geographic coordinate system as the NDVI images. Because the spatial resolution of the species data (10 by 10 km) was different from the NDVI data (7.6 by 7.6 km), the point maps representing species data were overlaid on the NDVI raster images. For every grid cell of 10 by 10 km of species data overlaid on the interannual average NDVI image (Figure 2a) and standard deviation of NDVI image (Figure 2b), the mean values of average NDVI as well as standard deviation were computed. The interannual maximum NDVI variables (viz. average NDVI and standard deviation)

**Figure 2.** Spatial distribution of interannual (1982–1993) maximum NDVI variables in Kenyan rangeland districts. (a) Average NDVI image. (b) Standard deviation image.

<table>
<thead>
<tr>
<th>District</th>
<th>Variable</th>
<th>Species Richness</th>
<th>Number of Individuals</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baringo</td>
<td>A</td>
<td>-0.612</td>
<td>-0.489</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.662</td>
<td>0.576</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.835</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td>Laikipia</td>
<td>A</td>
<td>-0.513</td>
<td>-0.314</td>
<td>80</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>ns</td>
<td>ns</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.729</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kwale</td>
<td>A</td>
<td>-0.620</td>
<td>-0.552</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.527</td>
<td>0.217</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.847</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Narok</td>
<td>A</td>
<td>-0.340</td>
<td>ns</td>
<td>97</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.608</td>
<td>0.479</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.680</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Samburu</td>
<td>A</td>
<td>ns</td>
<td>ns</td>
<td>125</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.722</td>
<td>0.613</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.612</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combined</td>
<td>A</td>
<td>-0.195</td>
<td>-0.199</td>
<td>378</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>0.223</td>
<td>0.204</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I</td>
<td>0.567</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 1.** Coefficient of Correlation (r) Between Variables: Inteannual Maximum NDVI Variables (A-Average NDVI, S-Standard Deviation) and Biodiversity Indicators (Species Richness and Number of Individuals) as well as Species Richness and Number of Individuals (I) in Five Districts of Kenya. Combined Represents all the Five Districts Analyzed Concurrently, as STANDS for Correlation not Significant at \( p < 0.05 \) Confidence Intervals, while \( n \) is the Number of Sample Points

PHOTOGNAMETRIC ENGINEERING & REMOTE SENSING
were extracted using lower left corner coordinates of the sample unit. Thus, each sample unit finally contained four variables—NDVI variables (average and standard deviation) and biodiversity indicators (number of individuals and species richness). Regression lines between the dependent variables (biodiversity indicators) and the independent variables (NDVI variables) were calculated, as well as the 95 percent confidence interval.

Results
Table 1 shows that the interannual average NDVI has a negative correlation with species richness and number of individuals, whereas the standard deviation of NDVI showed a positive correlation with biodiversity indicators.

Plots of interannual average NDVI against species richness and number of individuals reveal a unimodal pattern (Figures 3a and 3b) where the number of species and individuals increase at intermediate levels of interannual average NDVI but decrease at both lower and higher levels of interannual average NDVI. In addition, the relationships between the standard deviation of NDVI and species richness and number of individuals at regional scale roughly show a unimodal pattern (Figures 3c and 3d), though the data points are relatively more dispersed. The relation between species richness and number of individuals in individual district and combined districts data was also investigated. Table 1 shows that species richness is positively correlated with the number of individuals, confirming the ecological rule that species diversity of any higher level taxon generally increases with the group's total population size (Diamond, 1988).

Furthermore, Table 1 reveals that maximum NDVI variables are more strongly correlated with species richness than with the number of individuals. Presumably, in assemblages of biological species, there are generally several species represented...
by a few individuals, and a few species that are very abundant (Legendre and Legendre, 1998). This could have contributed to the dispersion of data points that most likely reduced the strength of association between number of individuals and NDVI variables (Figures 3a and 3b).

The three-dimensional plots (Figures 3a and 3b) demonstrate that, at regional scale, species richness and number of individuals are higher at intermediate levels of interannual average NDVI and standard deviation of NDVI. The species richness and number of individuals are high in regions where interannual average NDVI is less than 0.55 and the standard deviation of NDVI is more than 0.03 (Figures 3a, 3b, 3c, and 3d) while, in the Kwale district, Figure 5 illustrates that species richness and abundance of individuals are higher in areas where interannual average NDVI is less than 0.40 and the standard deviation of NDVI is more than 0.03.

