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Understanding the Production of Cultural Ecosystem Services and Benefits

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Abstract

As natural systems become increasingly threatened by global change and anthropogenic disturbances, the sustainable provision of ecosystem services has emerged as a global priority. Ecosystem services are essential for human wellbeing, and measuring, assessing and communicating their contribution has become ubiquitous in sustainable management practices. Despite the impressive body of research on ecosystem services, empirical evidence on the production of cultural ecosystem services is limited. Cultural ecosystem services represent a class of service that is largely intangible and that contribute primarily to subjective measures of human wellbeing, including life satisfaction, happiness and sense of belonging. Given the difficulty of measuring intangible services, our understanding of the production of cultural services and benefits remain poorly understood. I addressed gaps in knowledge on cultural ecosystem services by exploring important linkages at different levels of ecological and social organisation that contribute to the production of cultural ecosystem services.

Using birds as a case study through which to explore the concept of cultural ecosystem services, I adopted an interdisciplinary mixed-methods approach involving quantitative and qualitative interview methods. I conducted interviews about 491 bird species with 401 respondents in South Africa. I analysed the data quantitatively and used ancillary datasets to complement my findings. I focused on four interlocking themes.

First, I used functional traits associated with cultural ecosystem services of birds that respondents identified in interviews (i.e. cultural functional traits) to determine whether a consistent typology of cultural functional groups could be established. Using a K-means cluster analysis, I found that there are six consistent cultural functional groups associated with birds. Respondents reported significantly greater benefits from birds with interesting movement and behaviour, whereas bird species with perceived negative visual/oral traits were not well regarded by local users. My findings demonstrate how evaluating cultural ecosystem services through a functional trait lens enables the

translation of complex, intangible attributes that contribute to cultural ecosystem services into discrete units through which cultural benefits can effectively be explored.

Second, the extent to which cultural ecosystem services are co-produced through the interaction between people's personal beliefs, values and experiences and their environment remains poorly understood. Exploring these interactions at the level of an individual provides important insight into the specific socio-cultural factors that drive demand for cultural ecosystem services. I compared perceptions of cultural functional groups across a socially disaggregated sample population to determine whether an individual's socio-demographic characteristics, including where they live, is related to how they perceive cultural functional groups. I found that age, gender, race, language and education determined how people perceived cultural functional groups. My findings highlight the importance of disaggregating ecosystem users by a range of socio-demographic characteristics to better understand the social processes that inform the co-production of cultural ecosystem services.

Third, social-ecological interactions that co-produce cultural ecosystem services occur at different scales and levels, from organism, to community, through to landscape. However, the influence of multi-scale and multi-level variation on cultural ecosystem service production has received limited attention. Thus, the extent to which cultural benefits that are perceived at the level of organisms are in fact produced by broader landscape-level attributes is unknown. To address this gap, I drew on ancillary data that found that perceptions of bird communities had a relatively limited effect on cultural benefits received from birdwatching. By analysing the contribution of landscape-level attributes to birder benefits, I found that biome, variation in elevation and vegetation type contributed significantly to the receipt of birder benefits. My findings demonstrate the importance of incorporating multi-scale and multi-level variation in cultural ecosystem service production, even when the benefits associated with the service appear to be linked to individual organisms and communities.

Fourth, despite widespread application of the functional group approach in ecology, there have been limited studies on spatial variation in functional diversity. Understanding the distribution of functional groups across space can offer insight into how functional richness effects the capacity of the system to produce ecosystem services. I compared the distribution of ecological functional groups (described through measurable phenotypic functional traits) and cultural functional groups (described through human perception of and preferences for cultural functional traits). I found that ecological and cultural functional groups were correlated across South Africa and highly correlated in national parks. Moreover, some ecological functional groups are specifically associated with certain cultural functional groups. These results show that ecological functions influence the capacity of a system to produce cultural ecosystem services and moreover, that cultural ecosystem services are more strongly associated with ecologically relevant functional traits in areas that have lower levels of human influence (i.e. national parks).

In sum, I show that cultural ecosystem services are produced through complex social-ecological interactions at different scales and levels. I have thus demonstrated the importance of recognising and incorporating linkages between people, society and the environment in the assessment of cultural services. Adopting a framework for cultural ecosystem service assessment that deconstructs social-ecological interactions is of critical importance for understanding each step in the flow of cultural ecosystem services, and enables the processes informing the co-production of ecosystem services to be identified.

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1 Introduction

In this thesis, I explore the production of cultural ecosystem services by evaluating the contribution of different components of ecological and social systems to the production of cultural benefits.

First, I describe the conceptual framework I adopt in this thesis in Fig. 1.1 before providing a general outline and some relevant background on the ecosystem services concept. I then detail how the ecological and social components described in Fig. 1.1 address current gaps in ecosystem service research.

