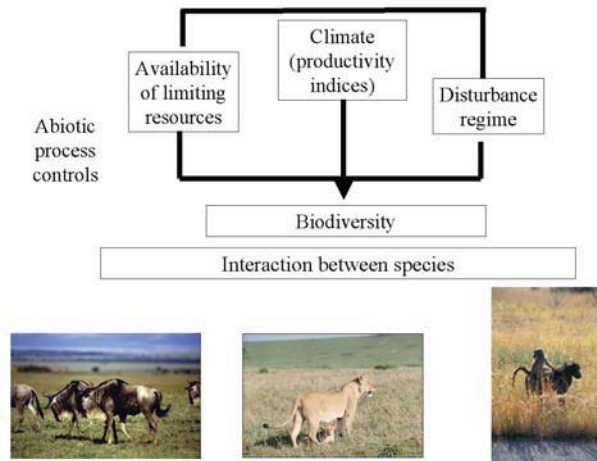


CHAPTER 3

MAMMALIAN SPECIES RICHNESS IN RELATION TO RAINFALL IN EAST AFRICA: DO SIMILAR PATTERNS EXIST AMONG TAXONOMIC GROUPS?

The aim of this study was test species richness – productivity of various taxonomic grouping (based on class, order and family groupings) was similar. In this study we restricted our focus to mammalian species, chose a single productivity variable and conducted the study in East Africa.



Chapter 3

Mammalian species richness in relation to rainfall in East Africa: do similar patterns exist among taxonomic groups?

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Abstract

The aim of this study was to test whether different species groupings had similar species-productivity patterns. We focused our study on East Africa, which to a large extent has retained the full diversity of its large mammal species and covers microhabitats ranging from desert-like conditions to tropical forests. The species richness of the various animal groups (11 orders and 10 families) was regressed against rainfall, using linear, polynomial, logarithmic and exponential models. The study revealed that five out of 11 orders (Artiodactyla, Hyracoidea, Rodentia, Macroscelidea and Carnivora) exhibited a unimodal pattern. The productivity-richness was dependent on taxonomic scale of the investigation, with signs of high variations at lower levels than at the level of orders and class. We conclude that species richness – productivity relationship is clearly scale-dependent. On a sub-continental scale the geographical patterns in species richness were similar among a number species groupings and tended to converge towards the same level (intermediate productivity) especially at the higher taxonomic level. The high variation of patterns at lower taxonomic level may reflect partitioning of energy gradient among families or group of species. This may be a result of different processes controlling richness at different spatial scales for various species groups.

3.1 INTRODUCTION

Studies conducted at sub-continental or continental scale have indicated that productivity and energy flows through an ecosystem are major determinants of species diversity (Abramsky and Rosenzweig, 1984; Owen, 1988; Currie, 1991; Said *et al.*, in press). Additional factors such as resource competition and facilitation (Sinclair, 1975; Sinclair, 1979; McNaughton, 1985; Prins and Olf, 1998), land use change through human

interference (Chaplin *et al.*, 2000; Sala *et al.*, 2000) and climatic disturbances (Sinclair, 1983b; Chaplin *et al.*, 2000) also contribute to variation in species diversity and assemblages of animals at this scale. Literature on the relationship between species diversity and productivity is abundant but often contradictory (see reviews Grace, 1999; Waide *et al.*, 1999), and the general theory has not been consistent (Grime, 1973; Tilman, 1982; Rosenzweig and Abramsky, 1993; Huston, 1994; Abrams, 1995).

Several studies have shown that the choice of geographical and ecological extent, taxonomic hierarchies or indices of productivity can lead to a multitude of patterns (Owen, 1990; Guo and Berry, 1998; Grace, 1999; Waide *et al.*, 1999). Waide *et al.* (1999) in their assessment of more than 200 productivity-diversity relations concluded that it requires careful attention to spatial and ecological scales to detect and understand patterns. A number of studies have addressed the effects of scaling on species diversity, with emphasis on data resolution (Anderson and Marcus, 1993; Bohning-Gaese, 1997) and sampling methods (Moore and Keddy, 1989; Rose and Legget, 1990; Lyons and Willing, 1999). Few studies have examined how groups of animals (based on taxonomic hierarchy) respond to productivity within a biogeographical area (see Currie, 1991; Kaufman and Willing, 1998; Rose and Legget, 1990). Such studies on interactions among the various taxonomic groups may further improve the theoretical framework of species diversity-productivity patterns.

