



Spatial and temporal dimensions to the taxonomic diversity of arthropods in an arid grassland savannah



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ABSTRACT

Quantifying the drivers of biodiversity variation is a key topic in contemporary ecology. While the geographic distribution of biodiversity is broadly determined by water and energy, local environmental conditions may be important. We evaluated the relative effects of spatial and temporal variation on taxonomic diversity of ground living arthropod communities in central South Africa. Seasonal climate variation was a major driver of arthropod abundance, but seasonal effects differed between habitats. We did not find any evidence for modular community structures, even across different habitats, or any evidence for a nested pattern across seasons. Instead, we observed a spatial nestedness which was only partly related to specific habitats. Our results suggest that neutral processes had influenced arthropod community structure, but also that very local processes may have been pivotal in determining local and regional arthropod diversity. Such processes may not necessarily have been neutral, but could have been caused by niche deterministic processes acting at scales smaller than the distinct habitat classes we used for our study. We further suggest that alterations in climate likely will have substantial effects on the spatial and temporal distribution of arthropod diversity in this arid region.

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1. Introduction

Understanding drivers for the distribution of biological diversity across spatial and temporal scales has emerged as key a topic in contemporary ecology (Reiss et al., 2009). This interest has at least partly been fuelled by a realization of the critical roles biodiversity has for the functioning of ecosystems (Hooper et al., 2005), and subsequently also for the sustenance of humanity (Cardinale et al., 2012). The geographic distributions of biological organisms are broadly determined by interactions of available water and energy (Hawkins et al., 2003). These factors have generated a large scale latitudinal diversity gradient in which the equatorial zones generally contain more diverse biological communities than temperate or polar ones (Hillebrand, 2004). However, although this latitudinal

diversity gradient sets the ecological boundary conditions for patterns of biodiversity (Hubbell, 2001), both local conditions as well as neutral processes such as genetic drift and random dispersal events may impose strong effects on the composition and structure of ecological communities (Rosensweig, 1995; Alonso et al., 2006). Such effects can not be ignored if we aim to fully understand how ecological communities have formed and are maintained.

Taxonomic diversity, which can be regarded as a discrete classification of phylogenetic relationships, may relate to both functional and phylogenetic aspects of diversity and can be seen as a proxy for these more specific diversity dimensions (Hooper et al., 2002). Taxonomic diversity is often partitioned into α , β and γ components to distinguish between different scale-dependent characteristics of variation (Whittaker, 1960). Alpha diversity quantifies the local diversity within a specific site, β diversity quantifies the variability among sampling units for a given area at a given spatial scale, whereas γ diversity quantifies the total diversity of a group of locations and therefore represents regional diversity.

However, although diversity metrics are useful for assessing the

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amount of variation within and among biological communities, they do not fully describe patterns of species distributions across time and space (but see Anderson et al., 2011). In particular, both nested and modular patterns of the spatial distributions of species may be highly relevant for ecosystem properties, but are not readily quantified by various diversity metrics. Nested patterns of species distributions have been recognized since the early half of the past century (Hult  n, 1937). Spatial nestedness indicates a distribution pattern where the distributions of the most widespread species also encompass the distribution of more localized ones (Galeano et al., 2009). Hence, with a truly nested spatial pattern all of the species present within species-poor locations are present within species-rich locations. The species rich locations therefore contain unique species and as a consequence species-poor locations do not contribute to the overall species richness of an area (Slipinski et al., 2012). Modularity describes the extent to which species are clustered into ‘modules’, where species are more ecologically associated within modules than they are across modules (Olesen et al., 2007). Modular patterns remain poorly incorporated into spatial ecology (Th  bault, 2013). This is somewhat surprising, since the extent of modularity is expected to be an important property of ecological communities (Olesen et al., 2007).

Despite ample attention to spatial partitioning of diversity (e.g., Lande, 1996; Crist et al., 2003; Gering et al., 2003; Ulrich et al., 2009), limited attention has been given to the temporal partitioning of species communities (Tylianakis et al., 2005). This is unfortunate, since temporal variation may have significant impact on both regional diversity as well as spatial variation of diversity among different habitats (Tylianakis et al., 2005; Rollin et al., 2015). Repeated studies on tropical invertebrate assemblages have suggested that temporal variation in species turnover may account for up to 20–25% of overall diversity within regions, which are values that are very close to the variation attributed to spatial variation related to different habitats (DeVries et al., 1997; Tylianakis et al., 2005; see also Rollin et al., 2015). The temporal scale of sampling may also introduce substantial methodological bias in quantification of both species richness and diversity measures even in non-seasonal environments (Summerville and Crist, 2005), and seasonal variation in climate may have profound variation on ecological communities as well (Wolda, 1988).