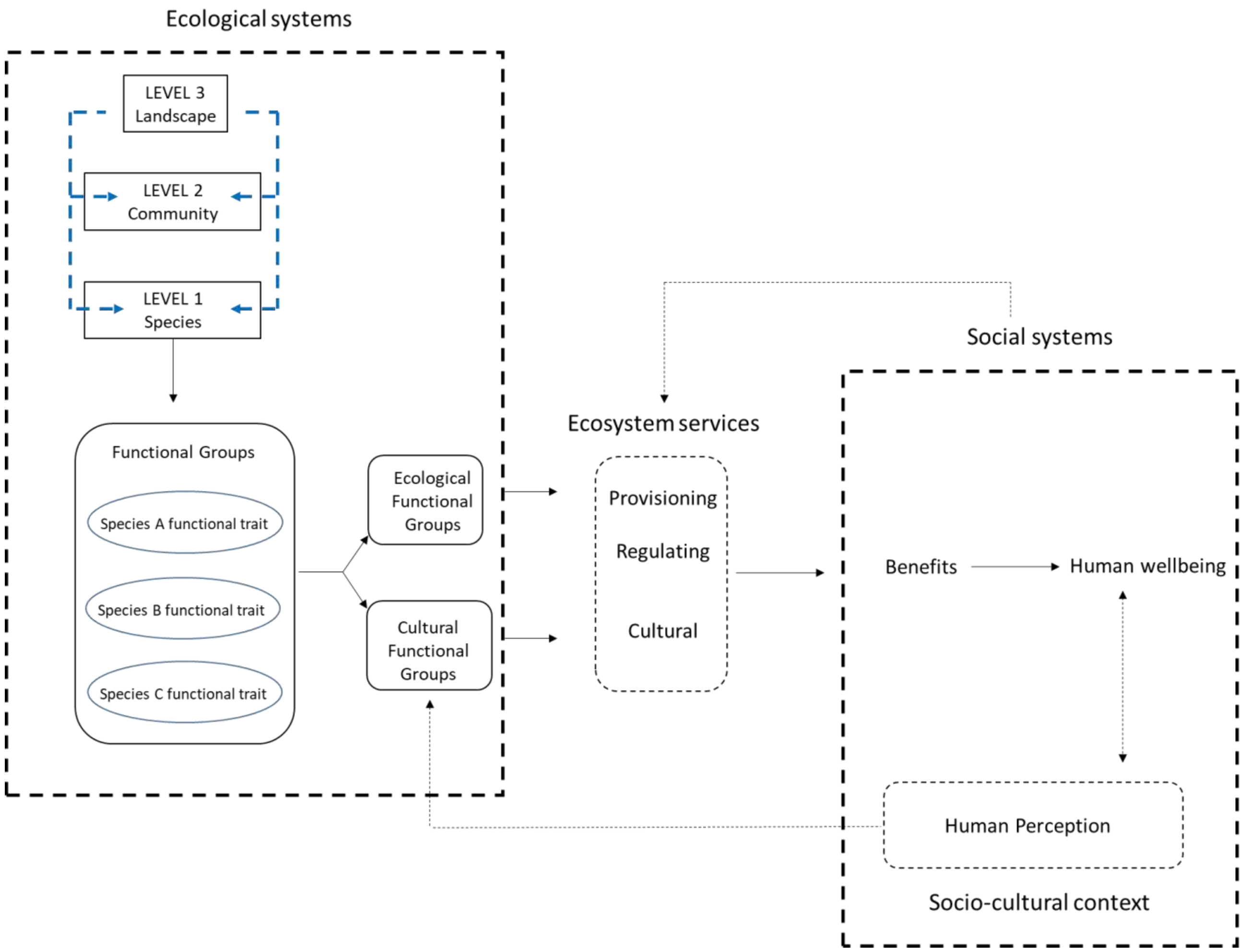


Figure 1.1 Adaptation of an ecosystem cascade model informing the conceptual framework of this thesis. I situate cultural ecosystem services at the interface between ecological and social systems to better understand how different components of each system interact to produce cultural ecosystem services. Ecological systems comprise hierarchically organised levels of ecological systems (i.e. species and communities nested within landscapes) (Hutchinson, 1975). Species that

share specific functional traits can be grouped together to form functional groups. Functional groups are considered to be the primary indicator to identify the effect of biodiversity on ecosystem service production (Echeverri et al., 2019). Functional groups underpin either provisioning or regulating services (defined as ecological functional groups) or cultural services (defined as cultural functional groups). Ecosystem services are co-produced through the interaction between ecological and social system processes, delivering benefits that contribute to human wellbeing. The way ecosystem services are co-produced is strongly shaped by co-construction: the interaction between individuals and their society that influences how ecosystem services are perceived. Individual human perception is thus informed by the individual's socialisation in their specific socio-cultural context. Perceptions of ecosystem benefits feedback to affect the nature of cultural functional groups.