The aim of this study was to test whether different species groupings (based on class, order and family groupings) had similar species-productivity patterns. In this study we restricted our focus to mammals, chose a single productivity variable and conducted the study in East Africa (sub-continental scale). East Africa is a natural experimental area to study species diversity-productivity interactions. It has to a large extent retained the full diversity of its large mammal species (Sinclair, 1995; Prins and Olf, 1998), and encompasses a number of microhabitats, ranging from desert-like conditions to tropical forests (Pratt and Gwynne, 1977).

3.2 MATERIAL AND METHODS

3.2.1 The study area

East Africa is situated approximately between longitudes 12° South and 6° North and latitude 29° West and 42° East. The study area covers Kenya (569,260 km²), Tanzania (886,220 km²) and Uganda (207,950 km²). The vegetation of East Africa is highly heterogeneous, with great variability in structure and productivity (Coe *et al.*, 1976; Pratt and Gwynne, 1977; East, 1984; van Wijngaarden, 1985; McNaughton *et al.*, 1989). The principal modifying factors that control productivity are fire, herbivory and soil nutrient (Bell, 1982; McNaughton, 1985; van Wijngaarden, 1985; Belsky, 1986; Dublin *et al.*, 1990; Sinclair, 1995). The vegetation is composed mainly of open *Acacia* grassland, dwarf shrub grassland and sparsely vegetated xeric grasslands, shrublands, bushlands and montane forests (Pratt and Gwynne, 1977; Bourliere and Hadley, 1983).

Productivity is highly influenced by spatial and seasonal distribution of precipitation (Deshmukh, 1984; McNaughton, 1985; Nicholson *et al.*, 1990). The range of precipitation varies between and within the three countries. Uganda has the highest rainfall

(900 – 1300 mm), with moderate rainfalls in Tanzania (600 – 1230 mm), and Kenya having drier areas (200 – 1300 mm). The three main rainfall patterns in the region are: year-long rainfall (around Lake Victoria), single season rainfall (northern Uganda, northwestern Kenya, most of Tanzania) and bimodal rainfall (rest of Kenya) (Pratt and Gwynne, 1977).

3.2.2 Mammalian and climatic data

Digital data on large mammalian distributions at regional level were acquired from the African Mammal Databank (Boitani *et al.*, 1999). A total of 163 species, belonging to 11 orders and 10 families were included in the analysis (Table 3.1).

Table 3.1: Listing of order, family and the number of species included in the study. The common names for order and family are indicated in brackets. The figures in parentheses are the number of species observed at continent level.

Order	Family	Number of Species	
Artiodactyla (Even-toed ungulates)	<i>Bovidae</i> (Horned antelopes)	51(79)	
	<i>Giraffidae</i> (Giraffes)	2(2)	
	<i>Hippopotamidae</i> (Hippopotamuses)	1(2)	
	<i>Suidae</i> (Pigs)	5(6)	
	<i>Tragulidae</i> (Chevrotains)	1(1)	
Perissodactyla (Odd-toed ungulates)	<i>Equidae</i> (Horses)	2(4)	
Hyracoidea (Hyraxes)	<i>Procaviidae</i> (Rock hyraxes)	5(6)	
Tubulidentata (Aardvark)	<i>Orycteropidae</i> (Aardvark)	1(1)	
Carnivora (Carnivores)	<i>Canidae</i> (Dogs and allies)	5(12)	
	<i>Felidae</i> (Cats)	7(10)	
	<i>Herpestidae</i> (Mongoose)	15(24)	
	<i>Hyaenidae</i> (Hyaenids)	3(4)	
	<i>Mustelidae</i> (Mustelids)	6(10)	
	<i>Viverridae</i> (Genets and civets)	8(15)	
	Insectivora (Insectivores)	<i>Erinaceidae</i> (Hedgehogs)	1(6)
		<i>Tenrecidae</i> (Otter shrews)	2(3)
	Lagomorpha (Hares)	<i>Leporidae</i> (Hares)	
	Macroscelidea (Elephant shrews)	<i>Macroscelididae</i> (Soft-furred elephant shrews)	7(15)
Pholidota (Scaly ant-eaters)	<i>Manidae</i> (Pangolins)	4(4)	
Primates	<i>Cercopithecidae</i> (Monkeys)	16(39)	
	<i>Galagonidae</i> (Bushbabies)	9(12)	
	<i>Hominidae</i> (Man and apes)	2(3)	
	<i>Loridae</i> (Lorisids)	1(3)	
	Rodentia (Rodents)	<i>Hystricidae</i> (Porcupines)	3(3)
	<i>Pedetidae</i> (Spring hares)	1(1)	