Arthropoda is one the most diverse animal phyla with an estimated species richness of between 5 and 10 million extant species (  degaard, 2000). Arthropod communities are important ecological components and have direct consequences on plant communities both through top-down processes and as a food source for organisms at higher trophic levels (Walker and Jones, 2001). Since arthropods are both abundant and relatively easy to sample, they are frequently used as model organisms for studies evaluating how local environmental factors influence diversity (McGeogh, 1998). However, rigid species-level evaluations of hyper-diverse taxa such as arthropods are logistically daunting and may be subject to taxonomic uncertainty (Williams and Gaston, 1994; Lawton et al., 1998; Cagnolo et al., 2002; B  ldi, 2003). Although the diversity and richness of higher taxon levels may be poor indicators of the diversity of other organism groups (B  ldi, 2003), they seem to correlate well with the diversity of finer taxonomic resolutions within these coarser groupings (Williams and Gaston, 1994; Vanderklift et al., 1998; B  ldi, 2003; Bang and Faeth, 2011). These observations are supported by theoretical arguments for diversity patterns to be robust against taxonomic scale (Storch and   zling, 2008).

Although climate may impose the ultimate boundary conditions for species ranges (Hawkins et al., 2003), the characteristics of local plant communities directly influence the abundance and composition of arthropod communities by acting both as a food source

and as refugia (Southwood et al., 1979). Although stochastic processes may be important for local community assembly (Chase and Mayers, 2011), there is generally a positive association between plant and arthropod diversity which may suggest that niche related processes are important for the composition of local arthropod assemblages. These patterns may be related to the ability of richer plant communities to host richer communities of herbivorous arthropods (Siemann et al., 1998), but also because of a positive secondary effect on predatory and parasitic arthropods (Southwood et al., 1979; Siemann et al., 1998). Furthermore, within the effects imposed by local vegetation characteristics, temporal variation in local climate may also influence the abundance and composition of arthropods at any given time (Wolda, 1988).

Here we use data from a survey of ground living arthropods in central South Africa to evaluate how spatial variation within and across four distinct habitats and temporal variation primarily related to climate influenced abundance as well as α and β diversity of local arthropod communities. Because most arthropods have relatively limited dispersal abilities, we expect that broad scale environmental variables, including climate, have dictated the regional taxonomic pool of arthropods, but that local variation primarily in plant communities has defined the spatial variation in arthropod communities within this regional pool. Furthermore, we expect that temporal variation in climate has defined the community of arthropods within a specific site at any given time. We specifically evaluated the following predictions: (i) there will be an increase in abundance for all taxonomic groups during the wet compared to the dry season, (ii) there will be an increase in both alpha and beta diversity with increasing spatial scale, (iii) there will be an increase in both alpha and beta diversity with increasing temporal scale, (iv) there will be a modular spatial pattern of arthropods among different habitats, and (v) there will be a nested temporal pattern of community composition within these modules, caused by seasonal variation in climate. We conducted the analyses at the taxonomic resolution of order, except for members of myriapods and arachnids, which were grouped across higher taxonomic ranks.

2. Materials and methods

2.1. Study area

We conducted the study on a 11,400 ha privately owned reserve, Benfontein Nature Reserve. Benfontein is situated 10 km south of Kimberley in the Northern Cape province of South Africa (28  50’S, 24  50’E, Fig. 1), and lies within a transitional zone between dry Karoo, grassland and Kalahari thornveld (Schulze and McGee, 1978). The study area has a semiarid climate, with a dry season comprising March to August and a wet season September to February (Kotze et al., 2012).

There are four distinct habitats on the reserve, grassland, pan, savannah and scrubland. The grassland habitat is situated in the eastern part of the reserve, runs through the central part and stretches to the south-western section of the reserve. The two most common grasses in this habitat are *Cymbopogon plurinodis* and *Panicum stapfianum*. Less common species include *Enneapogon desvauxii*, *Tragus koeleriodes* and *Eragrostis lehmanniana* with the karroid shrub *Pentzia incana* growing amongst the grasses. The grassland area surrounding the savanna is a mixture of *Stipagrostis uniplumis* and *E. lehmanniana*. The north-western part of the reserve is covered by a pan area. The majority of the pan habitat is covered by *Salsola exalata* and *Suaeda fruticosa* shrubs but these are frequently intersected by open areas. Another shrub that occurs on the pan is *Psilocaulon articulatum* and there are a few grasses such as *E. bicolor* and *E. truncata*. The entire area has a clay-rich soil

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