Commentary

Community structure of bats in the savannas of southern Africa: influence of scale and human land-use

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Abstract

In this review we provide a conceptual framework of the evolution of bat diversity patterns in the Savanna Biome in southern Africa, focusing on different niches and variables across spatio-temporal scales. At a regional scale, speciation mediated by historic geomorphic and climatic events has driven bat diversity of the regional species pool. The high taxonomic and phylogenetic diversity in the region is maintained by stable wet and warm climatic conditions and high habitat heterogeneity. Low replacement rate among bioclimatic regions suggest the selective extinction of savanna species with large or small body sizes and small geographic ranges. Processes at the meso-scale appear to play a minor role as the high mobility of bats enables them to select habitat patches even in human-dominated urban and agricultural landscapes. Multiple biotic processes, including competition and prey defenses operate at a local scale as well as a point scale, but non-random patterns are not ubiquitous within and across variables. Long-term data on births, deaths, migration and range expansion over many generations are necessary to quantitatively describe the feedback loop between local and regional scales. Additionally, data are needed to conceptually link the regional and biogeographic species pools. We provide suggestions for fields particularly worthy of future research with respect to bat assemblages in savanna ecosystems.

Introduction

The Savanna Biome dominates the African continent and covers 54% of southern Africa (Scholes, 1997; Rutherford et al., 2006, Fig. 1). In southern Africa, the savanna biome extends from the tropics in central Africa to the Nama-Karoo Biome on the central plateau, the Grassland Biome at higher altitudes towards the east, and down the eastern parts of the region into the Albany Thicket in the Eastern Cape. There is no widely accepted overarching classification system for southern African savannas (Scholes, 1997). Werger and Coetzee (1978) identified three broad vegetation units in the region's savannas: Open *Acacia* savanna of the southern Kalahari; *Colophospermum mopane* vegetation; and Other woodland, savanna, thicket and bushveld vegetation. By contrast, Huntley (1982) recognized two broad classes of savanna: moist/dystrophic (broad-leaved) savanna and dry/eutrophic (fine-leaved) savanna. At a broad spatial scale, there is a gradient of sharply decreasing diversity of tree and larger shrub species from east to west within the Savanna Biome (O'Brien et al., 1998). The temperature gradient may be the strongest predictor of regional species richness in southern African savanna and grasslands (Cowling et al., 1997).

Common to savannas around the world are a tropical climate (a hot wet season of four to eight months and a mild dry season for the rest of the year), and frequent grass-layer fires (Scholes, 1997). In southern Africa, annual rainfall in the savanna biome is around 750–1000 mm and occurs in the summer between October and April (Scholes, 1997; Schulze, 1997). Vegetation can be varied but consists mainly of open woodland with mopane, *Colophospermum mopane*, and *Acacia* trees, good grass cover, and various shrub species (Scholes, 1997; Rutherford et al., 2006). Many dominant grass genera of southern Africa savanna are shared with savannas of other continents, including *Heteropogon*, *Andropogon* and *Themeda* (Rutherford et al., 2006).

The vegetation history of the savanna has undergone various transitions during glacial, stadial and interglacial conditions. The development of modern savannas is linked with vegetation that flourished during the Tertiary, specifically the evolution of C4 grasses in the Oligocene (Christin and Osborne, 2014). Forest changed to open woodland between 12.8–6.8 mya in the Tugen Hills, Kenya (Jacobs, 2004). Pliocene uplift in southern Africa coupled with cooling corresponds with a transition from closed to more open woodland (Vrba, 1985, 1995). Open grassy savanna occurred between 2.6–2 mya on the boundary between the current Savanna and Grassland Biomes (Rutherford et al., 2006).

In the southern African region, savannas are well known for their high diversity of vertebrates including amphibians, reptiles, birds, and mammals (Drinkrow and Cherry., 1995; O'Brien et al., 1998; de Klerk et al., 2002; Van Rensburg et al., 2002), yet invertebrate groups including dragonflies (Samways, 1999) and ticks (Cumming, 2000) are also well represented. Bat species richness decreases from east to west with greatest species richness in the savannas of north-eastern South Africa and Zimbabwe, and lowest richness in the arid zones of western South Africa, south-western Botswana and southern Namibia (O'Brien et al., 1998; Schoeman et al., 2013). Savanna bat assemblages at local and regional scales may comprise more than 15 and 30 species, respectively (Monadjem and Reside, 2008; Schoeman and Jacobs, 2008; Schoeman and Waddington, 2011; Schoeman et al., 2013). Generally, no other group of mammals is known to approach such high degrees of alpha and gamma diversity in the savanna sub-region. This leads to the question of whether these species-rich assemblages are structured in any way. For example, does competition lead to partitioning of available