The total number of species of these taxa in the study area are as follows: all mammalian species ($n = 163$), Artiodactyla ($n = 60$), Perissodactyla ($n = 2$), Hyracoidea ($n = 5$), Tubulidentata ($n = 1$), Carnivore ($n = 44$), Insectivora ($n = 3$), Lagomorpha ($n = 5$), Macroscelidea ($n = 7$), Pholidota ($n = 4$), Primates ($n = 28$) and Rodentia ($n = 4$). We combined Artiodactyla, Hyracoidea, Perissodactyla, Tubulidentata, Proboscidea (note that

data on the distribution of elephant and rhinoceros were not available) and Sirenia (species absent in the study area) into a larger group: the ungulates or hoofed animals. The second grouping consisted of all herbivore species. We followed the mammalian classification system of Wilson and Reeder (1993).

In this study we used rainfall as a descriptor of productivity. Studies in sub-Saharan Africa have shown that productivity generally relates well to average rainfall (Le Houerou and Hoste, 1977; Deshmukh, 1984; McNaughton, 1985; van Wijngaarden, 1985). In addition, a number of studies have related species richness to rainfall as a measure of productivity in the semi-arid and arid environments (Brown, 1973; Abramsky and Rosenzweig, 1984; Owen, 1988). The rainfall and topographic data were derived from the ACTS database developed by Texas A&M (ACTS, 1994).

3.2.3 Analytical procedures

The species richness was established by overlaying individual species maps with a 3° x 3° regional quadrat map, similar to methods used in studies conducted by Currie (1991), Owen (1990) and Schall and Pianka (1978). Earlier studies of Currie (1991) and Kerr *et al.*, (1998) failed to find any indication that variation in quadrat area have a significant effect on the diversity of any vertebrate, plant, or invertebrate taxa. The total number of species occurring in each quadrat was taken as the species richness for that quadrat. Next, we examined the bivariate plots of species richness and each of the explanatory variables to determine the relationship. Later, we regressed species richness against rainfall, using linear, polynomial, logarithmic and exponential models. A higher polynomial model was fitted if there was a statistical improvement in fit based on the *F*-procedure (Zar, 1996). Tests for independence of the residual (Durbin-Watson test) and normality (Kolmogorov-Smirnov test) were conducted for each model. The statistical analysis was performed in Systat 7.0 (SPSS, 1997).

3.3 RESULTS

Maps of the spatial distribution of species richness of Mammals, Ungulates, Carnivores and Primates are shown in Figure 3.1. Descriptive and correlation statistics for species richness in the quadrat system of Figure 3.1 are as follows: Ungulates ($\bar{x} = 27$, CV = 16) with Carnivores $r = 0.76$, with Rodentia $r = 0.72$, with Primates $r = 0.36$; Carnivores ($\bar{x} = 28$, CV = 7) with Rodentia $r = 0.66$, with Macroscelididae $r = 0.66$, with Primates $r =$ not significant; Primates ($\bar{x} = 10$, CV = 42) with Insectivora $r = 0.75$, with Pholidota $r = 0.72$; Insectivora ($\bar{x} = 2$, CV = 48) with Pholidota $r = 0.80$, with Rodentia $r = 0.56$, with Lagomorpha $r = 0.56$; significant at $P < 0.05$.