1.1 Ecosystem services

Global changes to climate, biodiversity loss, and increased levels of pollution are adversely affecting the world's ecosystems. These global changes are characteristic of the Anthropocene, an era defined by the proliferation of industry, a growing human population and its increasing demands on natural systems (Cumming, 2016). The consequent outcome has been a rapid global overexploitation of non-renewable resources, resulting in increasingly degraded ecological systems (Wu, 2013). As ecological systems are degraded, non-material dimensions of human wellbeing that contribute to quality of life (i.e. those not captured by monetary estimates, such as life satisfaction) are being reduced (Saunders, 2010). The capacity of nature to contribute to the wellbeing of future generations is thus being diminished, raising issues of intergenerational justice (Barry, 2017). Recognising that measures were needed to mitigate against these threats, sustainability science was developed to enhance an understanding of complex interactions between society and nature (Ehrlich and Ehrlich, 1981).

Fundamentally, sustainability science recognises that nature produces benefits that contribute to human wellbeing and explores the interaction of global processes with ecological and social systems in specific contexts (Kates et al., 2001; Clark and Harley, 2020). In addition, sustainability science recognises that environmental stresses and economic development are inextricably linked, and suggests that minimising the harmful effects of economic development on the environment requires fostering sustainable interactions between people and nature (Turner, 1997; Clark and Harley, 2020). This requires strategies to meet the essential needs of the global population within the bounds of nature's capacity to contribute to these needs (Cassen, 1987). One of the key advances in the sustainability movement has been the development of boundary concepts between social, ecological and economic systems to manage sustainable development (Kates et al., 2001; Braat and De Groot, 2012).

The ecosystem services concept is arguably the most critical boundary concept between social, ecological and economic systems. Ecosystem services are defined as the innate characteristics, functions or processes of the environment that produce benefits that contribute to human wellbeing (Daily, 1997; MA, 2005). The ecosystem services concept was developed toward the end of the 1970's by ecological economists who were dissatisfied with the absence of ecological limits to growth from neoclassical economic theory (Ehrlich and Ehrlich, 1981; Gómez-Baggethun et al., 2010). Ecosystem services thus serve as an interface through which economic interests and sustainable development could meet by identifying and valuing the benefits ecosystems provide (MA, 2005). The ecosystem services framework became ubiquitous upon publication of the Millennium Ecosystem Assessment (MA, 2005), which represented a key progression in the ecosystem services approach by highlighting the impact of environmental change on human wellbeing, and promoting its uptake in policy agendas (Gómez-Baggethun et al., 2010).

Since the release of the MA, research on ecosystem services has increased exponentially (Fisher et al., 2009), and recently, has pivoted from value-driven ecological economics to interdisciplinary social-ecological systems research (Bruckmeier, 2016). However, despite the need for integrated approaches, economic value is the primary metric by which public and private decision-makers are informed of the benefits of ecosystem services (Heydinger, 2016). While economic estimates of ecosystem value are effective in providing a platform to communicate ecological worth to policy makers, land managers and the general public (Chan et al., 2012), this approach requires commodifying ecosystem services (Costanza et al., 1997). The commodification of ecosystem services has become increasingly contentious, particularly when the benefits derived from these services do not adhere to strict economic frameworks (Scholte et al., 2015). This implies that economic estimates of ecosystem services can undermine the value of their benefits, and may not account for benefits that are difficult to measure (Gould et al., 2015; Scholte et al., 2015). As a result, priority measures that result from economic assessments may not be sufficient in conserving the flow of ecosystem services (Polasky and Segerson, 2009). Addressing these challenges requires integrating novel methods into existing frameworks for measuring ecosystem services and their benefits.

I have adopted the Common International Classification of Ecosystem Services (CICES) for measuring and assessing ecosystem services. While recognising that alternative approaches have been implemented (e.g. the International Platform on Biodiversity and Ecosystem Services and The Economics of Ecosystems and Biodiversity), the CICES system provides a useful international standard for describing ecosystem services. Ecosystem services are categorized by CICES into provisioning (e.g. fresh water, firewood), regulating (e.g. climate regulation), and cultural services (non-material services) (Mensah et al., 2017; Echeverri et al., 2019).

The CICES system was adopted over alternative approaches in this thesis because it enables different elements of social and ecological systems that co-produce benefits for people to be identified (Haines-Young and Potschin-Young, 2018). However, it is important to note that efforts to understand the interactions between people and nature are still developing. As a result, this is an evolving field of study that produces novel approaches and promotes conceptual reframing for describing social-ecological interactions (Mastrángelo et al., 2019). The International Platform on Biodiversity and Ecosystem Services (IPBES) in particular has produced significant advances in our understanding of social-ecological interactions. Under the IPBES framework, the term “ecosystem services” is replaced by “nature’s contribution to people” (NCP) in recognition of a need for broader framing of people’s relationship with nature (Díaz et al., 2015). As a result, the IPBES conceptual framework promotes the inclusion of Indigenous Local Knowledge and incorporates a pluralistic approach to knowledge and values (Díaz et al., 2015; Kenter, 2018). However, the NCP concept is still being refined and limitations associated with its use have been identified. Of particular concern is the unidirectional nature of NCP and the subsequent underdevelopment of co-production in assessments (Kenter, 2018; Peterson et al., 2018), as well as limited understanding of feedbacks between social and ecological systems (Mastrángelo et al., 2019). Given the restrictions associated with IPBES and the widespread application of the CICES system, I chose to adopt the latter's approach. This enables me to contribute to the prolific volume of research on ecosystem services, and develop a novel approach for understanding social-ecological interactions within a well-established framework.