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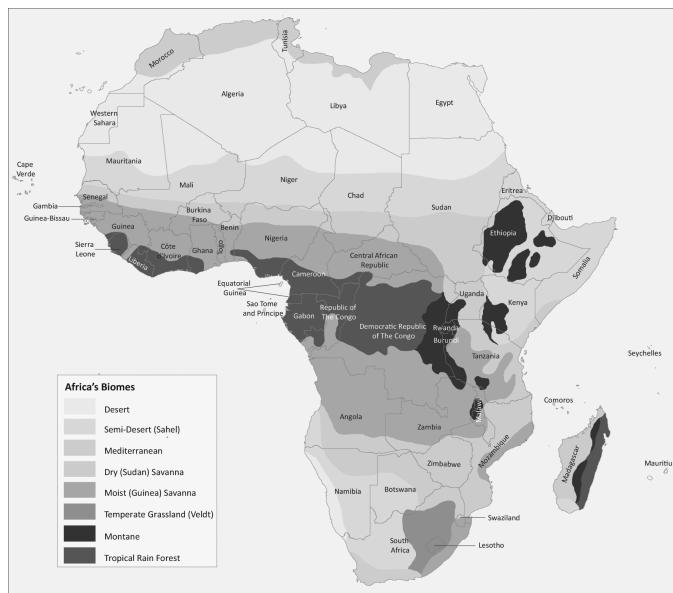*Email address:* schoemanc@ukzn.ac.za (M. Corrie SCHOEMAN)

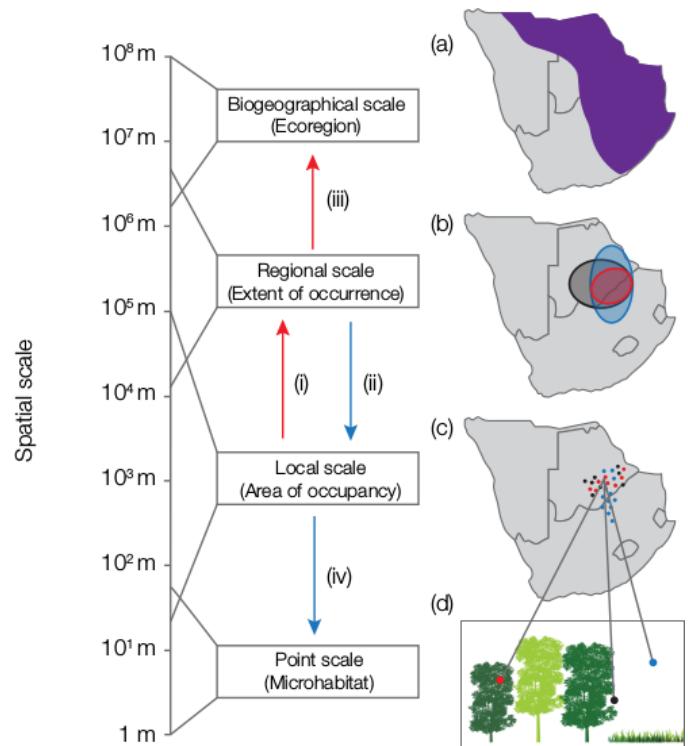Figure 1 – Map of Africa's biomes (https://na.unep.net).

Figure 2 – The hierarchical spatio-temporal distribution of insectivorous bats (a) from the biogeographical scale (estimated as the ecoregion where the species occur), (b) regional scale (represented as the extent of occurrence, estimated by the overlap in potential suitable habitat of species), (c) local scale, denoted by point localities of occurrence, and (d) the point scale, which represents the short-term movements of species between microhabitats. Numbered arrows indicate how patterns may interact at different scales. (Adapted from Buschke et al. (2014)).

resources (Patterson et al., 2003), or are these assemblages merely species that happen to co-occur (Arita, 1997)?

Traditionally, studies of bat community ecology have compiled detailed information on patterns of species organization on relatively limited geographic and temporal scales. The main conclusion from these studies is that the important factors that influence local species composition differ, often markedly, from system to system (Findley, 1993; Patterson et al., 2003). Because the kind of processes that can be identified as operating on a local scale is largely dependent upon the organisms and environments examined, there may be no "universal rules" on a local scale (May, 1986; Lawton, 1999). Useful rules and generalizations in community ecology may only emerge with a hierarchical perspective of abiotic and biotic filters that control which species existing in the regional species pools appear in local assemblages (Brown, 1995; Gaston and Blackburn, 2000; Algar et al., 2011) (Fig. 2). In this review we provide a conceptual discussion of the emergence of bat diversity patterns in the Savanna Biome in southern Africa, from the fundamentals of community ecology, relying heavily on a distinction between different niches and variables and the importance of scale.

Results and discussion

Ecology of Bats at Multiple Spatio-temporal Scales

Within a macroecological framework, community assembly is viewed as a multi-stage, multi-layered process that links diversity patterns across spatio-temporal scales (Morin, 2011). Membership in the regional species pool is mediated by evolutionary processes such as speciation and extinction of different numbers of species in taxonomic groups or habitats, and historical dispersal. Historical dispersal includes accidents of biogeography. For example, rhinolophid bats are absent from the savanna-like regions of Madagascar (Goodman, 2011) despite possessing physiological adaptations that allow them to inhabit climatically similar conditions in the savannas on the African mainland (Monadjem et al., 2010). Contrastingly, closely related Rhinonycteridae (*Paratriaenops* spp.) did disperse from the mainland savannas to Madagascar (Russell et al., 2008; Benda and Vallo, 2009).