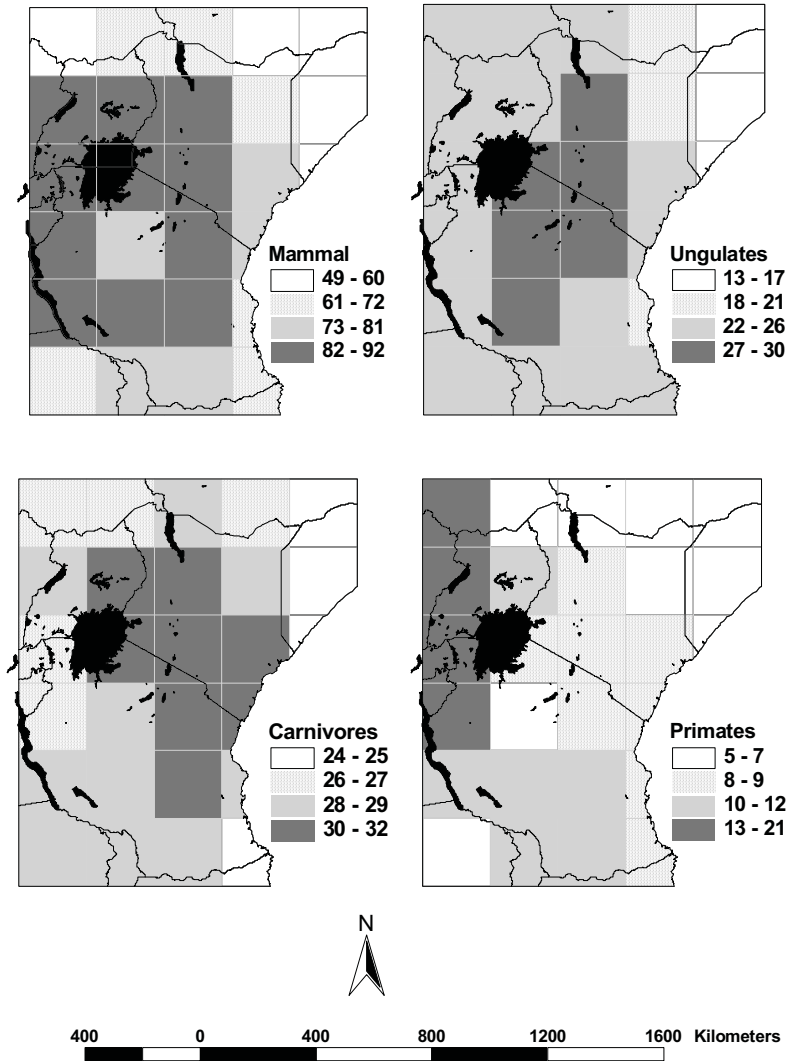


Figure 3.1: Geographical variation in species richness of mammals, ungulates, carnivores and primates in East Africa. Protected areas are symbolized in broken lines, and lakes indicated in continuous black colour. Each map is based on the overlay of species maps aggregated to 3° by 3° grids.

Table 3.2 present a summary of the relation between species richness of various faunal groups and rainfall. The richness of all mammals combined shows a unimodal or a humped-shaped pattern ($y = 14.99 + 0.142x - 0.0000736x^2$, $r^2 = 0.74$, $P < 0.001$, Figure 3.2a). The relationships between rainfall and species richness for five of the 11 orders (Artiodactyla, Hyracoidea, Carnivora, Macroscelidea and Rodentia) show a strikingly similar unimodal pattern (Figure 3.2b-e). The Primates (Figure 3.2f) and Insectivora revealed an exponential pattern. There was no significant relation between species richness and rainfall for the orders Perissodactyla, Tubulidentata, Pholidota and Lagomorpha.

Figure 3.3 shows the relationship between species richness at the lower taxonomic levels of the family (refer to Table 3.2 for the equations). A strong unimodal relationship between species richness and productivity was observed with the Bovidae ($r^2 = 0.81$, $P < 0.001$, Figure 3.3a). Procavidae (Figure 3.3b) and Macroscelididae (Figure 3.2d) showed similar pattern. Figure 3.4 displays combines (orders and family with similar pattern) the relationships between species richness and productivity.

