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Interaction patterns within a multi-herbivore assemblage derived from stable isotopes

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ABSTRACT

The ecological effects of consumer guilds are strongly driven by the relative resource use of included species. Here we use stable isotopes in faecal samples from 6 co-occurring mammalian herbivores in an African savanna to identify species-specific trophic niches and detect patterns of interactions between herbivores and their feeding resources. Species-specific foraging strategies were reflected in the faecal $\delta^{13}C$ values, with species aligning along both a browser-grazer gradient and a niche breadth gradient. Within the broad foraging strategies outlined by $\delta^{13}C$, $\delta^{15}N$ indicated a seasonal shift in resource use for some herbivores. We expected that ^{13}C isotope niches would overlap in a nested fashion, with the niches of grazers and browsers being included in those of mixed feeders, and that ^{15}N niches would separate into discrete modules reflecting leguminous and protein content of respective diets. However, the observed structure was more complex, with combined modular and nested patterns of interactions between herbivores and ^{13}C isotopes. We identified an isolated module comprising eland and its exclusive $\delta^{13}C$ values, and a series of nested structures with a set of specialist herbivores (hartebeest and sable) which $\delta^{13}C$ values were nested within those of more generalist herbivores (impala, waterbuck and zebra). Networks based on $\delta^{15}N$, however, reflected a higher level of overlap in resource use with random patterns in herbivore interactions with resources, and only a significant modular interaction pattern during the dry season. We suggest that the combined modular and nested pattern of $\delta^{13}C$ interactions reflect the simultaneous mutualistic and antagonistic characteristics of plant–herbivore interactions. We argue that such interaction patterns could stabilize ecosystems by constraining effects of perturbations to specific modules and by increasing functional redundancy through nested interactions.

1. Introduction

Consumer–resource interactions pervade ecosystems, where the links between organisms through trophic exchanges form the core of modern ecosystem definitions (Smith and Smith, 2012). The overall effects of a consumer guild (i.e. groups of consumers with similar resource requirements) are determined by the resource use of each species as well as the overlap between them (Dalerum et al., 2012a). Increasing overlap in resource use is expected among consumers with increasing physiological, ecological or genetic

similarity and in turn, ecologically or genetically similar resources are expected to be utilized by the same range of consumers (Gómez et al., 2010). Such ecological redundancy has been linked to the stability and resilience of ecosystems (Dalerum et al., 2012a; Holling, 1973). Therefore, quantifying the nature and structure of resource use within consumer guilds is important for understanding the functioning of ecological systems and for adopting efficient conservation strategies in the face of human driven environmental change (Laliberté and Tylianakis, 2010; Memmott et al., 2007).

Large terrestrial herbivores are critically important for ecosystem dynamics and often regulate both lower and higher trophic levels (Hunter and Price, 1992). From a consumer perspective, three major functional groups of large mammalian herbivores have traditionally been distinguished: browsers, grazers and mixed feeders (Hofmann and Stewart, 1972). This is an evolutionary response to morphological and chemical differences of plant resources, with herbivores evolving different physiological adaptations in order to maximize

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energy and nutrient extraction from the diverse plant material available (Iason and van Wieren, 1999; Robbins, 1993). In African savannas, the highly diverse plant communities combined with the high spatial heterogeneity and temporal variability of resources has lead to the evolution of equally diverse large herbivores assemblages that consist of species with different morphology, physiology, behaviour and life history traits (Fritz and Loison, 2006). This high diversity of both consumers and resources makes African herbivore assemblages an ideal model in which to address consumer–resource interaction patterns (Dobson, 2009).

Analysis of naturally occurring stable isotopes has become well established as a tool for investigating the resource use of consumers (Dalerum and Angerbjorn, 2005; Martínez del Río et al., 2009). For large African herbivores, stable isotopes of carbon and nitrogen in faeces, bone collagen, tooth enamel and hair have been utilized as useful proxies to quantify resource use (Cerling et al., 2003; Codron et al., 2007a; Sponheimer et al., 2003a). Different photosynthetic pathways cause plants to differ in their ^{13}C content so that grasses, which in African savannas follow the C4 pathway, are enriched in ^{13}C compared to forbs and woody plants that follow the C3 pathway (Farquhar et al., 1989). Determining ^{13}C/^{12}C isotope ratios in herbivores thus allow for discrimination between consumption of plants with different photosynthetic pathways, and subsequently to place herbivore foraging strategies along a grazing-browsing gradient. In contrast, plants differ in ^{15}N/^{14}N ratios primarily as a response to environmental conditions such as aridity, soil type, climate, source of N but also to plant and herbivore physiological mechanisms (Ambrose, 1991; Ambrose and De Niro, 1986; Codron et al., 2005a; Evans, 2001; Handley and Raven, 1992; Heaton, 1987; Sealy et al., 1987). Therefore, a combined evaluation of C and N may provide useful insights of the foraging ecology of herbivores beyond information strictly contained in the amount of C3 versus C4 plants in the diet.