Since the development of the ecosystem services concept, efforts to operationalise the ecosystem services framework have produced various conceptual models to measure and monitor their benefits (Potschin and Haines-Young, 2016). Under the CICES system, the ecosystem services cascade model provides a foundational basis for classifying ecosystem services (Haines-Young and Potschin-Young, 2018). The ecosystem services cascade model represents a pathway for the flow of ecosystem services, from production in ecological systems to delivery in social systems (Potschin-Young et al., 2018). In this model, ecosystem services represent the interface between processes and functions in ecological systems (i.e. supply) and their conversion to benefits in social systems (i.e. demand) (Potschin and Haines-Young, 2016). Traditional cascade models identify five linear steps in the production of ecosystem services (Daw et al., 2011; Potschin and Haines-Young, 2011; Fisher et al., 2014). Specifically: biodiversity gives rise to ecosystem functions (step 1). Ecosystem functions underpin ecosystem services (step 2), which then contribute to human wellbeing in social systems (step 3). The contribution of ecosystem services to human wellbeing is converted into use and non-use values (step 4), which are ultimately used to inform policy and decision-making (step 5) (Cook et al., 2020). My thesis addresses limitations associated with traditional step-wise cascade models and proposes a detailed framework to explore the complex socio-ecological interactions that produce ecosystem services (Fig 1.1).

1.2 Cultural ecosystem services

I specifically explore the production of cultural ecosystem services. The CICES defines cultural ecosystem services as the non-material benefits people obtain from ecosystems, including spiritual enrichment, cognitive development, reflection, recreation and aesthetic experiences. Cultural ecosystem services are differentiated from other categories of ecosystem services through their capacity to contribute to life-enriching and life-affirming aspects of human wellbeing (Fish et al., 2016), and consequently, promote deep attachment of local communities to the environment (Chan et al., 2012). Aside from the contribution to people's wellbeing, cultural ecosystem services are crucial to fostering support for conservation and other forms of nature stewardship. Since the sustainable provision of ecosystem services necessitates fostering deep attachment to promote willingness to support conservation action, empirical research on cultural ecosystem services is of critical importance in the sustainability movement (Milcu et al., 2013b). Indeed, cultural ecosystem services are often valued ahead of other services, suggesting that they are ubiquitous in the conservation decisions (Milcu et al., 2013b; Cumming and Maciejewski, 2017). Facilitating the provision of cultural ecosystem services creates a positive feedback loop, wherein conservation action is tailored to contribute to the cultural identity of individuals, and individual preferences for these services support conservation (Turpie, 2003). For example, biodiversity conservation provides intangibles non-market values that contribute to human wellbeing. In turn, communities support biodiversity through willingness to pay for services, such as birdwatching (Turpie, 2003; Cumming and Maciejewski, 2017).

Despite their important contributions to sustainability, research on cultural ecosystem services and the benefits they deliver remains nascent (Milcu et al., 2013b), especially compared with scholarship focused on other services. Much of the discourse on cultural ecosystem services still centers on the supply of ecosystem services from ecological structures and functions, and not the social constructs that drive demand for these services (Fischer and Eastwood, 2016; Arbieu et al., 2017). Cultural ecosystem service assessments are thus at risk of minimising the extent to which people are central in driving the production of ecosystem services (Echeverri et al., 2019). My thesis investigates and challenges commonly held assumptions about cultural ecosystem services by exploring the drivers of their production, and not just the services at hand.

To align with the utilitarian nature of the ecosystem services framework, it is critical that the value of cultural ecosystem services is measured. However, the benefits associated with cultural ecosystem services are largely intangible and thus difficult to measure, communicate and methodically replicate (Jones et al., 2021). Recognising that traditional economic approaches of describing the value of cultural ecosystem services through monetary estimates cannot capture the full range of benefits that are present, there has been increased effort to evaluate cultural ecosystem services by drawing on principles from a range of disciplines, including ecology, economics, and the social sciences (Milcu et al., 2013b). A particularly useful strategy for capturing the value of cultural ecosystem services relies on translating people's perception of nature into quantifiable terms. Perceptions in this context refer to the ways an individual relates to the environment through their personal observations and interpretations which are constructed through their values, norms, beliefs, knowledge, and experiences (Bennett et al., 2016).

1.3 Research gaps and relevant literature

In this thesis I address 4 broad research needs relating to ecological and social systems in the production of cultural ecosystem service literature identified in Figure 1.1. More specific research gaps are discussed in the relevant chapters (Chapters 3 to 6).

