Abstract – Measuring the complexity of species in (semi) natural environments is time consuming and expensive. In this paper we summarise remote sensing techniques developed for mapping and monitoring biodiversity of herbivores and vegetation. In particular, methods involving interannual variation of NDVI with respect to mammal and bird species richness in Kenya will be described. We show it is possible to predict species richness at a regional scale using NDVI derived from NOAA satellites, and that these relationships are unimodal. Further work relating species richness to climate parameters showed that these relationships are also unimodal. We also show that climate parameters are better predictors of species richness than NDVI alone.

I. INTRODUCTION

Biological diversity is defined as the variability among living organisms from all sources including inter alia, terrestrial, marine, and other aquatic ecosystems, and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems. As the living world is mostly considered in terms of species, biological diversity is commonly used as a synonym of species diversity, in particular of 'species richness', which is the number of species in a site or habitat (Groombridge, 1992). Explaining patterns of species diversity at the species level is one of the most complex problems in ecology because diversity is usually the outcome of many contributing factors whose relative importance varies with spatial and temporal scale (Diamond, 1988).

The relationship between diversity and productivity has been the subject of a longstanding debate in ecology. The productivity hypothesis predicts that when resources are abundant and reliable, species become more specialized, allowing more species per unit area. In the last decade NDVI has been related to the distribution of both plant and animal species diversity. Walker et al. (1992) correlated plant species richness to aggregated NDVI in California, while Jorgensen and Nohr (1996) related bird diversity to landscape diversity and biomass availability in the Sahel. However, empirical evidence shows that higher productivity can be either negatively or positively correlated with species richness. In fact, in many systems a unimodal pattern is found, with highest species richness at intermediate levels of productivity; above the point of central tendency species richness decreases as productivity increases, while below the point of central tendency species richness increases as productivity increases (Grime, 1979). A number of explanations of this apparent paradox have appeared (Rosenzweig and Abramsky, 1993), but no single theory has been accepted by ecologists. NDVI has been related to NPP at broad spatial scales (Box et al., 1989; Prince, 1991). The chain of relationships from NDVI to NPP and NPP to species richness encouraged us to investigate whether a relationship could be established between NDVI and species richness.

Various studies have shown that NDVI integrates the influence of climatic variables and other environmental factors (Cihlar et al., 1991). This suggests that NDVI is a better predictor of NAPP and, compared with climatic indices, may reveal a stronger relationship with species diversity. Since NDVI integrates the influence of climatic variables and environmental factors such as soil fertility, it is hypothesized that NDVI would better predict species diversity than would climatic variables.

Spatial heterogeneity is another popular hypothesis use to explain pattern of species richness (Stoms and Estes, 1993). The heterogeneity hypothesis states that diverse ecosystems support richer assemblages of biological species compared with simple ecosystems (Podolsky, 1994). The within-region variability of NDVI values, for instance defined as the standard deviation of maximum NDVI, should relate to the heterogeneity of habitats, and have a positive relationship with species richness of mammals and plants.

NDVI is based on the spectral properties of green vegetation contrasting with its soil background. This index has been found to provide a strong vegetation signal and good spectral contrast from most background materials. NDVI is a measure derived by dividing the difference between near-infrared and red reflectance measurements by their sum. NDVI provides an effective measure of photosynthetically active biomass (Tucker and Sellers, 1986). NDVI has been shown to be well correlated with climate variables including rainfall and evapotranspiration in a wide range of environmental conditions (Justice et al., 1986; Cihlar et al., 1991). NDVI may therefore be considered to represent the integration of climatic variables at a given location and time (Anyamba and Eastman, 1996).

National Oceanic and Atmospheric Administration (NOAA) AVHRR data have been used to document interannual variation in vegetation in Sub-Saharan Africa (Tucker et al., 1986). Although the AVHRR-NDVI data are normally of low spatial resolution (1 km at best, but more typically 7.6 km), they possess a remarkably high temporal resolution. Images are commonly dekadal (every ten days) or monthly; they thus provide a very effective source for the examination of intra- and interannual climatic variations (Anyamba and Eastman, 1996). Yearly variations in vegetation can take the form of changes in the spatial distribution of plant growth (Tucker et al., 1986), or may involve differences in species dominance from year to year (Pitt and Heady, 1978).

The interannual variation of the maximum NDVI can be used to assess whether vegetation cover over a number of years is actually stable in an area, or highly variable. For example, calculating the standard deviation for a number of years describes the variability of vegetation cover for an AVHRR-NDVI image pixel. Pixels with high standard deviations correspond to areas with large variations in vegetation composition and growth. Such areas are likely to have diverse habitats that may support richer assemblages of species (Podolsky, 1994). However, there are numerous examples of communities with high species diversity in...
environments with large variation in vegetation composition and growth which are unpredictable, unstable or frequently disturbed (Huston, 1994).

The aim of this work is firstly to evaluate whether climate-based or remote sensing based productivity indices better predict species richness. The second aim is to examine the relationships between the species richness of vascular plants and large mammals with interannually integrated maximum NDVI variables at a landscape scale. This article summarizes recent work by Said et al. (2003) as well as Oindo and Skidmore (2002).

II. METHODS

The study area is East Africa - covering Kenya (569,260 km²), Tanzania (886,220 km²) and Uganda (207,950 km²). It is situated approximately between longitudes 12° South and 6° North and latitude 29° West and 42° East. The great diversity of ungulates is one of the most noticeable features of the East African region. Out of 95 ungulate species found in Africa, 55 are found within this sub-region.