Table 3.2: Models predicting species richness as a function of productivity based on faunal grouping

Taxonomic aggregate			Model	r^2
Class	Order	Family		
Mammalia			$14.99 + 1.42*10^{-1}x - 7.36*10^{-5}x^2$	0.74***
	Ungulate		$-1.32 + 7.67*10^{-2}x - 4.47*10^{-5}x^2$	0.70***
		Artiodactyla	$-0.99 + 6.24*10^{-2}x - 3.63*10^{-5}x^2$	0.69***
		Bovidae	$-6.41 + 6.89*10^{-2}x - 4.04*10^{-5}x^2$	0.81***
		Hyracoidea	$-0.11 + 7.9*10^{-3}x - 4.52*10^{-5}x^2$	0.47**
		Procavidae		
		Perissodactyla		ns
		Tubulidentata		ns
		Rodentia	$-2.55 + 1.27*10^{-2}x - 702*10^{-5}x^2$	0.53**
		Macroscelidea	$-3.63 + 1.63*10^{-2}x - 9.38*10^{-5}x^2$	0.59**
		Macroscelididae		
		Carnivora	$17.74 + 2.76*10^{-2}x - 1.59*10^{-5}x^2$	0.46**
			$5.4128e^{-0.0003x}$	0.32**
		Canidae		
		Felidae		ns
		Herpestidae	$1.4922\text{Ln}(x) - 2.3022$	0.58***
		Mustelidae	$2.1835\text{Ln}(x) - 10.193$	0.66***
		Viverridae	$2.1037\text{Ln}(x) - 8.8128$	0.55***
	Primates		$4.037e^{0.001x}$	0.66***
		Cercopithecidae	$2.192e^{0.001x}$	0.60***
		Galagonidae	$-8.13*10^{-1} + 1.19*10^{-2}x - 6.43*10^{-6}x^2$	0.32*
	Insectivora		$0.6809e^{0.0008x}$	0.36*
	Pholidota			ns
	Lagomorpha			ns

