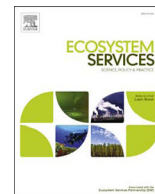




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Large mammal diversity matters for wildlife tourism in Southern African Protected Areas: Insights for management

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ABSTRACT

Relationships between biodiversity and cultural ecosystem services have been little studied compared to other ecosystem services, although fundamental for environmental management. Recreational ecosystem services like wildlife tourism are specific cultural ecosystem services that often involve relationships between the supply of opportunities to interact with biodiversity and the demand of wildlife tourists. Here, we first investigated whether different biodiversity measures based on three metrics applied to four components of large mammal diversity influenced the distribution of visitors within four Protected Areas (PAs) in Southern Africa. Second, we explored whether these effects were context-specific across the four PAs. We counted large mammals and visitor numbers along 196 road transects to test these relationships. All species-mammal diversity metrics related positively to visitor numbers. Subsets of mammal diversity were also positively associated with the distribution of visitors in all PAs. Relationships between supply and demand for the recreational service of wildlife tourism were mainly context-specific: the relationships between biodiversity measures and visitor numbers differed among PAs. Our results could help managers to optimize the use of recreational services within PAs, by diversifying viewing opportunities while reducing disturbance to wildlife. The supply-demand approach presented here offers promising avenues for further assessments of recreational ecosystem services.

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1. Introduction

Biodiversity is assumed to provide multiple benefits to human societies through ecosystem services; yet little is known on the actual relationships between biodiversity and ecosystem services (Balvanera et al., 2013; Mace et al., 2012). In particular, there is a lack of studies investigating the inter-linkages between cultural ecosystem services (CES) and biodiversity (Cardinale et al., 2012). Cultural ecosystem services are the “non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation and aesthetic experience” (Millennium Ecosystem Assessment, 2005). These non-material benefits provided by biodiversity contribute to shaping people's relation to nature (Chan et al., 2016; Cooper et al., 2016; Hausmann et al., 2016) and can improve human well-being (Hausmann et al., 2016; Milner-Gulland et al., 2014; Naem et al., 2016). Investigating the relationships between biodiversity

and CES is, however, problematic because these relationships are often indirect, difficult to measure and to manipulate experimentally (Balvanera et al., 2016; Cardinale et al., 2012). Further, because CES are inherently co-produced by bio-cultural and social-ecological processes (Díaz et al., 2015; Palomo et al., 2016), it is also difficult to ascertain to what extent biodiversity is contributing to CES (Dallimer et al., 2012). Consequently, little is known on the quantitative relationships between biodiversity and CES (Cardinale et al., 2012; Hevia et al., 2017; Mace et al., 2012), even though they are recognized as important in environmental management and conservation policies (Laurila-Pant et al., 2015).

Recreational ecosystem services have been the most studied form of CES (Milcu et al., 2013). Recreational services represent the potential contribution of landscapes and biodiversity to specific recreation opportunities, involving people's physical, intellectual and representational interaction with ecosystems and biodiversity, as defined in the Common International Classification of Ecosystem Services (CICES, Haines-Young and Potschin, 2013). Novel approaches have emerged to estimate the recreation potential associated with biodiversity, involving the collection of local

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field data (Arbieu et al., 2017; Grünwald et al., 2016; Winterbach et al., 2015), social-media data (Hausmann et al., 2017a,b; Martínez Pastur et al., 2016; Willemen et al., 2015), or economic methods such as choice experiments (Veríssimo et al., 2009) or social-ecological approaches to assess wildlife tourists' preferences (Maciejewski and Kerley, 2014). These novel approaches offer promising evidence that biodiversity can support recreational services in different places, particularly in Protected Areas (e.g. Hausmann et al., 2017a; Martínez Pastur et al., 2016).

Protected Areas (PAs) are prime conservation units expected to achieve several objectives such as the conservation of biodiversity and ecosystem services (Watson et al., 2014). PAs play a prominent role in providing recreational services, particularly for nature-based tourism, as they receive worldwide approximately 8 billion visitors per year (Balmford et al., 2015). Nature-based tourism, and in particular wildlife tourism (defined here as a form of nature-based tourism involving encounters with non-domesticated animals), represents a unique opportunity to study the capacity of biodiversity to provide recreational services (Daniel et al., 2012; Wood et al., 2013). Despite this, only few recent studies have demonstrated positive relationships between biodiversity and wildlife tourism in PAs. For example, Siikamäki et al., (2015) showed that PAs with high biodiversity were most attractive for visitors in Finland. Similarly, Booth et al., (2011) highlighted the importance of rare bird species in attracting visitors to PAs in the United Kingdom. Therefore, a comprehensive assessment of how various components of biodiversity actually affect the recreational service of wildlife tourism is currently lacking.