**Discussion**

The species diversity of natural communities is hypothesized to either increase or decrease monotonically with ecosystem productivity or to be unimodally related to productivity, with maximum diversity occurring at intermediate levels of productivity (Tilman, 1982; Rosenzweig and Abramsky, 1993). Plots of interannual average NDVI, which is an index of ecosystem productivity, against species richness and number of individuals (Figures 3a and 3b) demonstrate a unimodal relationship. The species richness and number of individuals are highest at the intermediate levels of interannual maximum average NDVI. Apparently, intermediate levels of average NDVI coincide with environments with intermediate levels of productivity (Box et al., 1989) that support high production of grass resources. In turn, this enables more individual organisms to coexist, and thus more species at abundances that make it possible for them to maintain viable populations that over time allows an increase in species richness and number of individuals (Gaston, 2000). Moreover, at intermediate levels of productivity, predators (carnivores) can maintain diversity among prey by reducing interspecific competition (Morin, 2000). This mechanism breaks down in low- and high-productivity environments, where predators are, respectively, too infrequent to thin their prey or so numerous that only the best defended prey persist (Morin, 2000).

Furthermore, natural ecosystems with low productivity environments lack niche or resource diversity to allow various species to coexist (Stoms and Estes, 1993), encouraging species adapted to the more productive niche to dominate the community, thereby decreasing overall species diversity (Kassen et al., 2000) and, hence, abundance of individuals. In higher productivity areas, resource diversity declines due to increased production of woody species, which in turn reduces the primary production of grass resources (because of shading by trees) (Prins and Olff, 1998). Consequently, the reduced variety of resources results in more individuals per few species (Begon et al., 1990) rather than more herbivore species.

Although the unimodal patterns suggest that productivity is a primary factor determining species richness and number of individuals, productivity could simply be correlated with factors that actually generate diversity. One such factor may be temporal variation of productivity (Morin, 2000), in this case estimated from the standard deviation of NDVI. Presumably, variability in maximum NDVI represents a seasonally changing environment where different species may be suited to conditions at different times of the year. Hence, more numbers of species and individuals might be expected to coexist in a seasonal environment than in a completely constant one (Begon et al., 1990)

Some investigators suggested that, when the entire range of productivity is considered, species richness is highest at intermediate levels. Tilman's (1982) model of the number of plant species that can coexist competitively on a limited resource base, Abramsky and Rosenzweig (1984), using rainfall as an index of productivity, were consistent with Tilman's (1982) model for the relationship between species richness of rodents and productivity in the Israeli arid lands. They showed that species richness of rodents reached a peak at moderately low productivity, then declined as resources continued to increase. Tilman's (1982) model offers a way to reconcile the conflicting findings reported in the literature on the relationship between productivity and species richness. Both positive and negative responses of richness to productivity may be expected among different ranges, perhaps taxon specific, of productivity values (Owen, 1990). If the hump-shaped model of Tilman (1982) is general in scope, then the differing relationship between richness and productivity reported in the literature may reflect only sampling from different slopes of a fundamental richness-productivity function (Owen, 1990). In the present study where the range of interannual average NDVI (productivity) represented is 0.29 to 0.63, the response of large mammal species richness and abundance to ecosystem productivity is at least consistent with the predictions of Tilman's (1982) model.

**Conclusion**

This study has provided an assessment of multi-temporal reflectance data for the purpose of predicting large mammal species richness and abundance of individuals. The results demonstrate that AVHRR-NDVI data can provide temporal quantitative information on vegetation reflectance that can be used to estimate relevant environmental factors influencing patterns of species richness and abundance of individuals. However, the predictive power of NDVI variables was relatively weak — with a few exceptions (Table 1). In addition, only a relatively small number of mammals were studied. It is believed that using finer pixel resolution imagery and increasing sample size of the number of species studied may improve the accuracy of the results. In the future, as finer pixel-resolution satellite images become available at a frequency similar to NOAA AVHRR imagery, the mix of surface types in each pixel will be reduced (Box et al., 1989), thereby increasing the accuracy of results at the landscape level. Until then, AVHRR-NDVI data remain the most useful imagery available for monitoring vegetation (Tucker and Sellers, 1986) and predicting mammal species richness as well as abundance of individuals at a landscape scale in Kenya.

**Acknowledgment**

The financial support of The Netherlands Government Fellowship Program through the International Institute for Aerospace Surveys and Earth Science (ITC) is highly acknowledged for the success of this research. Appreciation goes to H. Mwendwa, Director of Department Resource Surveys and Remote Sensing, Ministry of Environment, Kenya (DRSRS) for providing animal species data. The USAID/FEWS Project provided the AVHRR-NDVI time series images, which were accessed through the Internet.

**References**


Figure 4. Three-dimensional relationships among variables in the districts (Baringo, Kwale, Laikipia, Narok, and Samburu) analyzed as lumped data set: Interannual average NDVI (INDVl) versus standard deviation of NDVI versus (a) large mammal species richness and (b) number of individuals.

Figure 5. Maps of Kwale district at spatial resolution of 10 by 10 km showing the distribution of (a) number of large mammal species, (b) average number of individuals, (c) interannual average NDVI, and (d) standard deviation of NDVI in the period 1982 to 1993.


(Received 17 April 2001; accepted 28 September 2001; revised 16 October 2001)