1.3.1 Ecological systems

1.3.1.1 Hierarchical levels in ecological organisation

The delivery of cultural ecosystem services have typically been assessed from the viewpoint of the service at hand, predominantly at the species level (Kunz et al., 2011) or landscape scale (Pastur et al., 2016). However, ecological systems comprise multiple levels of ecological organization, and it has been suggested that the nature of hierarchical organization of ecological levels (i.e. organisms and communities nested within ecosystems) has important implications for the delivery of ecosystem services (Bruley et al., 2021). Moreover, landscapes exhibit substantial variation within ecosystems, and yet geographic and spatial relationships, particularly as they relate to multi-scale variation (i.e. site to landscape), have been poorly incorporated into ecosystem service analyses (Potschin and Haines-Young, 2011). Understanding spatial relationships at different scales represents an important frontier in our understanding of ecosystem service delivery and can offer insight into how local and regional supply and demand of cultural ecosystem services is mediated by social-ecological interactions. I address this gap by determining how variation in landscape characteristics at different scales and levels contributes to the provision of cultural ecosystem services.

1.3.1.2. Ecosystem functions

The concept of ecosystem functions is rooted in community ecology and was originally used to understand the impact of morphological differentiation of species traits on ecosystem processes (Blondel, 2003). Species with specific functional traits are allocated into groups that represent a suite of similar functional traits (i.e. functional groups), providing simplified descriptions of ecological organisation that support decision making in the management of ecosystems (Bellwood et al., 2019; Haller-Bull and Rovenskaya, 2019). Ecosystem functions underpin a system's capacity to generate ecosystem services, and are thus critical in safeguarding the production of ecosystem services (Bellwood et al., 2019). Functional ecology has subsequently emerged at the forefront of conservation discourse, and has fundamentally improved our understanding of the ecosystem processes that promote the delivery of ecosystem services (Ovaskainen et al., 2017). Ecosystem functions are thus a useful tool for translating complex ecological structures and processes into discrete ecological units that underpin ecosystem service production (de Groot et al., 2002)

Since ecosystem functions are described by measurable ecological traits of an organism, such as physiological, structural, behavioural, or phenological characteristics (Blondel, 2003), traditional ecosystem cascade models consider ecosystem functions to be mediated only through ecological processes (Braat and De Groot, 2012). Human preferences and perceptions are thus regarded as exerting limited selective pressure on how functional groups are organised and where they are distributed in the landscape (Diaz et al., 2011; Lefcheck et al., 2015). However, the cascade model's translation of ecosystem functions minimizes the extent to which demand for ecosystem services and benefits in social systems have feedback effects on human-mediated management decisions on ecological systems (Tengberg et al., 2012; Clements and Cumming, 2017). This suggests that ecological functions may not be the exclusive drivers underpinning ecosystem services. Cultural ecosystem services in particular are produced through subjective perceptions; their production depends on human responses to specific traits, such as the aesthetic value of an organism. I address this gap in knowledge on the functional drivers behind cultural ecosystem services by adopting a trait-based framework and exploring the extent to which cultural and ecological functions are aligned in the provision of cultural ecosystem services.

1.3.2 Social systems

1.3.2.1 Co-production and co-construction

The delivery of ecosystem services is inherently anthropocentric, since it is the presence of people that enables complex ecological processes to be translated into services (de Groot et al., 2002). The social-ecological interaction between people (organised in social systems) and their environment (organised in ecological and biophysical systems) that produces ecosystem services is referred to as co-production, and is at the heart of the ecosystem services concept (Fischer and Eastwood, 2016). Co-production is not a uniform function, however; it can exhibit substantial heterogeneity between people as it is influenced by a myriad of interdependent, individual-specific factors, including socialisation, stakeholder perception, place attachment and the type of knowledge people hold (Milcu et al., 2015; Scholte et al., 2015; Fischer and Eastwood, 2016). The way in which ecosystem services are co-produced is therefore also strongly shaped by co-construction: the interaction between individuals and their society that influences the meanings people assign to ecosystem services (Fischer and Eastwood, 2016). Identifying the linkages between co-production, co-construction and the delivery of ecosystem services is important to improving empirical research on cultural ecosystem services, particularly since the contribution of these service to human wellbeing is subjective and therefore unlikely to be homogenous within a society. However, most studies that focus on cultural ecosystem services do not examine heterogeneity in the socio-cultural dynamics that produce preferences for these services (Plieninger et al., 2013; Zoderer et al., 2016). These analyses tend to rely on aggregate values (i.e., those that relate to the population as a whole), despite the influence of differing social constructs on perceptions of cultural ecosystem services (Daw et al., 2011). I address the critical gap in our understanding of co-production and co-construction by adopting a socially-disaggregated approach to cultural ecosystem service delivery, focusing on how an individual's identification with a particular socio-demographic context affects their perceptions of the cultural ecosystem services and contributes to the co-construction of their value (Martín-López et al., 2012; Fischer and Eastwood, 2016).

1.3.2.2 The ecosystem cascade model

Current cascade models have been criticized for over-emphasizing the contribution of natural capital to ecosystem services while overlooking important social processes at different intersections of cultural ecosystem service delivery (Cook et al., 2020). As a result, potentially important interactions between ecology, people and society that produce cultural ecosystem services are poorly understood (Bruley et al., 2021). I expand on current cascade models to incorporate deeper complexity in the provision of cultural ecosystem services (See Fig. 1.1 for more detail).