Patterns and processes at regional scales

The high bat richness in the Savanna Biome (O'Brien et al., 1998; Schoeman et al., 2013), compared to richness in the other biomes, mirrors richness patterns of mammals, birds, and plants across southern Africa (Andrews and O'Brien, 2000; Jetz and Rahbek, 2002; Qian et al., 2009). Non-spatial and spatial models reveal that both habitat heterogeneity and climate are the most important predictors of bat species

richness at broad spatial scales (Schoeman et al., 2013). Evolutionary processes associated with spatial heterogeneity establish barriers to dispersal, and isolate populations, potentially favouring adaptations to new environmental conditions and speciation events. The spatial scale of mammalian geographic ranges, ecoregions, and life zones is the scale over which these processes operate (Ricklefs and Schluter, 1993). Major zones of uplift and faulting in the southern African region are associated with rifting in the East African Rift System. Tectonic activity started here at the end of the Miocene, and in tandem with palaeo-climatic processes, has been invoked as the ultimate cause of allopatric speciation events in mammals including antelopes (Cotterill, 2003), mole-rats (Faulkes et al., 2010), and bats (Taylor et al., 2012b). For example, divergence within certain lineages of the *Rhinolophus hildebrandtii* complex in southern Africa occurred during the late Neogene (Plio-Pleistocene), when seasonal woodland/forest habitats were being replaced by more open woodland (Cerling et al., 2011; Taylor et al., 2012b). Past climate-driven forest dynamics can also be invoked to have driven species-level diversification in both forest and savanna adapted species further south. For example, genetic differentiation in the savanna molossid *Chaerephon pumilus* has been attributed to habitat fragmentation, during glacial maxima, when vicariance of subtropical forests isolated ancestral populations (Taylor et al., 2009; Naidoo et al., 2013 but see Naidoo et al., 2016).

Bat species richness in savanna is also correlated with current climate where day-to-night temperature oscillation is low compared to summer-to-winter oscillation, and minimum temperatures, mean annual temperatures and annual mean precipitation is relatively high (Andrews and O'Brien, 2000; Qian et al., 2009; Schoeman et al., 2013). Under these climatic conditions the amount and temporal availability of food resources is greatest, as is plant diversity, hence the significantly positive relationship between bat richness and plant richness at broad spatial scales (Andrews and O'Brien, 2000; Qian et al., 2009). Further, the timing of parturition of African insectivorous bats is constrained by rainfall, because insect abundance peaks approximately a

month after the rainfall season starts (Cumming and Bernard, 1997). Bimodal birth peaks of *Epomops franqueti* and *Micropteropus pusillus* in West African tropical savannas coincide with fruit availability (Thomas and Marshall, 1984). Similarly, savanna fruit bats such as *Epomophorus wahlbergi* give birth to pups close to peak abundance of preferred fruit (Cumming and Bernard, 1997). However, in Swaziland the two birth peaks of the species coincide with the onset of the rains (October-November) when fruit availability is high and the beginning of the dry season (April-May) when fruit availability is low (Monadjem and Reside, 2012).

Recently, Pio et al. (2014) used phylogenetic analyses, species distribution modeling (see below), and climate change projections to investigate if threats driven by climate change may result in loss of phylogenetic diversity (PD) in southern African bats, two of the largest plant families in the Cape Floristic Region (Proteaceae and Restionaceae), and an herbivorous insect genus (*Platypleura*) in the family Cicadidae. PD was quantified as rooted PD (Rodrigues and Gaston, 2002) because it was one of the most appropriate ways of accounting for evolutionary history and relatedness between taxa in a conservation context compared to many alternative measures of PD (Pio et al., 2014). Although PD of bats was notably high in the savanna region, it will contract considerably within the next 70 years under likely climate change scenarios. However, changes in PD for these animal and plant clades reveal congruence: PD losses are not significantly higher under predicted extinction than under random extinction simulations.

Underlying the areas of broad-scale distribution of savanna species are three important factors (Soberón and Peterson, 2005): (i) the dispersal capabilities of species, (ii) the spatial distribution of environmental conditions favourable to the establishment and fitness of the individuals (these non-interactive, scenopoetic variables establish the broad spatial limits of distribution), and (iii) the biotic environment determined by competitors, predators and pathogens, together with the availability of resources (these interactive, bionomic variables determine the fine-grained structure of distributions). There has been much progress in modeling the species' potential distribution range or suitable habitat space at broad spatial scales using distribution models or environmental niche models (ENMs) (Warren, 2012). ENMs define the Grinnellian niche and can be used to understand coarse-scale ecological and geographic properties of species (Grinnell, 1917; Peterson, 2003; Soberón, 2007) and assemblages (Schoeman et al., 2013; Pio et al., 2014) as well as assess biogeographic similarity between phylogenetically closely related species (Schoeman et al., 2015). For example, Lamb et al. (2008) investigated the relationships between predicted distributions based on ENMs and phylogeography of populations of giant mastiff bats (*Otomops martiensseni*). The ENMs predicted a potential distribution for *O. martiensseni* largely coinciding with mesic to humid savannas, woodlands, and forests, particularly in areas of rough topography, and two environmental variables, mean maximum temperature in October and topographic roughness, contained the most useful information by themselves in the models. Further, the authors found no evidence of an apparent gap in the Grinnellian niche between records belonging to the north-east lineage and south-east-central-west lineage, suggesting that factors other than habitat suitability under current climatic conditions have resulted in the observed phylogeographic structure. Theses results are not surprising given that molossids such as *Otomops* species have flight characteristics that are adapted for long-distance foraging and dispersal (Norberg and Rayner, 1987). Indeed, among African molossids, there is a significant inverse relationship between wing loading values and genetic structuring (Taylor et al., 2012a).

