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Original Research Paper

Factors that Affect the Species Richness of the Raptor Guild of the Carnivore Community in the Afro-Alpine Sections of the Bale Mountains National Park (BMNP)

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ABSTRACT

The Afro-alpine moorlands of the Bale Mountains National Park (BMNP) constitute a diverse guild of avian carnivores. The response of the species richness of this guild to ecological processes is evaluated in this paper. Importance of elevation, topographic physical features, patch heterogeneity of habitat and prey were evaluated in explaining the species richness of the guild of diurnal raptors. The spatial variation in the moorland ecosystem as result of associations of these explanatory process variables was determined through a Principal Component Analysis. This showed there were three spatial clusters of census patches that held significantly different number of species of the guild. Importance of the variables that defined the spatial variability of the ecosystem in explaining the changes in the species richness of the raptor guild was explored through simple correlation analyses and step-wise multiple linear regression that made use of PCA components of covarying explanatory variables. The first axes of the PCA mainly defined by elevation, patch physical features, habitat heterogeneity, diversity of relatively small birds and relatively large sized avian and mammalian prey was selected as a significant predictor. In this model, species richness responded negatively to the environmental variables. Heterogeneity of patches in vegetation type and species richness of prey communities that included birds and mammals such as hare and hyrax affected the species richness of the raptors significantly positively. A simple linear regression model showed interspecific niche overlap declined as a function of species richness.

INTRODUCTION

Since the last half of the 20th century, community ecologists have been depicting patterns in structuring of species assemblages that are results of processes in a system that determine interspecific interactive associations (Wiens 1989, Real & Levin 1991, Begon 1996, Krebs 2000). An accurate depiction of community patterns and making scientific predictions is an essential part of a study of a community for it to have an applied relevance (Keddy 1992). This essentially requires predicting that which subsets of a given species pool will occur in which habitat or environmental component within the defined ecological boundary of the community. This practically is determining the natural rules that determine why a collection of species that makeup a community are assembled in a manner they do within a given environment. The accuracy of the predictions made regarding patterns of community organization is thus mainly dependent on a refined determination of functionally equivalent species as members of a given community. Although, the concept of functional equivalence is widely applied for a refined selection of guilds in a community (Keddy 1992), a whole scale lumping of species members of a higher taxon such as birds results in an erroneous mixing of the community structuring forces with a functional group the organization of which is naturally affected by them. This contradiction is nowhere more apparent than where raptors and other birds that occupy different layers of trophic hierarchy are concerned. The avian predators more appropriately must be recognized as members of a wider carnivore community that constitutes species at the top of the pyramid of forager organization. Thus, the raptors are foragers of other birds that are parts of a lower functional layer which outrightly demands postulating a predictive community hypothesis that must drive for modelling the predator's organizational response as a function of changes in the attributes of the prey community. Without such clear and naturally relevant distinction between the pattern variable and the process responsible for it, making scientifically valid evaluations and predictions is impossible particularly where an avian predator assemblage is concerned. With this premise, we treated the raptor assemblage in the Afro-alpines of the Bale Mountains National Park as a major guild of a carnivore community and evaluated the impact of factors that include prey on spatial patterns of its species richness.

There are a number of factors to which the species richness of a community can be related to (Kelt & Brown 1999). Environmental variables that affect species richness patterns include latitude and altitude to which many other factors are correlated. Productivity of the environment is also a very important underlying factor in bringing about observed patterns of species richness. The physical and biological heterogeneity of the environment plays a key role in affecting the structuring of predatory communities by being the main ecological force that determines their interactive spatial associations.

The Afro-alpine moorlands of the BMNP constitutes a 25 species large guild of diurnal raptors (Clouet et al. 2000) and it was determined that they had strong functional relationships with a very diverse community of mammalian and avian prey at the population level (Shimelis 2008). At the community scale, the carnivore community, in general, and the raptor guild in particular, have not been studied before. In this paper we haver evaluated the spatial variation in the species richness of the raptor guild focusing on the relevance of environmental, habitat, prey and interaction variables. The main hypothesis is, interactively or alternatively, factors such as altitude, habitat heterogeneity and prey diversity strongly influence the aggregation of species spatially providing the impetus for the constraining effects of niche overlap on interspecific co-occurrence.