This study seeks to contribute to this assessment of the recreational service of wildlife-tourism by exploring the role of different components of biodiversity in the actual use of this service. Biodiversity metrics, such as species richness, phylogenetic diversity and abundance, can be relevant measures of biodiversity that are essential for the recreational service of wildlife tourism. People may be interested in interacting with many species (high species richness), with dissimilar species (high phylogenetic diversity) or with many individuals (high abundance) (Winterbach et al., 2015). However, these metrics can also be applied to specific subsets of biodiversity in the assessment of the service of wildlife tourism, since people may also be attracted to specific groups of species. In particular, they may prefer charismatic (Arbieu et al., 2017; Di Minin et al., 2013; Di Minin and Moilanen, 2014), rare (Angulo and Courchamp, 2009; Booth et al., 2011) or threatened species (Siikamäki et al., 2015). Assessments of the recreational service of wildlife tourism should therefore cover different components of biodiversity that reflect different recreational opportunities (see Fig. 1), not only considering all species present in an area, but also subsets of charismatic, rare and threatened species (see Dallimer et al., 2012; Siikamäki et al., 2015).

The recreational service of wildlife tourism can be assessed from the perspective of the relationship between supply and demand (Fig. 1). The supply-side refers to the biophysical components and properties, often in combination with human capitals (e.g. infrastructure, machines or knowledge), that are required to provide an ecosystem service in a particular area over a period of time (Burkhard et al., 2012; Geijzendorffer et al., 2015; Palomo et al., 2016; Wei et al., 2017). The demand-side refers to the consumption, use or desire to enjoy a particular ecosystem service by stakeholders to fulfil their needs in a particular area over a period of time (Geijzendorffer et al., 2015; Wei et al., 2017; Wolff et al., 2015). In the context of the recreational service of wildlife tourism, the supply-side refers to the different biodiversity components (*i.e.* all species, subsets of charismatic, rare and threatened species) and metrics (*i.e.* richness, phylogenetic diversity, abundance) that offer opportunities of recreational experiences

(Fig. 1). The demand of wildlife tourism can be expressed by the number of visitors (Balmford et al., 2015; Schägner et al., 2016), their preferences and desires to encounter or see particular species (Ament et al., 2017; Arbieu et al., 2017) or their actual costs and willingness to pay for seeing particular species (Di Minin et al., 2013; Naidoo et al., 2016). This demand can be also influenced by human infrastructure, such as tourism facilities, development of roads or available tourist information (Fig. 1).

The supply- and demand-sides of wildlife tourism can vary across space because of variation in ecosystem capacity, such as habitat structure, and variation in infrastructures, such as tourism facilities (de Vos et al., 2016; Lacitignola et al., 2007; Martínez Pastur et al., 2016; Torres-Sovero et al., 2012). The spatial heterogeneity of the supply- and demand-sides of recreational services is difficult to jointly assess, and few studies have shed light on this (see Crouzat et al., 2015; Paracchini et al., 2014). However, understanding the spatial variation in supply and demand can inform management decisions in PAs (Palomo et al., 2014). For example, the distribution of wildlife tourists can reveal spatial patterns of potential disturbances to wildlife (Lunde et al., 2016, Mulero-Pázmány et al., 2016). Therefore, analysing the spatial variation of the supply and demand of the recreational service of wildlife tourism might provide useful guidance for management within and across PAs.

The main objective of this research was to test the spatial relationship between different biodiversity measures and wildlife tourism in order to understand the supply and demand dimensions of this recreational service within and across four PAs in three countries (Namibia, Botswana, South Africa). We specifically aimed to: (1) test the influence of biodiversity metrics (species richness, phylogenetic diversity, abundance) applied to four components of biodiversity (all species, and subsets of charismatic, rare and threatened species) on visitor numbers along road transects within the four PAs, while testing whether factors related to infrastructure affected the spatial distribution of visitors in the PAs; and (2) to test whether the effects of biodiversity measures on visitor numbers were consistent across the four PAs. In doing so, we conducted transect counts of mammal diversity and abundance (*i.e.* supply) as well as visitor numbers (*i.e.* demand) along road transects in the four PAs. This study offers a novel approach to assess the recreational service of wildlife tourism by considering different biodiversity metrics and components relevant for its supply and by taking into account the spatial variation of its supply and demand.

2. Methods

2.1. Study area

We conducted fieldwork in four PAs (Fig. 2), namely Etosha National Park (Namibia), Chobe National Park (Botswana), Kruger National Park and Hluhluwe-Imfolozi Park (South Africa). The four PAs were selected because they cover a wide gradient in environmental conditions, in particular in rainfall (mean annual rainfall was obtained from the WorldClim database (<http://www.worldclim.org>)), and represent a variety of savannah landscapes (Methods S1 in Supporting Information, see also Table 1 in Arbieu et al., 2017). Savannah ecosystems harbour a unique diversity of large mammals, such as large ungulates and predators, and are prime destinations for wildlife tourists (Akama and Kieti, 2003; Boshoff et al., 2007; Di Minin et al., 2013; Okello et al., 2008). The four PAs were also selected because they contain predator and especially lion populations (the most abundant species of predators and the most sought after by tourists, see Arbieu et al., 2017), and offer the possibility for visitors to use own vehicles or tour-operators (*i.e.* guided drives). All data were collected during

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