There is also support for the corollary prediction that populations of slow-flying clutter-adapted species should exhibit more constrained Grinnellian niches and distinct phylogeographic structure. For example, Stoffberg et al. (2012) found five genetically supported geographic groups of *Rhinolophus clivosus* sensu lato in South Africa, with two distinct groups occurring in the Savanna Biome. These groups are corroborated by echolocation and wing morphology data, and MaxEnt modelling shows a strong correlation between the Grinnellian niches of
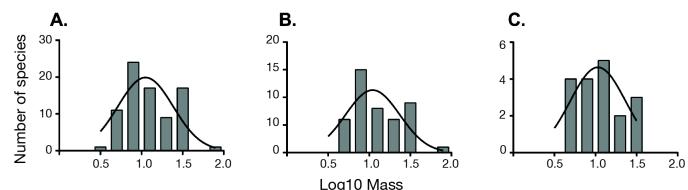

Figure 3 – Distribution of body sizes of insectivorous bats at the A. southern Africa, B. savanna biome, and C. savanna ensemble scale. The expected normal distribution is also shown.

the detected groups and ecoregions. Based on molecular clock calibrations, the authors suggest that climatic cycling and related vegetation changes during the Quaternary may have facilitated diversification both genetically and ecologically. Jacobs et al. (2013) reported distinct Grinnellian niches for two distantly related clades historically lumped in *Rhinolophus darlingi* with similar body sizes: the potentially suitable habitat space for the *darlingi* clade occurs in the south-eastern savannas and is limited by temperature seasonality and favoured by precipitation in the wettest quarter ranging 500–1100 mm, whereas that of the *damarensis* clade occurs in the more arid western part of the sub-region and is limited by mean annual precipitation (>1000 mm) and precipitation and temperature in the wettest quarter.

Body size distribution of savanna insectivorous bats appears to be scale-dependent, becoming progressively more right-skewed and less evenly spaced from local to regional levels (Schoeman and Jacobs, 2008; Fig. 3). Although the regional species pools of the arid zones, fynbos and forest biomes are subsets of the Savanna Biome regional species pool (Schoeman and Jacobs, 2008), small and large-bodied bat species present in savannas are absent from the other biomes. One hypothesized process that may explain the low replacement rate of these species between habitats and geographic regions is the selective extinction of species with large (or small) body sizes and small geographic ranges (Brown and Nicoletto, 1991). Indeed, there is evidence that the extinction risk of bat species is significantly correlated with small geographic ranges (Jones and Purvis, 2003) and there are large-bodied savanna bat species such as *Rhinolophus mossambicus* (20 g) that have smaller geographic ranges than their smaller-bodied congenerics such as *R. darlingi* (9 g) (Monadjem et al., 2010; Taylor et al., 2012a).

Patterns and processes at intermediate, landscape scales

The high spatial heterogeneity of the Savanna Biome (see above) promotes the persistence of high bat species richness by creating new habitats and enlarging environmental gradients (Ruggiero and Kitzberger, 2004). Daylight roost availability in caves and trees can be invoked to explain meso-scaled control over bat assemblage structure, specifically the richness hotspots in southern African savannas (Schoeman et al., 2013). Its influence may be exemplified in the abundance of roosts in crevices and caves across Zimbabwe's "granite shield", and equally in karstic landscapes on dolomitic formations (Monadjem et al., 2010). Moreover, the granite shield is dominated by mature stands of Miombo woodland where a high proportion of large trees have hollow boles that arguably augment roost availability to woodland savanna bats, particularly those belonging to Vespertilionidae, Emballonuridae and Molossidae (Monadjem et al., 2010). In this context, Fenton et al. (1998) attributed the high abundance and species richness of savanna bat assemblages in northern Zimbabwe to the availability of daylight roosts in the Miombo woodlands not negatively impacted by dense elephant populations. Similarly, tree roosts are probably most abundant in the forested relief along the eastern and southern margins of the Great Escarpment and along mountain ranges (Mucina and Geldenhuys, 2006).

Habitat selection in heterogeneous savanna landscapes by relatively mobile animals such as bats operates at many spatial scales (Ober and Hayes, 2008; McConville et al., 2013). Habitat selection theory emphasizes the ability of species to disperse and colonize patches with the highest perceived quality; the resulting patterns of distribution are a function of spatial redistribution of individuals among habitat patches

(Binckley and Resetarits, 2005). Habitat selection can function as a selective filter between a developing assemblage and the regional species pool. Generally, bats move easily among habitats and actively select where they forage (Fenton et al., 1977), reproduce (Van der Merwe, 1975; Brown and Bernard, 1994) or roost (Fenton et al., 1985; Jacobs et al., 2005; Monadjem, 2005). Habitat selection provides one possible explanation for the conspicuous absence of bats from apparently suitable assemblages. However, chance events or exclusions caused by direct interactions with competitors or predators can produce similar results (see below), and therefore should be ruled out as alternative hypotheses before assuming habitat selection is the operative filter at work.