The vegetation of East Africa is highly heterogeneous, with great variability in structure and productivity. The productivity is greatly influenced by the spatial and seasonal distribution of precipitation and temperature. The range of precipitation varies between and within the three countries. Uganda has a range of 900 to 1300 mm, Tanzania 600 to 1300 mm, and Kenya 200 to 1300 mm.

A number of data sets were compiled for these studies. Lack of space precludes a description of the methods used, but interested readers are referred to Said et al (2003) and Oindo and Skidmore (2002). The following data sets were generated at a regional scale (1 km pixel): herbivore data on 55 species (Boitoni et al, 1999); climatic, soils and land cover data from the ACTS database (ACTS, 1994); solar radiation; multidate AVHRR imagery used to calculate NDVI generated from the African Data Dissemination Service (ADDS) and Global Inventory Monitoring and Modelling (GIMMS).

III. RESULTS

Figure 1 shows the relationship between species richness and four indices of environmental productivity for 55 ungulate mammal species in East Africa. The relationship between species richness and NDVI and rainfall is unimodal. The relationship between species richness and rainfall/potential evapotranspiration is linear and negative.

A similar unimodal pattern can be seen in data from Kenya at a district level (Narok district), for all mammals with a body mass greater than 4 kg observed by aircraft (Figure 2). Figure 2(a) shows mammal species richness against integrated maximum average NDVI, while 2b shows the coefficient of variation.

Continuing the exploration of species richness with vegetation data sets (instead of mammals), it can be seen that plant species richness is also related to mean NDVI and the coefficient of variation of NDVI, but exhibits a negative curvilinear relationship.
We then explored the relationship between mean NDVI and rainfall and uncovered a positive curvilinear relationship (NDVI = -0.7725 + 0.1613Ln(P), p < 0.0001, r² = 0.87, n = 69), with an asymptote beyond 1300 mm rainfall.

Table 1 summarizes the results of the statistical analysis (regression r²) between species richness and four environmental factors related to net primary production, for 55 mammal species across East Africa. The analysis was undertaken for the whole range of rainfall data (200-1300mm), as well as 2 subsets of the rainfall data (less than 1000 mm as well as 1000-1300 mm). The strongest correlates were rainfall and NDVI with 69% and 55% in the variance of species richness explained respectively. Climate variable (precipitation) is a better explanatory variable for species richness than NDVI, having consistently a higher r² value. Note that non-significant (ns) results from low sample numbers in table 1.

<table>
<thead>
<tr>
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<th>200 – 1300 mm</th>
<th>&lt; 1000 mm</th>
<th>1000-1300 mm</th>
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<tbody>
<tr>
<td>Precipitation</td>
<td>r² = 0.69</td>
<td>r² = 0.77</td>
<td>r² = ns</td>
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<tr>
<td>Temperature</td>
<td>r² = 0.47</td>
<td>r² = 0.66</td>
<td>r² = 0.21</td>
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<tr>
<td>Potential</td>
<td>evapotranspiration</td>
<td>r² = 0.44</td>
<td>r² = 0.56</td>
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<tr>
<td>NDVI</td>
<td>r² = 0.55</td>
<td>r² = 0.67</td>
<td>r² = ns</td>
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Table 1: r² between mammalian species richness and four environmental factors related to net primary production

IV. DISCUSSION

The results from this study reveal that the remotely sensed index was not a better predictor of species richness than integrated climatic indices (Table 1). This is contrary to our initial expectation and contradicts established literature (Nicholson et al., 1990; Walker et al., 1992; Stoms and Estes, 1993; Los, 1998b). The climatic model was more predictive than NDVI in areas with a rainfall range between 200 and 1300 mm; for the drier part of the rainfall gradient (<1000 mm) the difference was not significant. The difference in variance explained by the two models was investigated by reviewing the literature that related NDVI and climatic variables to NAPP. This observation is supported by a number of studies relating species richness to NDVI. Most of these studies have reported lower correlations between plant or mammalian species richness and NDVI (see Walker et al., 1992; Oindo et al., 2000; Oindo and Skidmore, 2002; this study) than those studies using climatic variables as proxy for productivity (refer to Prins and Olff, 1998; Olff et al., 2002).

The species richness in East Africa is best described as unimodal in pattern (refer to Figures 1 - 3). The strongest single factor that best predicted ungulate species richness was rainfall. Contrary to expectations that high productive areas would have high species richness (energy limitation theory - see Wright, 1983), ungulates were highest at the intermediate productivity level. The pattern is consistent with studies on variations in richness (plants and animals) as functions of productivity that show species richness reaches its maximum at intermediate productivity levels (see Grime, 1973; Huston, 1980; Rosenzweig and Abramsky, 1993; Prins and Olff, 1998; Huston, 1999; Olff et al., 2002). The hump-shaped curve of the species richness-productivity relationship appears to be composed of at least two phases: the positive (Kenya) and negative slopes (Tanzania and Uganda) that make up the two sides of the hump-shaped curve, with maximum species richness occurring in both Kenya and Tanzania.

Furthermore, why do maximum levels of species richness of mammals occur at intermediate levels of productivity (maximum average NDVI)? One possibility is that under conditions of low primary productivity in natural ecosystems, there is not much habitat or resource heterogeneity - the landscape is uniformly barren. As productivity rises, the average variety of micronutrient combinations in fertile soils increases (Rosenzweig and Abramsky, 1993). This leads to a more diverse community of plants that can support a greater number of herbivore species. But go beyond a certain point on the productivity gradient and the habitat heterogeneity that support mammalian diversity declines (Rosenzweig and Abramsky, 1993). This leads to the scarcity and low quality of graminaceous resource in forest gaps result in decrease of species richness of mammals (Prins and Olff, 1998). For further discussion and results please refer to Said et al. 2003 as well as Oindo and Skidmore (2002).

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