* $P < 0.05$; ** $P < 0.001$; *** $P < 0.0001$

Mammalian species richness in relation to productivity

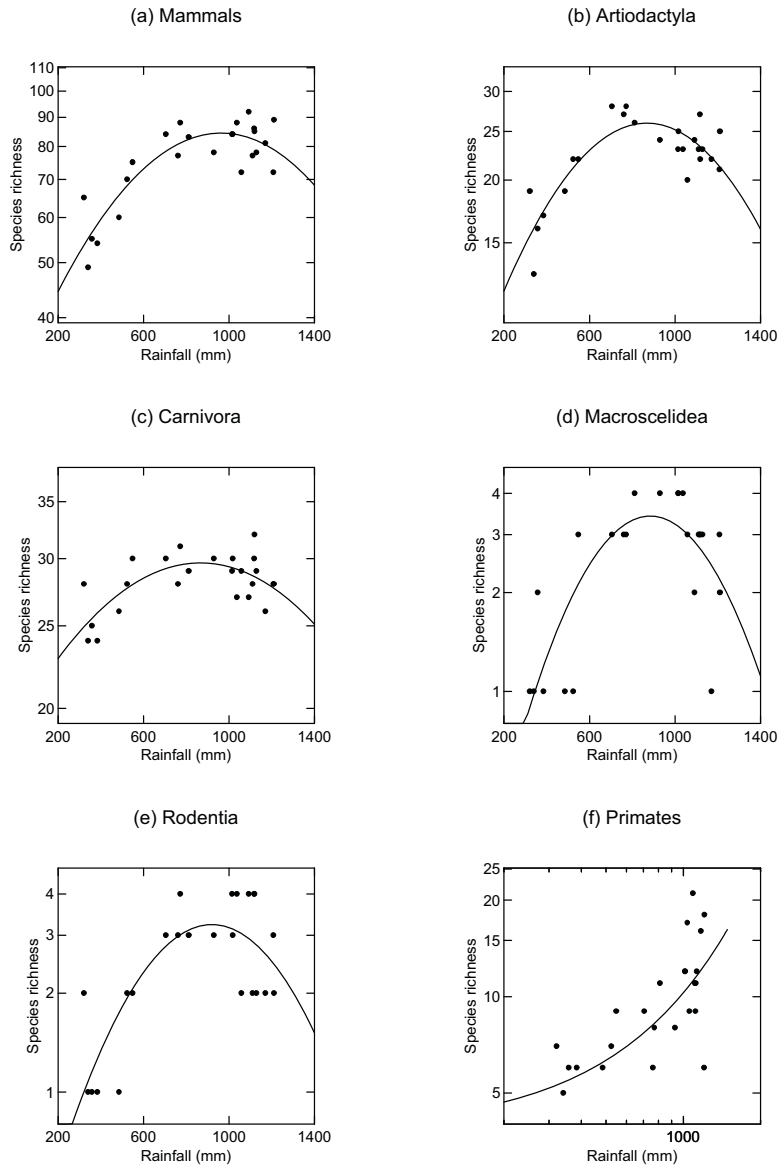


Figure 3.2: Relationship between species richness (at class and order level) and mean annual rainfall (refer to Table 3.2 for the detailed equation for each of the relationships).

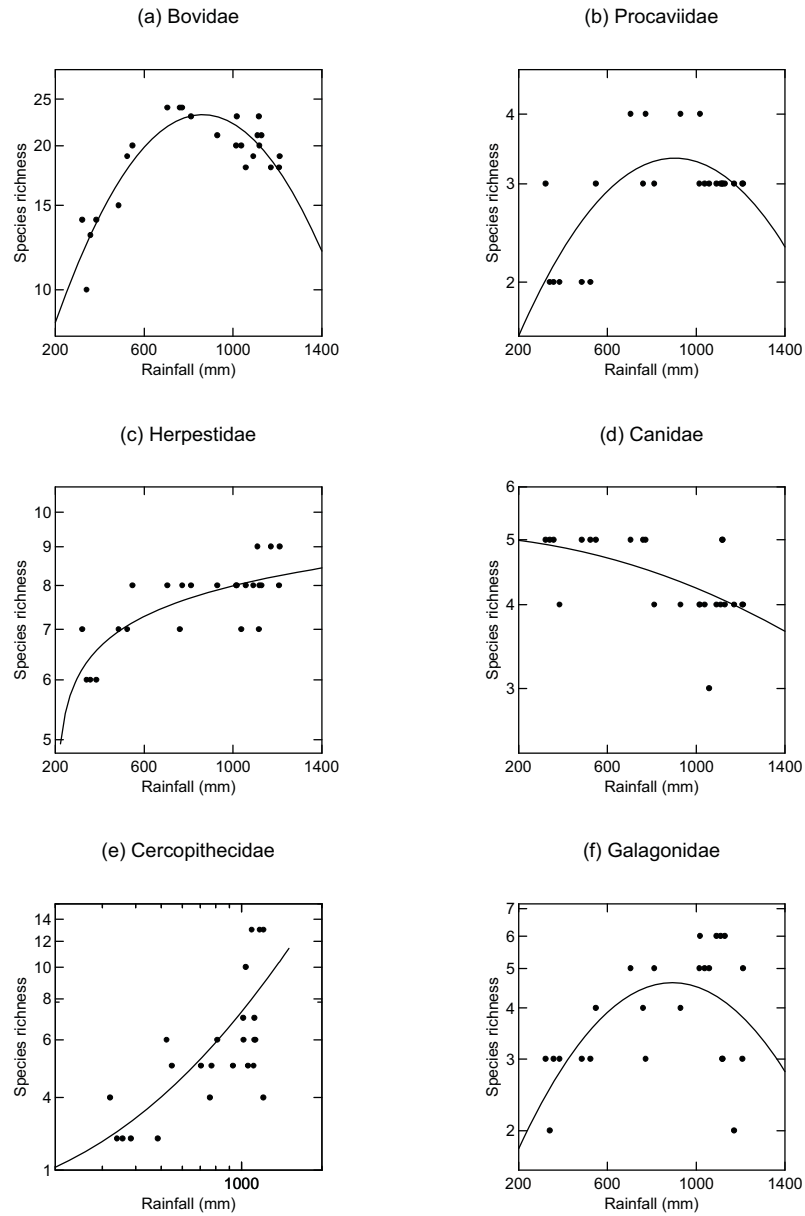


Figure 3.3: Relationship between species richness (family level) and mean annual rainfall (refer to Table 3.2 for the detailed equation for each of the relationships).