Correlations between bat incidence and habitat characteristics are *de facto* evidence for habitat selection. For example, Monadjem and Reside (2008) found higher bat activity, diversity, species richness and abundance in riparian habitat sites than in the surrounding savanna landscape in Swaziland's lowveld. Riparian habitats generally support higher concentrations of insect prey (Rautenbach et al., 1996) and fruiting trees (Lack, 1987). Riparian habitats may also be selected by bats due to the acoustically uncluttered environment above water (Warren et al., 2000), continuous distinct lines of vegetation that can be used for navigation (Racey and Swift, 1985) and water for drinking (Grindal et al., 1999). Fruit bats were up to 10× more abundant in the riparian habitats than the savannas (Monadjem and Reside, 2008), which was attributed to the availability of fruiting trees such as figs (*Ficus* species) that form an important part of the diet of these bats (Monadjem et al., 2010). In contrast, Rautenbach et al. (1996) found no differences in bat diversity and evenness between riverine habitats and woodland savanna in the Kruger National Park, South Africa. Nonetheless, several species (including *Neoromicia nana*, *Pipistrellus rusticus*, *Eptesicus hottentotus*, *Rhinolophus fumigatus*, *R. darlingi*, *Epomophorus wahlbergi*) were almost entirely restricted to riparian habitats. However, in both studies the species recorded in savanna sites represented a subset of the riparian species; bat assemblages in the riverine versus savanna habitats differed in the relative abundances of species rather than the presence or absence of species per se.

In agro-ecosystems in the Savanna Biome, Noer et al. (2012) reported that two coexisting species of African molossids, the little free-tailed bat, *Chaerephon pumilus*, and the Angolan free-tailed bat, *Mops condylurus* foraged more over sugarcane fields than other habitats available in the area: savanna, riparian forest and urban areas (Fig. 4). Although Noer et al. (2012) did not investigate the availability of insects in the different habitats in the area, molecular diet analysis revealed the presence of insect pest species such as boring moths (*Eldana saccharina* and *Mythimna phaea*) and stinkbugs, yet there was little evidence for trophic niche partitioning between the two species (Bohmann et al., 2011), suggesting that availability of insect prey over the sugarcane fields was not limiting. In an agro-ecosystem dominated by macadamia orchards further north in the Savanna Biome, activity of bats in macadamia orchards and in adjacent natural riparian habitat varied significantly with season, being elevated during mid-late summer when populations of Twin-Spotted (*Bathycoelia natalicola*) and Green (*Nazara* spp.) Stinkbugs peak (Taylor et al., 2013).

Urbanization fragments natural areas into protected or inaccessible patches that are disjunct and dispersed in a mixed human land-use matrix (Forman and Godron, 1986). Consequently, landscape-scale processes mediated by the dispersal of individuals among fragments that differ in size, shape and isolation may play an important role in the distribution and diversity of the resident bat fauna Gorresen et al. (2005). However, Moonsamy (2012) found little support for this hypothesis when accounting for diversity patterns of insectivorous bats in urban and peri-urban reserves of Durban, South Africa. Ensembles were significantly nested, i.e. species-poor ensembles were subsets of species from species-rich ensembles, yet nestedness was not correlated with isolation, size or shape of reserves. In addition, bat activity was positively correlated with the shape of the reserves, where irregular shaped reserves had higher activity than circular reserves. Irregularly shaped reserves probably comprise more edge habitats than circularly shaped
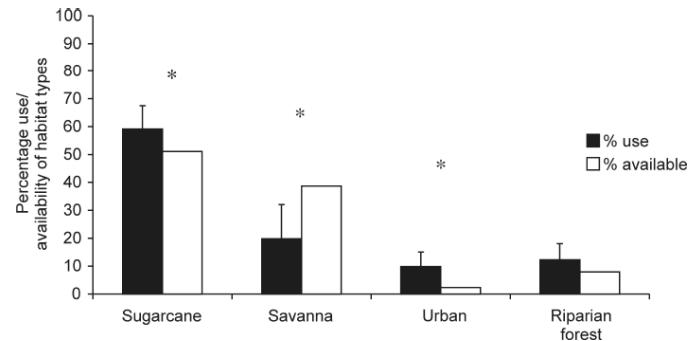

Figure 4 – Mean percentage utilization (± standard error) estimated as minimum convex polygons over the different habitats (sugarcane, savanna, urban and riparian forest) utilized by nine *Chaerephon pumilus* bats compared with the percentage distribution of available habitat within the maximum range circle of *C. pumilus*. * = Significantly different (*p*<0.05).

reserves, which, in turn, provide more habitat space and insect prey (Verboom and Huitema, 1997; Hogberg et al., 2002).

Patterns and processes at a local scale

When species make it through these non-interactive filters, local abiotic conditions and physiological adaptations that permit the establishment, reproduction and survivorship of populations, as well as interspecific interactions (i.e. biotic filters such as competition, predation, and co-evolution), determine the subsequent success or failure of a species to survive in the local community.

In contrast to the Grinnellian niche model, which is relevant to understanding coarse-scale ecological and geographic characteristics of species, the Eltonian niche axiom focuses on biotic interactions and resource–consumer dynamics, and is measured mainly at local scales (Soberón, 2007; Colwell and Rangel, 2009; Devictor et al., 2010). This hierarchical view of the niche is consistent with theories about how factors affecting the structure of biological diversity act at different scales (Mackey and Lindenmayer, 2001; Whittaker et al., 2001; Soberón, 2007).

