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Original article

Species richness – Energy relationships and dung beetle diversity across an aridity and trophic resource gradient

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A B S T R A C T

Understanding factors that drive species richness and turnover across ecological gradients is important for insect conservation planning. To this end, we studied species richness – energy relationships and regional versus local factors that influence dung beetle diversity in game reserves along an aridity and trophic resource gradient in the Botswana Kalahari. Dung beetle species richness, alpha diversity, and abundance declined with increasing aridity from northeast to southwest and differed significantly between dung types (pig, elephant, cattle, sheep) and carrion (chicken livers). Patterns of between-study area species richness on ruminant dung (cattle, sheep) differed to other bait types. Patterns of species richness between bait types in two southwest study areas differed from those in four areas to the northeast. Regional species turnover between study areas was higher than local turnover between bait types. Patterns of southwest to northeast species loss showed greater consistency than northeast to southwest losses from larger assemblages. Towards the southwest, similarity to northeast assemblages declined steeply as beta diversity increased. High beta diversity and low similarity at gradsect extremes resulted from two groups of species assemblages showing either northeast or southwest biogeographical centres. The findings are consistent with the energy hypothesis that indicates insect species richness in lower latitudes is indirectly limited by declining water variables, which drive reduced food resources (lower energy availability) represented, here, by restriction of large mammals dropping large dung types to the northeast and dominance of pellet dropping mammals in the arid southwest Kalahari. The influence of theoretical causal mechanisms is discussed.

1. Introduction

A global meta-study of regional ecological gradients indicates that rainfall, available energy, and water-energy balance are the strongest influences on geographical patterns of change in species richness (Hawkins et al., 2003). The relative importance of these factors varies with latitude. In cool temperate regions, where energy availability is low, energy or water-energy balance were, generally, the strongest correlates with species richness. However, under the higher temperatures of warm temperate to tropical regions below latitudes 45°–48°, there is a higher energy availability and, although energy would obviously remain important, its availability is limited by water variables so that species richness was most strongly correlated with rainfall. Thus, it may be hypothesized that towards the tropics increasing aridity leads to reduced resources (lower energy availability), leading to reduced species diversity. This is consistent with the suggestion of Hawkins et al. (2003) that for invertebrates, such as insects, species richness may be indirectly limited by water variables through their influence on plant productivity, which limits food availability. The present study examines how increasing aridity and diminishing trophic resources influence patterns of dung beetle diversity within game reserves across the Botswana Kalahari and discusses the possible response mechanisms (Evans et al., 2005) since understanding pattern and process at both landscape and local scale is important for conservation planning (Tscharntke et al., 2012).

An extensive literature confirms that patterns of species diversity across regional gradients are subject to both regional and local processes (e.g. Ricklefs, 1987; Lobo et al., 2006; Mykrä et al., 2007) and it may be said that regional gradients result from changing local effects across regional space overlain by historical or regional influence on local patterns. Most regional gradients are characterized by a number of co-varying or co-linear factors that, in terms of responses by insects, may be of greater, equal, or lesser importance. By their very nature, aridity gradients may include further co-varying ecological influences besides changes in the

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availability of food and energy, such as more open vegetation physiognomy and increasing temperature. Interpretation of influences of aridity may also be confounded by ecologically influential, independent variation across space, such as differences in soil texture. Thus, assessing the relative importance of variables and the scale at which they operate is problematical as is assessing whether or not a significant correlation equates to causality in a relationship between environment and apparent biotic response.

The Botswana Kalahari comprises a northeast/southwest gradient in aridity and trophic resources that is ideal for studying interactions between the various regional and local influences on dung beetle diversity including relationships between species richness and energy availability. The regional gradient in declining annual rainfall (>600 to <200 mm p/a) results in an opposing rainy season gradient of increasing average daily temperatures to the southwest that stems from reduced frequency of local rainfall events during summer when dung beetles were sampled (Tshikae et al., 2013a). Substantial rainfall is an initiator of high activity in dung beetles (Davis, 1995, 2002) and with greater frequency of events might increase both the temporal diversity of activity patterns and opportunities for breeding, leading to greater abundance and increased species richness in the northeast. A parallel regional gradient in declining mammal species richness (>100 to <70) (Andrews and O'Brien, 2000), density, and biomass (Tshikae et al., 2013a) results in reductions in energy availability through declines in dung type diversity, density of droppings, and amounts per dropping in arid southwestern localities (see Material and methods and Discussion). As a certain amount of dung type specialization has been recorded in dung beetles both in Botswana (Tshikae et al., 2008) and elsewhere (Fincher et al., 1970; Cambefort, 1982), this might result in reduced opportunities for dung type specialization and loss of certain specialist species with increasing aridity (Tshikae et al., 2013b).