In parallel with the re-emerging interest in community ecology, network analyses have been increasingly used to describe and quantify species trophic relationships (Ings et al., 2009; Miranda et al., 2013). A trophic network consists of at least two distinct sets of nodes (typically species) that are connected through resource utilization links (Elton, 1927; Harary, 1961). Quantifying the topology of such networks allows for formal evaluation of patterns of resource partitioning or overlap (Sugihara, 1984). Evolutionary processes acting at the multi-specific and multi-trophic levels seem to constrain such ecological networks towards specific structures that confer ecological stability (Allesina and Pascual, 2008). Nestedness and modularity are two such topological patterns that have emerged as particularly important for ecosystem stability (Bascompte et al., 2003; Bastolla et al., 2009; Stouffer and Bascompte, 2011; Thébault and Fontaine, 2010). Nestedness describes an interaction structure where the resources used by specialist consumers are a subset of the resources used by more generalist consumers (Bascompte et al., 2003). Modularity describes an interaction structure where there are delimited sub-communities of consumers and resources, with more frequent and stronger interactions within each sub-community than between them (May, 1973; Prado and Lewinsohn, 2004).

African savannas are expected to experience important climatic changes that combined with widespread management interventions could lead to major changes in herbaceous structure, basal cover and plant community composition (Buitenwerf et al., 2011; IPCC, 2013; Kirtman et al., 2013; Rutherford et al., 1999). Since African savannas are largely driven by plant–herbivore interactions, it is imperative that we understand the structure of trophic interactions between herbivores and their resources to fully understand the consequences of the expected environmental changes. In this study we use C and N stable isotopes from herbivore faeces to (I) quantify the relative feeding ecology within an African large herbivore assemblage, and (II) to quantify the structure of the relationship between herbivores and their feeding resources using network analyses. African herbivores follow a grazer-browser gradient where some species adopt intermediate mixed feeding strategies. This is expected to be reflected in corresponding δ^{13}C values. The ^{13}C isotope niches of mixed feeders are thus expected to include the niches of more specialist grazers in a nested hierarchical structure. We expect this nested structure to be stronger in the wet season compared to the dry season, because of the limited resource supply and quality during the latter. We subsequently also expect a reduced modularity in ^{13}C niches in the dry season. δ^{15}N values relate to the physiology of plants and herbivores. We expect lower δ^{15}N values in mixed feeders because of inclusion of ^{15}N-depleted, N$_2$-fixating legumes in their diets (Delwiche et al., 1979; Ambrose and De Niro, 1986). In addition, grazers recycle more ^{15}N-depleted urea due to their lower consumption of crude protein, which should further lead to higher δ^{15}N values in their faeces (Sealy et al., 1987). We predict a modular pattern in herbivore δ^{15}N networks, shaped by differences in dietary content in both leguminous plants and proteins between grazers and mixed feeders.

2. Methods

2.1. Study system and study species

The study was conducted in Kgaswane Mountain Reserve (KMR, 25°43′ S, 27°11′ E), a 5300 ha protected area in the Magaliesberg Mountain Range, North West Province, South Africa. The area is fenced and elevation ranges from 1230 to 1660 m. The topography is characterized by steep cliffs on the western and southern boundaries with a wide summit plateau of quartzite in the northern part of the reserve. Mean annual rainfall is 604 mm (coefficient of variation: 0.42 between 1980 and 2011, KMR weather station, 1119 m altitude), most of which falls during October–April, defining distinct wet and dry seasons. Annual average temperatures range from 11 to 27 °C being highest from December to February and lowest between June and August (KMR weather station).

The study area lies in the transition zone between the mixed bushveld and the rocky highveld grassland vegetation types (Low and Rebelo, 1996), and contains plant and animal species associated with both. The grassland is dominated by the grasses Themeda triandra, Hyparrhenia hirta, Trachypogon spicatus and Elionurus muticus (Nel, 2000). The woodland is dominated by Protea caffra and Acacia caffra (Nel, 2000). The reserve hosts a population of over 500 large herbivores including: red hartebeest Alcelaphus buselaphus (98, estimated numbers), zebra Equus quagga (90), eland Taurotragus oryx (85), impala Aepyceros melampus (81), waterbuck Kobus ellipsiprymnus (68), sable antelope Hippotragus niger (45), mountain reedbuck Redunca fulvorufula (41), kudu Tragelaphus strepsiceros (15), blesbok Damaliscus pygargus (10), springbok Antidorcas marsupialis (7), klipspringer Oreotragus oreotragus (6), oribi Ourebia ourebi (6), roan antelope Hippotragus equinus (3), and common reedbuck Redunca arundinum (5) (Nel et al., 2011). Carnivores occur in low numbers in the area and include caracal Caracal caracal, aardwolf Proteles cristata, black-backed jackal Canis mesomelas, and leopard Panthera pardus.

Our focal species were the six most abundant large herbivores in the reserve: red hartebeest, zebra, eland, impala, waterbuck, and sable antelope. Eland has been described either as a browser (Watson and Owen-Smith, 2000) or mixed feeder favouring browsing (Gagnon and Chew, 2000), depending on local environmental conditions and resource availability in the study region (Sponheimer et al., 2003b). Impala is regarded as a mixed feeder