MATERIALS AND METHODS

Study area: Bale Mountains National Park (BMNP) is found on the southeast plateau of Ethiopia. It is located between 6°29' and 7°10'N, and 39°28' and 39°58'E. The area of BMNP is 2200 km sq varying in altitude from 1500 to 4377 m above sea level (Hillman 1993, EWNHS 1996). BMNP is the largest extent of protected Afro-alpine habitat on the African continent. The major habitat types in the Afro-alpine sections of the NP include (a) boulder fields with many small shrubs such as *Artemesia afra, Huperzia* spp., *Kniphophia doliosa,* and *K. isoietifolia,* (b) river valleys and swamps dominated by plant species such as *Calamagrostis epigejos* var. *capensis, Alopercurus baptarrhenius* and several other grasses and herbs, (c) flat meadows that is marked by the presence of plants such as *Helichrisum* spp., and *Alchemila hammani* (Kingdon 1990, Hillman 1993, Sillero-Zuburi & Mackdonald 1997).

Raptor census: Fieldwork focused on three 100 km^2 areas of BMNP: The Lower Web Valley (B), the Upper Web Valley (A), and the Senetti Plateau (C) (Fig. 1). In each of the three study sites six random circular sampling sites with a 1 km radius were established and counts were conducted from a suitable vintage point (Shimelis 2008). The samples were separated by a 2.5 km minimum distance. Raptors were counted in the morning for three hours per scanning plot. From these data raptor presence/absence in each sample plot was determined.

Habitat assessment: From quadrats that were set for assessment of the physical and vegetation structure of habitat described in Shimelis (2008) the presence/absence of types of vegetation types and habitat types by topographic fea-

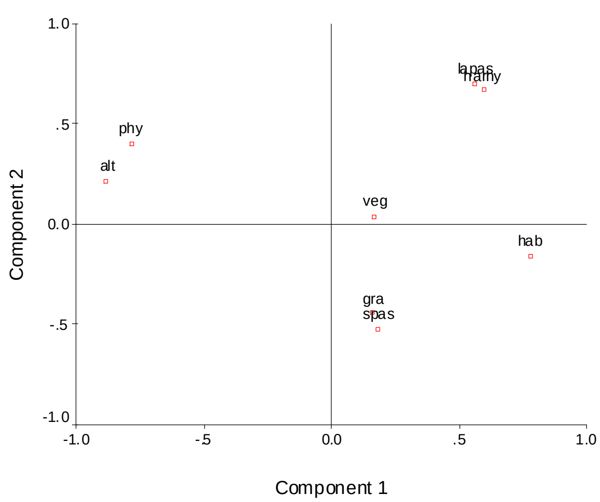

Fig. 1: The distribution of the three study sites across the Afro-alpine sections of the BMNP.

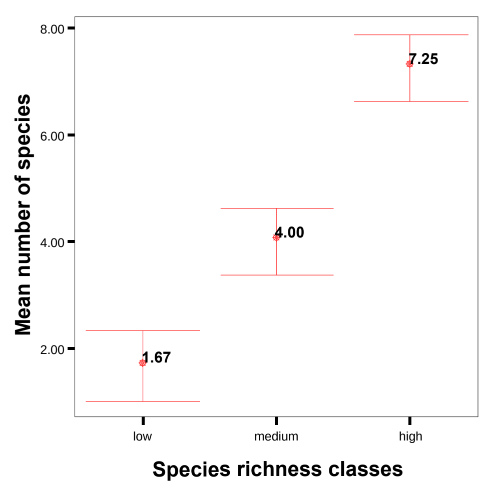

Fig. 2: Spatial variation of samples in variables important for raptors and the difference in mean number of species richness along this spatial divisions of similar samples.

tures in each raptor censusing patch were determined according to all existing categories that included the flat valley meadow, rocky valley mounds/outcrops, boulders on cliff tops, cliff ridges/walls, mezes and wetlands. This generated the number of topographic features in each spatial sample unit.