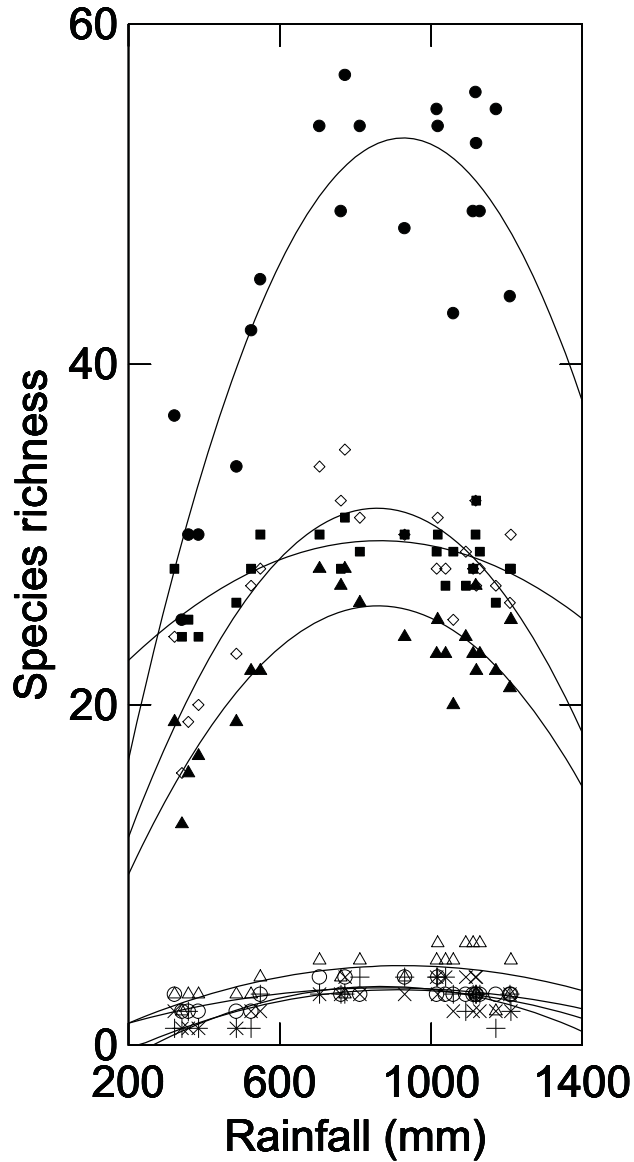


Figure 3.4: Relationship between species richness and productivity showing similar patterns among a number of fauna and taxonomic groups. The following notations represent: all Herbivores (●); Ungulates (◇); Carnivores (■); Artiodactyls (▲); Galagonidae (△), Rodentia (○), Macroscelidea (+), Hyracoidea (x).

The relationship between the second largest group, the Carnivora and productivity was also humped-shaped ($17.74 + 0.027x - 0.0002x^2$, $r^2 = 0.46$, $P < 0.002$, $n = 24$). The five families under the order Carnivora showed two distinct patterns: the species richness of Herpestidae (Figure 3.3c), Mustelidae and Viverridae increased as productivity increased, whereas the species richness of Canidae (Figure 3.3d) and Hyaenidae decreased as productivity increased. The Cercopithecidae or monkeys had an exponential pattern (Figure 3.3e), which was similar to its higher class the Primates, while Galagonidae or bushbabies (lower taxonomic level) showed a unimodal pattern (Figure 3.3f). For the other families the correlation was generally weaker and more variable, with no significant pattern.

3.4 DISCUSSION

3.4.1 Species diversity – productivity patterns

The result of this study shows that species richness had a different response to productivity depending on the species grouping (order and family). Five out of 11 orders (Artiodactyla, Hyracoidea, Rodentia, Macroscelidea, and Carnivora) showed a unimodal pattern. The results are also consistent with the findings of most earlier studies, showing that species richness first rises and then declines with continued increase of biomass (see also Grime, 1973; Huston, 1980; Tilman, 1982; Abramsky and Rosenzweig, 1984; Al-Mufti *et al.*, 1984; Owen, 1988; Rosenzweig and Abramsky, 1993; Prins and Olf, 1998; Huston, 1999; Balmford *et al.*, 2001; Olf *et al.*, 2002). The second important pattern revealed in this study is that the relationship between species richness and rainfall at family level was different for various species group. The pattern of carnivores was more related to food type (Schoener, 1974) than habitat type (for example highly correlated to bovine distribution. At family level the species richness of Herpesitade (Mongoose), Mustelidae (Mustelids) and Viverridae (Genets & civets) increased monotonically with productivity, whilst the Canidae (Dogs & allies) decline monotonically with rainfall. The results for the other family groups (Bovidae, Procavidae, Macroscelididae and Galagonidae or the bushbabies) were consistent with the unimodal pattern.