There are many statistical and ecological benefits to using body size, skull and wing morphology, or echolocation attributes for inferring resource utilization and ecological relationships amongst bats (for a full discussion see Stevens and Willig, 1999; Patterson et al., 2003). Studies of bat community structure in savannas have described phenotypic niche patterns indicative of resource partitioning. For example, Aldridge and Rautenbach (1987) showed that wing morphology and echolocation determines the selection of foraging habitats in coexisting savanna bats, and suggested differences in morphological niches among sympatric species may indicate partitioning of spatial (microhabitat) resources. Findley and Black (1983) and Schoeman and Waddington (2011) described savanna bat ensembles in natural and urban landscapes, respectively, as comprising a large number of morphologically similar species packed together in morphospace, and a small number of morphologically dissimilar species dispersed more distant from this cluster, and therefore presumed to be released from competitive interactions. Nonetheless, with increasing species richness, species packing among morphologically similar species increased (Schoeman and Waddington, 2011).

To disentangle deterministic patterns of community assembly from random expectations, observed patterns in local assemblages can be contrasted to those simulated by null models (Gotelli and Graves, 1996; Myers et al., 2013). If competition influences phenotypic structure, then differences between species should be greater than distances chosen at random from a particular distribution of distances representing the actual or potential regional pool. Alternatively, phenotypic distances between species should be less variable — i.e. species should be more evenly spaced — than distances expected by chance (Schoeman and Jacobs, 2008). Among coexisting savanna species at a local scale, body mass was more evenly spaced than expected from chance (Schoeman and Jacobs, 2008; Fig. 3). Functional group members also exhibited non-random wing and echolocation patterns, particularly in

species rich ensembles. In contrast, Schoeman and Waddington (2011); Pierce (2012) found no evidence that competition influenced body size in urban and peri-urban bat ensembles in the Savanna Biome, yet non-random patterns in wing and echolocation parameters were found at both ensemble and functional group (specifically between open-space bats) levels. However, differential habitat use can also be considered to be an adaptive process without invoking competition through, for example, habitat choice that permits phenotypic segregation (Ravigné et al., 2009).

Evidence that competition drives the divergence in the diets of coexisting bats is conflicting. Findley and Black (1983) developed a model of dietary specializations based on volant or non-volant prey types in diets of coexisting savanna bats, which essentially mirrored their phenotypic niche structure. Closely related species occupy narrow trophic niches near the community centroid and are restricted in resource use because of competitive interactions with near neighbours whereas species on the periphery of the community centroid are taxonomically and ecologically very different from neighbours and hence have broad dietary niches. Conversely, numerous studies show that insectivorous bats foraging in similar habitats of the African savannas consume the same types of prey (Aldridge and Rautenbach, 1987; Jacobs and Barclay, 2009; Schoeman and Jacobs, 2011). Contrary to predictions from competition, dietary overlap between coexisting bats in the Savanna Biome was significantly higher than expected by chance (Schoeman and Jacobs, 2011). However, most published papers on the diet of insectivorous bats are typically at the resolution of insect order. Techniques that allow more detailed dietary analyses, such as DNA barcoding from faeces (Bohmann et al., 2011) may help to better determine the influence of competition on the prey composition in the diets of bats, but have yet to be applied to savanna bats in Africa. The selection of prey size classes by coexisting species may be another important dimension along which the partitioning of food resources takes place (Schoener, 1974). Although species such as *Rhinolophus clivosus* and *Scotophilus dinganii* with larger skulls take larger prey than congeneric species with smaller skulls, the small differences in prey size taken is unlikely to facilitate coexistence of species via resource partitioning (Jacobs et al., 2007; Jacobs and Barclay, 2009). Instead, larger bats take insects over a large range of prey sizes whereas small bats feed predominately on small prey (Aldridge and Rautenbach, 1987; Jacobs and Barclay, 2009).

In addition to, or instead of competition, insect prey defenses may influence both trophic and phenotypic niches of insectivorous bats. The interaction between bats and moths is one of the most cited examples of a coevolutionary arms race (Rydell and Jones, 1995; Waters, 2003). There is strong phylogenetic evidence that at least seven insect orders have independently evolved auditory systems that allow them to detect the echolocation calls of attacking bats (Conner and Corcoran, 2012). There is some evidence that in response, bats may have evolved echolocation calls and/or foraging behaviour that make them less detectable by these hearing defences. For example, the allotonic frequency hypothesis (AFH) proposes that some bat species have evolved echolocation frequencies that are either below (<20 kHz) or above (>60 kHz) the frequency range at which insects, specifically tympanate moths, hear best. The AFH therefore predicts that the percentage of eared moths should be highest in the diet of allotonic bats whose peak echolocation frequencies are relatively inaudible to moths and lowest in syntonic bats, i.e., bats using echolocation frequencies that are audible to moths (Fenton and Fullard, 1979; Fullard, 1982). This appears to be the case in southern Africa both at local and regional scales (Jacobs, 2000; Schoeman and Jacobs, 2003, 2011).