Prey assessment: From the abundance data on prey communities collected in Shimelis (2008) presence/absence of each mammalian and avian prey per raptor censusing patch was determined. This provided the species richness of prey communities per spatial sample unit.

Data analysis: To determine the spatial variation of the Afro-alpine moorland and also to construct a collective gradient of interrelated explanatory variables Principal Component Analysis (PCA) was conducted. The number of spatial differences of the study area determined as such was used to predict group membership of spatial sample units using K-means clustering. Along this spatial sample segregation one way analysis of variance (ANOVA) was conducted to determine the spatial variation in the species richness of the raptor community. To further explore the possible impact of the key explanatory variables simple correlation analysis was carried out. The collective constructs of explanatory variables generated in the PCA were used in building a multiple linear regression model for species richness as a function of the surrounding environment. Simplified Moritsa index (Krebs 1989) was computed to determine the mean spatial niche overlap amongst co-occurring species pairs. The constraining effect of niche overlap on the co-occupancy of space was evaluated using regression modelling.

RESULTS

Association of explanatory variables: The PCA results showed the Afro-alpine moorland had three distinct differences regarding the distributional association of variables that were considered as important for explaining the community patterns in the raptor guild (Fig. 2). The analysis selected the first four components that accounted for more than 87 % of the variance in the whole data set. The first component is characterised by environmental variables that separated high and low areas in relatively large-sized prey diversity (Table 2). The second component was defined by differences in the species richness of small and large prey groups. The third component encapsulated differences in the species richness of small mammals and small birds. The fourth component represents mid altitude areas with very high vegetation diversity but with low species richness of the large passerine community.

Spatial variability in raptor species richness: The surveys generated a total list of 14 species of raptors in the Afro-alpine sections of the BMNP. Spatial sample units grouped according to the distribution of the explanatory variables was used to evaluate mean differences in species richness (Fig. 2). These species were assembled with species richness levels that significantly varied amongst the three sample

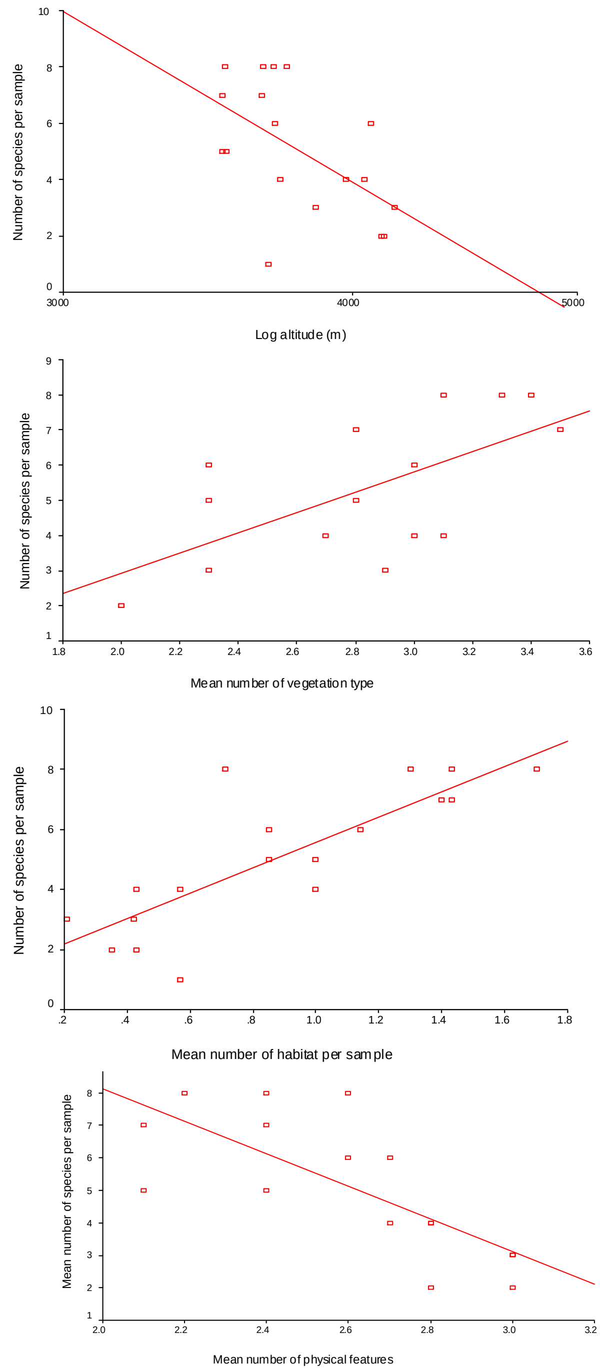

Fig. 3: Relationship of raptor species richness with physical and vegetation features of census patches.