1.4 Thesis aims

In this thesis, I aim to contribute to a better understanding of the complex social-ecological interactions at different scales and levels that produce cultural ecosystem services, using birds as a case study. I address my aim and contribute to filling the research gaps that I identify through four objectives, each corresponding to a thesis chapter:

1. Determine if cultural functional traits of birds that underpin cultural ecosystem services can be used to create a consistent typology of cultural functional groups (Chapter 3).
2. Determine if the ways in which people perceive cultural functional groups are related to the socio-demographic characteristics and residential location of ecosystem users (Chapter 4).

3. Determine the extent to which landscape attributes contribute to the cultural benefits people experience from birding (Chapter 5).
4. Determine whether cultural services are produced by birds with different ecological functions (Chapter 6).

1.5 Birds as a case study

My thesis focuses on the cultural services provided by birds in South Africa. Using a specific taxon is a specific reflection of the more general need to develop model taxa and datasets that can help us interrogate and test ecosystem service concepts more deeply. Birds are useful species with which to explore the production of cultural ecosystem services, since they are prevalent and conspicuous in most ecosystems, and hold particular salience for ecosystem users (Whelan et al., 2015). The contribution of birds to cultural ecosystem services has predominantly been explored at the level of individual species or communities (Sekercioglu, 2002; Whelan et al., 2008), but the way that a person experiences a bird is embedded in the context in which that bird lives. The bird is also dependent on that landscape for resources like food and habitat (Whelan et al., 2015). Despite their capacity to produce cultural ecosystem services, studies on birds are limited to ecosystem benefits associated with recreation and tourism (Sekercioglu, 2006; Wenny et al., 2011; Whelan et al., 2015). Understanding the cultural ecosystem services provided by birds will thus enable the identification of cultural benefits at multiple scales and levels and further, enable disaggregated values to be captured to account for variation in co-construction.

1.6 Study region

My thesis focuses on five provinces in South Africa: Western Cape, Northern Cape, Eastern Cape, Mpumalanga, and Limpopo. These selected areas contain six of the country's nine biomes: Albany Thicket, Forest, Fynbos, Grassland, Savanna, and Succulent Karroo. This diversity in vegetation supports South Africa's rich birdlife, with 856 species recorded, 68 of which are endemic (Taylor and Peacock, 2018). Birdwatching is prevalent in South Africa, and has contributed significantly to conservation and tourism, with avitourism contributing ZAR ~1 billion to South Africa's economy annually (Rogerson et al., 2013). Moreover, South Africa has progressed research in avifauna through the Southern African Bird Atlas Projects 1 and 2 (SABAP and SABAP2). Despite extensive opportunity for research on avifauna in South Africa, their contribution to cultural ecosystem services has been limited (Cumming and Maciejewski, 2017).

South Africa encompasses a diverse population, recognising 11 official languages, and four distinct ethnic groups: Black (80.2%), Coloured (i.e. person of mixed ancestry) (8.8%), Indian/Asian (2.5%) and White (8.4%) (Census, 2011). Birds hold important symbolic value for South Africans, particularly around ancestral relations and providing a sense of place and identity (Gijsbertsen, 2012).

1.7 Thesis outline

I address my thesis objectives in four data-based chapters, adapted from manuscripts prepared for peer-reviewed publication.

In **Chapter 3**, I address my first objective to determine if cultural functional traits of birds can be used to create a consistent typology of cultural functional groups. Ecological functional traits of birds have previously been described for provisioning and regulating services (Sekercioglu, 2002). This chapter elaborates on the foundational work of avian functional groups by using interview data from a range of respondents with varying socio-demographic characteristics to identity cultural functional traits of birds that underpin their cultural ecosystem services. These traits are then used to create cultural functional groups, and their significance is explored in detail.

I build on **Chapter 3**'s findings in **Chapter 4** by exploring how a respondent's socio-demographic characteristics and location are related to perceptions of cultural functional group. This chapter draws on the literature on access (Ribot and Peluso, 2003) and emerging work taking a socially disaggregated approach to ecosystem service (Lau et al., 2018) to identify key social constructs that may influence how individuals interact with cultural functional groups.

In **Chapter 5,** I address my third objective of determining the extent to which landscape attributes contribute to the cultural benefits people experience from birding. I expand on work by Cumming and Maciejewski (2017), who found that bird-related variables contributed to a relatively small proportion of benefits people experience from birding. By quantifying the effects of variation in landscape-level attributes to the cultural benefits of birdwatching, this chapter helps to disentangle the relative contributions of different levels and scales of ecological organization to the provision of cultural benefits.