There is also support for the corollary prediction that peak echolocation frequency should be a better predictor of diet than size or wing parameters (Schoeman and Jacobs, 2003, 2011). However, the support for the AFH in trophic niches is largely based on correlation, and correlation need not indicate causation. This means that alternative hypotheses cannot be discounted, for example relationships between habitat structure and peak frequency (Odendaal et al., 2014, but see Stoffberg et al., 2011), as well as between diet and call intensity (Schuchmann and Siemers, 2010) and sensory bias (Safi and Siemers, 2010). Moreover,

bats that take moths may not be less audible to moths than bats that eat fewer moths; for example there is evidence that African moths have a broader hearing range (5–110 kHz) suggesting that their ears may function at frequencies usually considered allotonic (Fullard and Thomas, 1981; Fullard et al., 2008; Jacobs et al., 2008).

Consistent with predictions from the prey defenses hypothesis, echolocation parameters of coexisting bats were more similar than expected from chance (i.e. under-dispersed) in both urban and natural savanna landscapes (Schoeman and Jacobs, 2008; Schoeman and Waddington, 2011). However, habitat filtering processes may also result in under-dispersed phenotypic patterns. For example, the under-dispersed sensory patterns may reflect the narrow but optimal range of echolocation frequencies used by urban insectivorous bats to exploit an abundant but widely distributed resource in open habitats (Jung and Kalko, 2011).

Recently, Minnaar et al. (2014) combined experimental and modeling work to show that at a small spatial scale, artificial light can have a significant, disruptive effect on interactions between *Neoromicia capensis* and their prey species. Specifically, eared moth consumption by *N. capensis* increased six-fold under lit conditions, whereas this prey type typically comprises a very low percentage of the bat's diet under naturally dark conditions (Schoeman and Jacobs, 2003, 2011). Given that several allotonic bat species avoid lit environments (Stone et al., 2009; Stone and Jones, 2012; Lewanzik and Voigth, 2014), this provides evidence that artificial light favours bats that echolocate within the hearing ranges of moths, which may eventually lead to more homogenous community structure (Schoeman, 2016).

A third biotic process that may operate on local scales to influence bat community structure is predation. Generally, bats encounter fewer predators than non-volant mammals of similar size (Sibly and Brown, 2007). Nonetheless, vertebrate predators such as birds, mammals, reptiles and amphibians and even invertebrates hunt bats on a regular basis (Speakman, 1991; Findley, 1993; Nyffeler and Knörnschild, 2013). In the Savanna Biome, predators, such as owls, hawks, and snakes are known to attack bats, often as they leave their roosts at dusk (Kemp and Rautenbach, 1987; Cotterill, 1992; Fenton et al., 1994; Fenton, 1995). Consequently, bats have several behaviours that make them less susceptible to predation, for example delayed time of emergence from day roosts and burst-emergences often accompanied by loud cries (Fenton et al., 1994; Fenton, 1975). Selective responses to high predation rates may involve the evolution of specific phenotypes, or enemy-free space (Jeffries and Lawton, 1984; Fernández-Juricic et al., 2006; Møller and Erritzøe, 2010). For example, species with smaller body sizes (e.g. *Cloeotis percivali*) may be less detectable to vertebrate predators, or those with larger body sizes and more pointed wings (e.g. *Scotophilus dinganii*) may be safe from getting tangled in spider webs or escape threats at greater distances. However, reports of predation on bats are mostly anecdotal and few studies test related hypotheses (Fenton, 1995). To test predation hypotheses age-specific mortality data is necessary that is seldom obtainable for bats (Barclay and Harder, 2003; Monadjem et al., 2015).

Short-term (i.e. days to months) variation in the timing of species invasion, arrival or activity can influence the outcome of biotic interactions and the establishment of species in assemblages. Simple Lotka Volterra competition models or more complex models (Holt et al., 1994) predict that small historical differences, for example differences in the initial abundances of competing species, can result in very different assemblages.

There are scant data on long-term temporal changes in activity and species composition in southern African bat assemblages. In savannas, arthropod and fruit availability is higher during the rainy season than the dry season (Sinclair, 1978; Rautenbach et al., 1988; Cumming and Bernard, 1997; Schoeman and Jacobs, 2011). In African Chiroptera, except for the molossids, the timing of parturition is such that young bats are weaned just before the period of maximum insect and fruit abundance (Cumming and Bernard, 1997). Various savanna bat species, including *Miniopterus natalensis*, *M. fraterculus*, *Myotis tricolor*, *Rhinolophus clivosus* and *Hipposideros caffer* markedly reduce their foraging activity during winter together with migratory habits and vari-

ous physiological and behavioural strategies to delay embryonic development between copulation in the autumn and parturition in midsummer (Bernard, 1980, 1982, 1983; Bernard and Meester, 1982; Van der Merwe et al., 1986; Van der Merwe, 1987; Van der Merwe and Rautenbach, 1987; Bernard and Cumming, 1997). Savanna bats also show different activity patterns each night. Many vespertilionids have bimodal foraging patterns, with high activity levels just after sunset and before sunrise when insect abundance is highest whereas molossids tend to forage on the wing throughout the night (Fenton, 1975; Fenton et al., 1980; Barclay, 1985; Fenton and Rautenbach, 1986; Aldridge and Rautenbach, 1987; Rautenbach et al., 1988). However, there is no evidence for increased roles of competition for food or prey defenses during winter when prey resources are lower in fairly pristine (Schoeman and Jacobs, 2011) or urban (Moonsamy, 2012) ensembles. In fact, temporal partitioning of resources by bats appears unlikely (Saunders and Barclay, 1992; Hickey et al., 1996; Patterson et al., 2003).