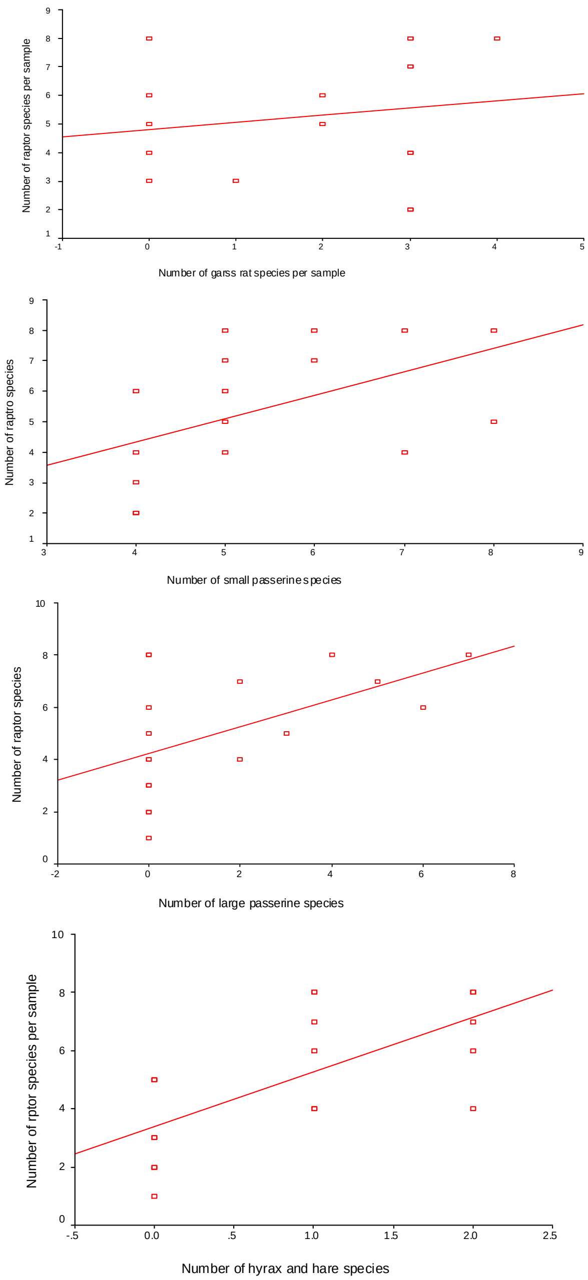

Fig. 4: Relationship of the species richness of the raptor species richness with diversity of prey communities.

classes ($F_2 = 59.6$, $P < 0.001$).

Effect of processes on raptor species richness: The observed species richness of the raptor community had a significant negative correlation with elevation (r = -0.54, P = 0.02) as most of the highest records were made in areas where elevation was relatively low (Fig. 3).