3.4.2 Trophic levels and secondary interactions

Competition, mutualism and trophic interactions frequently lead to secondary interactions among species (Chaplin *et al.*, 2000). The similarity in patterns in the fauna communities as presented in this study shows that assemblages of species may not be just random and the fauna of any region is attributable to several historical and ecological characteristics. A number of studies have shown that herbivore species diversity varies across gradients of plant abundance and quality (Western, 1975; Coe *et al.*, 1976; Bell, 1982; East, 1984; McNaughton, 1985; Prins and Olf, 1998; Olf *et al.*, 2002). Olf *et al.* (2002) further suggest herbivore species must encounter plants of both sufficient abundance and quality to

persist, and therefore the highest herbivore density is thus expected in locations that are neither so wet and/or infertile that average plant quality would be too low to sustain smaller herbivores, nor so dry and/or infertile that plant productivity would be insufficient to sustain larger herbivores. This hypothesis was strongly supported by the relationship between the Bovidae and productivity in the study area ($r^2 = 0.81$, $P < 0.001$, $n = 24$). The carnivores on the other hand were moderately related to productivity ($17.74 + 0.027x - 0.0002x^2$, $r^2 = 0.46$, $P < 0.002$, $n = 24$). However, the strongest correlate to the carnivore density was related to ungulate distribution ($r_s = 0.76$). At the family level the strength of the relationships was greater than at the order level. This observation supports the hypothesis that carnivores are related more to food type or prey than to habitat type (Schoener, 1974). However, at the family level the patterns were different from the higher taxonomic level. This may reflect the partitioning of energy gradient among carnivores species groups as shown in this study. And an additional explanation is that particular families and orders can have differing physiological tolerances for given environmental conditions supports this pattern (Sinclair, 1983a; Currie, 1991). Earlier works have shown partitioning of energy between species or species groups do occur at a local scale, (see Jarman and Sinclair, 1979; de Boer and Prins, 1990; Illius and Gordon, 1992; Murray, 1993; Murray and Brown, 1993; Illius and O'Connor, 2000), which be reflected in regional patterns. Kingdon (1997) suggests that the diversity of carnivores is one of the surest signs identifying a high diverse ecological area. East Africa savanna ecosystems still retain about 60% of the continental carnivore species richness. Ricklefs (1990) hypothesized that predators enhance diversity among their prey by reducing populations (and hence competition for resources), thereby easing conditions for coexistence.

The other important characteristic of the savanna ecosystem is the heterogeneity of the habitat, features such as soil characteristics (texture, porosity, salt concentrations, moisture), floral composition and physiognomy result in a mosaic of habitats (Sinclair, 1975; Happold, 1983; Belsky 1986). Each produces a slightly different environment or microhabitat, which are important habitats for smaller mammalian species. In this study relationship between the rodents, shrews and hyraxes, the species richness reached its maximum at intermediate productivity level. Happold (1983) observed that habitats with a high degree of heterogeneity had more rodent species and a larger biomass of rodents than less heterogeneous habitats. Similar patterns were observed for lagomorphs and shrews (Happold 1983; Kingdon 1997). The pattern of primates was at lower taxonomic level the patterns indicated the highest concentration of bushbabies was at intermediate level, while for the monkeys the richness increased with rainfall gradient. It highest peak was observed in the extreme western parts of the study area mostly located in Uganda and Tanzania.

We conclude that species richness – productivity relationship is clearly scale-dependent. It is interesting to note that at sub-continental scale the geographical patterns in species richness were similar among a number of taxonomic and species groups and tended to converge towards the same level (intermediate productivity) especially at the higher taxonomic level. While the high variation of patterns at lower taxonomic level it may reflect partitioning of energy gradient among families or group of species. This may be a result of different processes controlling richness at different spatial scales for various species groups.

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