Finally, in **Chapter 6**, I focus on the relationship between cultural and ecological functions. **Chapter 6** thus addresses my fourth objective of determining whether cultural services are produced by birds with different ecological functions. I approach this objective by determining the distribution of avian cultural and ecological functions and identifying whether their distributions suggest patterns of correlation. Determining the extent to which different functions are correlated allows me to address my fourth objective by describing whether specific cultural functions are associated with specific ecological functions. In so doing, I identify potential trade-offs between the provision of cultural services from birds and other avian ecosystem services.

2 Methodological approach, study sites, and data collection

In this chapter, I describe some general elements of the methodological approach that I adopted for my four data-based chapters. After summarising the key elements of my approach, I provide information on my study sites, sampling design and interview design.

2.1 Approach

To understand the production of cultural ecosystem services and benefits, I focused on the cultural services and benefits provided by birds (Aves) to a demographically diverse human sample population. Using a specific taxon is a useful way to address and test ecosystem service concepts, recognising that extrapolating these methods to alternative systems and taxa will benefit the body of research on cultural ecosystem services. I specifically focus on cultural ecosystem services associated with birds since these services capture important ways in which people relate to nature, and have the potential to be extrapolated to other systems (Echeverri et al., 2019).

All data chapters employed an interdisciplinary mixed-methods approach involving quantitative and qualitative interview methods. I used three datasets to address my objectives. Firstly, to understand the underlying cultural functional traits of birds that produce cultural ecosystem services, I used a mixture of convenience and purposive sampling to conduct semi-structured interviews with participants (Etikan, 2016). Through this approach, I was able to capture people's perceptions of bird species traits and using statistical approaches, I converted these perceptions to quantitative data that facilitated exploration of the concept of cultural functional groups. This dataset will hereafter be referred to as trait data, and is discussed in greater detail in Section 2.3. Secondly, I used an ancillary dataset on the subjective experiences of birders and their bird-related observations captured through interviews in survey format. This dataset is complemented by measurements of landscape attributes to address Objective 3. These data will hereafter be referred to as landscape data and discussed in greater detail in Section 2.4. Finally, I used quantitative data on the organisation of avian ecological functional groups and their distribution in South Africa to address Objective 4. These datasets will hereafter be referred to as ecological data, and include a refinement of Sekercioglu's (2006) classification of avian ecological functional groups based on bird distribution data from the Southern African Bird Atlas Project (SABAP2) (see Section 2.5 and Table 2.1).

These data will be discussed further in the relevant chapters.

Table 2.1 Dataset used in each of the data chapters.

Chapter	Title	Objective	Dataset
Chapter 3	Defining cultural functional groups based on perceived traits assigned to birds	1. Determine if cultural functional traits of birds identified by individuals that underpin cultural ecosystem services can be used to create justifiable cultural functional groups	Trait data
Chapter 4	The role of socio demographic characteristics in mediating relationships between people and nature	2. Determine if disaggregating ecosystem users by socio-demographic characteristics and location can explain differences in perceptions of cultural functional groups	Trait data
Chapter 5	The influence of landscape context on the production of cultural ecosystem services	3. Determine the extent to which landscape attributes contribute to the cultural benefits people experience from birding	Landscape data
Chapter 6	Cultural ecosystem services from birds relate closely to avian ecological functions	4. Determine whether human selection for cultural ecosystem services affects the range of ecological functions in a system	Ecological data; Trait data

2.2 Study sites

South Africa is a multicultural country comprising ~58.78 million people (Census, 2011). From 1948–1994, South Africa was governed by a policy of apartheid, characterised by legislation that institutionalised segregation of races and cultures (Butler, 2003). This legislation was partly enforced through physical separation of races, particularly through the creation of homelands (Promotion of Bantu Self-Government Act, 1956). This Act removed African people from urban and "white" areas into designated "Bantustans" based on cultural and linguistic markers (Chisholm, 2012). The resulting economic and social impacts included disparate wealth distribution along an urban-rural gradient, as well as independent cultural development (Amodio and Chiovelli, 2014). Despite progress in economic and cultural integration since the end of apartheid, South African society is still economically and socially divided (Amodio and Chiovelli, 2014). South Africa recognises 11 official languages and four distinct ethnic groups: Black (80.6%), Coloured (i.e. person of mixed ancestry) (8.7%), Indian/Asian (2.5%) and White (8.1%) (Census, 2011). Access to education, healthcare and amenities are locally dependent, with basic services more restricted in rural settings (34.7% of the population).

South Africa supports rich birdlife, with 856 species recorded, 68 of which are endemic (Taylor, 2018). South Africa's rich avian biodiversity contributes to the wellbeing of the population through a range of ecosystem services, including cultural (e.g. eco-tourism), regulating (e.g. pest control and waste decomposition), and provisioning services (e.g. supply of food) (Sekercioglu, 2006; Cox et al., 2018). Delivery of these services is critical for human survival, and additionally provides an important component of the South African economy (Taylor, 2018).

This research took place in five provinces in South Africa: Western Cape, Northern Cape, Eastern Cape, Mpumalanga and Limpopo (Fig. 2.1). My study sites were selected to fulfil criteria of encompassing both urban and rural environments, being safe, feasible and efficient to access, and comprising diverse socio-demographic groups.