Species richness generally increased significantly with

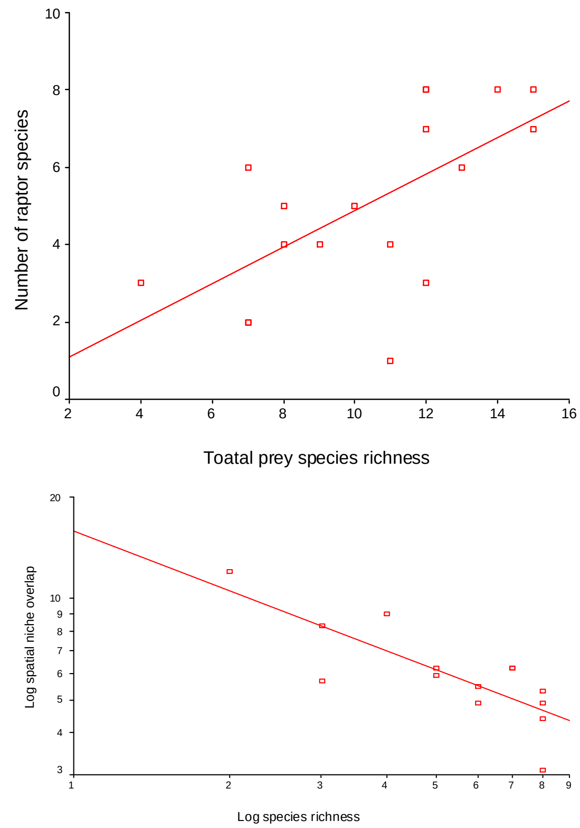

Fig. 5: The relationship of the species richness of the raptor guild with the combined diversity of avian and small mammal prey communities and interspecific niche overlap.

the rise in the magnitude of measures of spatial heterogeneity (Fig. 3). This was demonstrated by the significant positive correlation with the mean number of physiographic features (r = 0.635, P = 0.011) and the mean number of habitat types by vegetation (r = 0.81, P < 0.001). The number of raptor species declined significantly (r = -0.79, P < 0.001) as the mixture of the physical environment devoid of vegetation increased (Fig. 3).

The relationship of the species richness of the raptor community with the diversity of the available food varied depending on the potential prey community considered. The general species richness pattern did not have significant correlation with the diversity of the grass rat community (r = 0.441, P = 0.118). Figurative examination of this relationship showed that it could have been positively significant if not for the high magnitude of the response variable where such prey was not available (Fig. 4). The relationship with the number of species of the small passerine community was positively significant (r = 0.59, P = 0.015). Despite the significance of the positive relationship, the number of raptor species frequently differed amongst sites of the same

Table 1: Principal components and their relationship with environmental variables

Variable	Principal component loadings			
	One	Two	Three	Four
Altitude	-0.9	0.2	0.4	0.1
Vegetation type	0.2			0.9
Physical features	-0.8	0.4		0.3
Habitat patches	0.8	-0.2	0.4	
Grass rats	0.2	-0.4	0.8	0.1
Small Passerines	0.2	-0.5	-0.7	0.3
Large Passerine	0.6	0.7	-0.1	-0.2
Hare- and hyrax	0.6	0.7		0.2

number of the small passerine species. Samples did also have the same number of raptor species despite their differences in the magnitude of the species richness of the small passerine community. The number of species in the raptor community changed with positive significance ($r = 0.52$, $P = 0.012$) along a gradient of large passerine species richness. Like the previous prey communities the positive relationship with the number of large passerines was not consistent as there were sites with the same level of availability of large passerine species but the number of the raptor species differed. The combined presence of hyraxes and hares did also have significant positive impact ($r = 0.68$, $P = 0.002$) on the species richness of the raptor community. The sum total of the species richness of the small mammal and avian prey communities generated a prey diversity variable that had positive significant correlation ($r = 0.67$, $P = 0.002$) with the species richness of the raptor community of the Afro-alpine sections of the BMNP (Fig. 5).

The PCA components were regressed against the number of raptor species as a response variable in a stepwise manner. The multiple linear regression model that explained more than 61 % of the variability in the response variable included only the first component as a significant predictor ($F_1 = 25.4$, $P < 0.001$). This component's relationship with the species richness of the raptor community was positive ($P < 0.001$) and the relationship can be expressed via the following equation: $S = 1.8$ PC1+ 5.1. This relationship clearly indicated that the diversity of relatively large-sized prey and environmental heterogeneity are the most important overriding factors that determined aggregation of raptor species in space

The state of interspecific interaction: Spatial niche overlap amongst co-occurring raptors declined as species richness increased (Fig. 5). The simple linear regression that was conducted to measure the relationship between the two showed that there was significant negative relationship ($P = 0.02$) and expressed as $\log s = -0.8$ mean niche overlap + 1.24. This relationship clearly indicated the number of species increased in areas that allowed higher levels of niche divergence/specificity amongst similar species.