An analysis of species abundance structure at six study areas across the Botswana aridity gradient has identified two regional and six local components for dung-associated scarabaeine beetles, all but one representing 40–50% of total local variation (Tshikae, 2011). The two regional components are correlated most strongly to annual rainfall, temperature during sampling, and an index derived from the density of 25 mammal species across the gradient (Tshikae et al., 2013a). One southwest-centred regional component declined in proportional contribution to the northeast whereas the other component was centred in the northeast and declined to the southwest. The point of intersection between regression lines, fitted to these components, supported a major boundary zone in the centre of the aridity gradient that was consistent with the ecoregion classification of Olson et al. (2001).

The current work uses various measures of diversity and similarity to examine regional and local patterns of species richness, diversity (gamma, beta, alpha), abundance, and behavioural group distribution, either side of the boundary zone that bisects the Botswana Kalahari aridity gradient. Particular emphasis is placed on co-varying patterns of species richness with increasing aridity and reduced trophic/energy resources. One aim of the study was to determine if species richness and diversity declined between study sites that are ranked according to declining rainfall, and if any insights might be gained from a joint consideration of regional patterns between study sites and local patterns between dung types. A second aim was to determine if patterns of richness and diversity between five bait types (four dung types plus carrion) might change across the gradient owing to regional changes in food/energy availability. This aim was based on the observation that two dung types are not found naturally at the dryer southwest end of the gradient owing to the absence of surface water except after substantial rain (Moyo et al., 1993; Penry, 1994) causing the exclusion of mammal species that are both dependent on permanent water and drop the largest dung types (buffalo, elephants, zebra, rhinoceros) (Campbell, 1973; Chamaillé-Jammes et al., 2007). A third aim was to determine if patterns of species loss to the northeast and southwest of the boundary zone might reflect southwest and northeast biogeographical centres that have been demonstrated by Davis (1997) and Tshikae (2011). We also discussed other potential modifiers of patterns across the aridity and trophic gradient. These included variables independent of the gradients (landscape type – fossil lacustrine versus aeolian sands) as well as observed disturbances (livestock farming). These various empirical trends were discussed with regards to theoretical causal mechanisms for reduced species richness with reduced energy availability (Evans et al., 2005).

2. Material and methods

2.1. Study region and geographical gradients

The study was conducted from northeast to southwest across the deep sands of the Botswana Kalahari along an 1170 km gradient of increasing aridity (Fig. 1). Dung beetles were sampled from six study areas in three conserved regions; two areas per region and three study sites per area. These six study areas were in Chobe National Park (Chobe, Savuti), Central Kalahari Game Reserve (North CKGR, Khutse), and Kgalagadi Transfrontier Park (Mabuasehube, Transfrontier) (Fig. 1).

The northeast to southwest gradient in diminishing annual rainfall (Fig. 1), increasing summer temperatures, and decreasing annual temperatures (Scholes et al., 2002) is paralleled by changes in species richness and biomass of woody plants (O'Brien et al., 1998; Scholes et al., 2002). Strong shade cover occurred only in the woodland of Chobe in the extreme northeast whereas Savuti was characterized by dense but open shrubland (Tshikae, 2011). Further to the southwest, cover density of shrubs was increasingly and significantly lower so that grassland became dominant. Cover density of grass was highly variable but was significantly lower only in the extreme southwest in Transfrontier (Tshikae, 2011). Of four

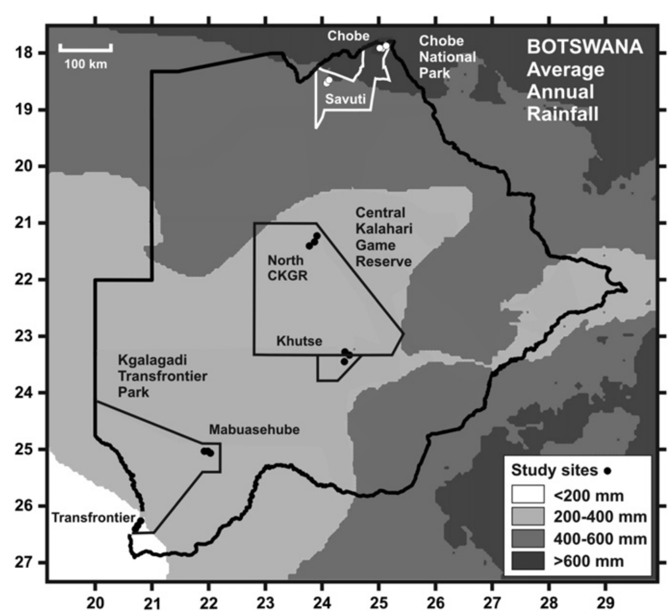

Fig. 1. Map showing the location of three study sites at each of six study areas within game reserves (= 18 study sites) relative to rainfall regimes across the Botswana Kalahari.