Linking patterns across spatial scales

Ecological processes that occur at a local scale (e.g. births, deaths and migration between breeding and overwintering sites) determine the area of actual occurrence of bat species. The aggregated effects of reproduction, range expansion and local extinction over many generations determine the Grinnellian niche of species (Soberón, 2007), often estimated by environmental niche models (Warren, 2012). In this framework, local scale processes may influence patterns at a regional scale. Processes operating at a regional scale (e.g. speciation and Grinnellian range expansion) may, in turn, affect patterns at a local scale, by geographically constraining the colonisation and establishment of local populations. This creates a feedback loop between local and regional processes that drive both statistical and conceptual associations between assemblage patterns at local and regional scales (Buschke et al., 2014), and therefore has been the focus of this review.

Recently, Carstensen et al. (2013) coined the new term "biogeographic scale" for spatial scales greater than the geographic area of the regional species pool (Fig. 2a), essentially incorporating multiple regional species pools. The biogeographic species pool is a representation of the geographical area in which species composition of aggregated assemblages is more similar than composition of assemblages from outside the geographical area. The spatial extent of this pool could be defined as the extent of the savanna ecoregions (Olson et al., 2001) or Afrotropical biogeographic (Procheş and Ramdhani, 2012; Holt et al., 2013) or region (Linder et al., 2012) in which the species occur. Specifically, the biogeographic species pool should be viewed as an emergent property of patterns and processes operating at finer spatial scales (Buschke et al., 2014). Consequently, patterns at the scale of biogeographical regions are the aggregated effect of processes occurring at local and regional scales, but not the other way around. However, new theories are needed to link the regional and biogeographic species pools conceptually because current ecological theories that link local assemblages to the regional species pools are inappropriate (Buschke et al., 2014).

By contrast, patterns at the point scale (Hortal et al., 2010) (Fig. 2d) are influenced by patterns and processes at larger spatial scales, and represent the utilizing of microhabitats of individual organisms in response to immediate stimuli. Specifically, bats will preferentially forage in microhabitats they are most adapted to — e.g. clutter versus clutter-edge versus open-space — and where insect availability is highest. The choice of microhabitat (point scale) is most likely constrained by the choice of foraging and roosting habitat (local and landscape scales) and interspecific interactions, rather than the other way around (Buschke et al., 2014).

Conclusions and future prospects

Clearly ecological community structure of savanna assemblages arises from a combination of abiotic and biotic processes operating at local and regional scales. At a regional scale, membership in the regional species pool is bolstered through speciation mediated by geomorphic and climatic evolution events across north-eastern southern Africa dur-

ing global cooling (Miocene) when seasonal woodland and forest habitats were being replaced by more open savannas, and warm interglacials when tropical forests expanded their ranges southwards. Stable wet and warm climatic conditions and high habitat heterogeneity sustain high taxonomic and phylogenetic diversity in the region. Nonetheless, low replacement rate among regions may indicate the selective extinction of savanna species with large or small body sizes and small geographic ranges. At the meso-scale, habitat fragmentation appears to play a minor role as the high mobility of bats enables them to select habitats across patches and habitats even in human-dominated urban and agricultural landscapes. There is evidence that multiple biotic processes, including competition and predator-prey interactions operate at a local scale as well as a point scale, but non-random patterns are not ubiquitous within and across variables. Although actual occurrences of savanna bat species in the sub-region have been fairly well documented (Monadjem et al., 2010), and used to estimate potential suitable habitats and community structure (e.g. Schoeman et al., 2013; Pio et al., 2014), long-term data on births, deaths, migration and range expansion over many generations are lacking, hence the feedback loop between local and regional scales is difficult to accurately quantify at this stage.

The following are suggested as fields particularly worthy of future research with respect to bat assemblages in savanna ecosystems:

1. Document the degree to which relationships between bat diversity and environmental and biotic processes, as well as stochastic processes and human disturbance, change from large to small spatial scales. This will have major relevance for determining the range of applicability of climatic niche models, global change predictions and macroecological processes (Belmaker and Jetz, 2011).

2. Contrast Grinnellian and Eltonian niches, and combine functional and phylogenetic indices for analysing patterns of community assembly with analyses from simulated and natural assemblages, embracing complexity at multiple scales (e.g. Cadotte et al., 2013; Schoeman et al., 2015). This approach holds the promise for identifying the species most vulnerable to habitat loss and climate change, and those more likely to maintain gene flow across fragmented landscapes, and persist, despite rapid environmental change.

3. Investigate how physical landscape and bat population/assemblage structure affect the epidemiology and genetic structure of their pathogens and parasites and how the pathogens and parasites, in turn, affect the bat assemblage structure and are able to emerge in new host species. Such insights will be critical for managing conservation and public health risk, as well as for forecasting the ecological impacts of changing climate regimes and the next emergent zoonotic disease. ✍

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