DISCUSSION

Amongst the issues that contemporary ecological theory has been focusing on since the 1950s was the problem of the number and relative abundance of species in a community (Wiens 1989, Real & Levin 1991, Begon 1996, Krebs 2000). As pointed out by May (1986), a major intellectual challenge facing modern ecologists is to discover those forces that determine the magnitude of species found in a community.

Environmental variables such as altitude, spatial heterogeneity, the range of resource available and interspecific interaction such as competition and predation are postulated as factors that primarily determine species richness of any given community (Wiens 1989, Begon 1996, Krebs 2000). Various workers elsewhere documented the significant effect of the availability and diversity of resources as an important predictor of species richness patterns of communities of various taxa (Rosenweig & Winakur 1969, Brown 1975).

The raptors in the Afro-alpine moorlands of the BMNP do have strong functional and aggregative relationships with the avian and mammalian prey communities (Shimelis 2008). The results in this paper demonstrated that species richness of the raptor guild varied significantly in space. This spatial variation in species richness was a result of the change in the magnitude of key primary and secondary processes. The decline in the number of raptor species as elevation increased indicated that highly positioned areas generally are less suitable to the majority of species of the community. In fact the amount of the different niches that was potentially available to the community as a whole declined with increase in altitude. As demonstrated by their component loadings (Table 1) virtually all the niche variables had their highest degree of presence in areas where elevation was at its relative lowest point (Fig. 2). Such areas were characterised by a high diversity of exposed soil and rock formations than the vegetation cover. As a result of this, the numbers of habitat patches at high altitude areas were at their minimum reducing the number of prey species colonizing them. Various workers have reported significant changes in species richness of avian communities along gradient of vegetation (Wiens 1989, Begon 1986, Krebs 2000) and the effect on raptors is indirect by limiting the availability of their herbivorous prey. Abundance of prey species in the Afro-alpine moorlands of the BMNP was dependent on the vegetation type and other structural features of habitat (Shimelis 2008, Talents 2007). In addition to its positive effect on raptor species richness through provision of niches to a diverse guild of prey, the diversity of habitat patches determine the availability of the spatial resource needs of the various raptor species. The nesting habits of the breeding species differ some choosing meze edges, some using relatively high rocky mounds at valley bottoms while others nest only on the sides of steep and high cliffs (Shimelis, unpublished data). Thus, high habitat patch diversity means more species of raptors per site. The prey community in total rather than each group on its own did serve as effective predictor of the species richness of the raptor guild. The increase in the overall prey diversity allowed localized foraging divergences boosting the number of species of overlapping requirements. Where niche overlap was high the number of species that co-occurred was small and species richness increased as the magnitude of interspecific competition was reduced enabling increased number of competing species to co-exist.

The Afro-alpine moorlands of the BMNP are increasingly simplified as result of human settlement, high livestock density and expansion of agriculture in areas that are suitable for such purposes. It is not yet determined how this affects the overall ecosystem, in general, and the raptor guild in particular. The site is a very important catchment and the existing plant-prey-predator interaction (Shimelis 2008) may play a key role affecting the different modes of regulatory functions of the moorland ecosystem. A threat to such ecologically integrated system may reduce significantly its ecosystem values resulting in region-wide negative effects. Our work demonstrated how and why the Afro-alpine moorland system at the top of the trophic hierarchy is organised spatially and this provides an understanding essential for the conservation and management of biodiversity in the NP.

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Appendix 1: The total list of raptor species encountered in the Afro-alpine sections of the BMNP.

Common Name	Scientific Name
Augur Buzzard	*Buteo augur*
Black Eagle	*Aquila verauxii*
Black Kite	*Milvus migrans*
Common Kestrel	*Falco tinninculus*
Golden Eagle	*Aquila chrysaetos*
Greater-spotted Eagle	*Aquila clanga*
Pallid Harrier	*Circus macrourus*
Imperial Eagle	*Aquila heliaca*
Lammergyer	*Gypaetus barbatus*
Lanner Falcon	*Falco biarmicus*
Lesser Kestrel	*Falco numani*
Red-chested Sparrow hawk	*Accipter rufiventris*
Step Eagle	*Aquila nipalensis*
Tawny Eagle	*Aquial rapax*