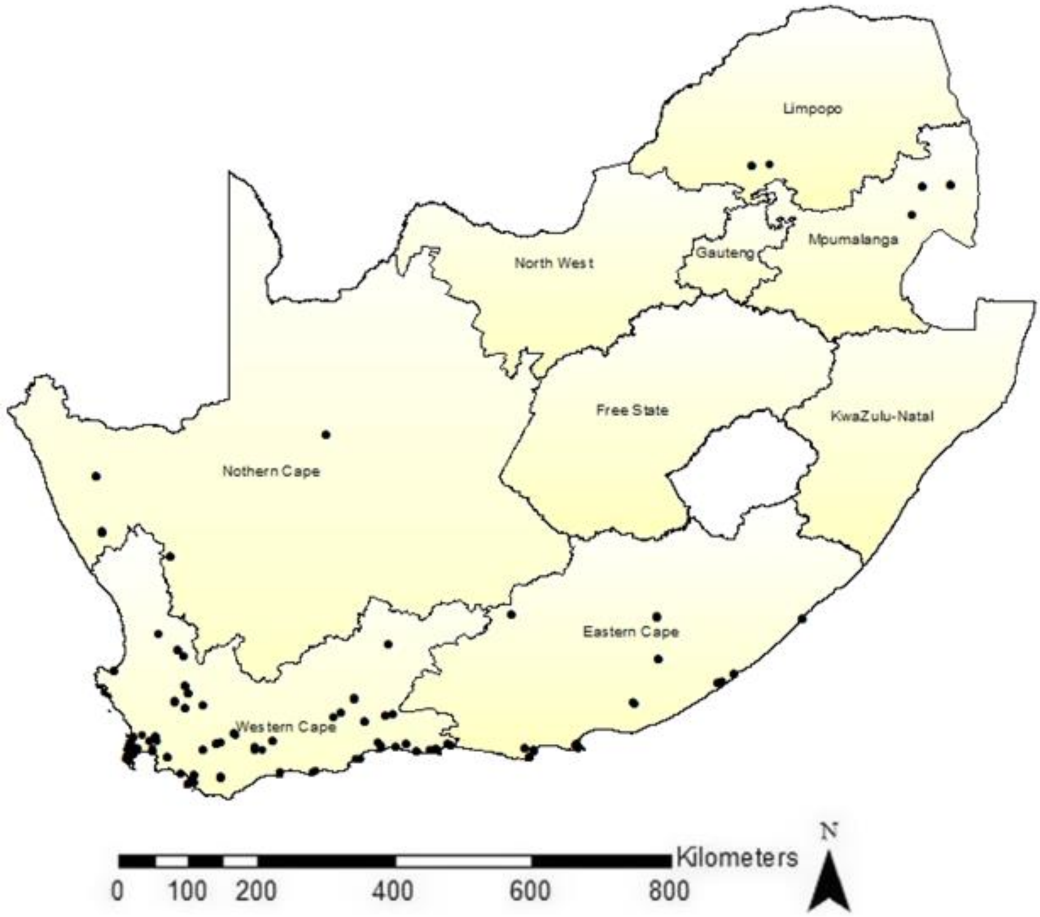


Figure 2.1 Map of study sites in five provinces in South Africa.

2.3 Trait data

2.3.1 Sampling respondents

To select respondents for semi-structured interviews, I used a mixture of convenience and purposive sampling. In total I interviewed 401 respondents from May 2016 to December 2017. Participating respondents were selected to enhance individual variation in social-demographic identity to allow investigation into differences in human perception. To recruit respondents, a focal person was selected in each site via the Birdlife South Africa network and tourism bureaus. Through the focal person, interested respondents were identified and interviewed. Potential respondents were also approached opportunistically in public spaces in each location and consenting individuals were interviewed. Given the variety of people this approach encompassed, my dataset included responses from inter alia the general public, land managers, farm managers and labourers, conservationists, students and tour guides.

While time and budget constraints concentrated interviews in the Western Cape, South Africa's demographic variability was well-represented in the sample (Census, 2011). However, varying responses to my requests to participate in the study resulted in an uneven distribution of socio-demographic characteristics, and in particular the underrepresentation of black South Africans in this sample (Table 2.2). I established differences in socio-demography by age, ethnicity/race and socio-linguistic markers in accordance with established definitions (Crenshaw and Robison, 2010). My dataset thus included individuals from three self-identified racial groups reflecting the approach undertaken in the 2011 South African census (Table 2.2). Respondents were sampled using a paired sampling design under which respondents from at least two different socio-demographic backgrounds were interviewed in urban locations and adjacent rural areas. Although the ratio of urban to rural respondents was not always consistent, a minimum of two respondents per environment (rural or urban) were interviewed within each location. Selecting respondents along an urban-rural gradient allowed me to capture responses from individuals from a diverse range of landscape structures and who rely on ecosystems with varying capacities to produce services (Herrero-Jáuregui et al., 2019). The dataset included individuals who occupied a range of locations along an urban-rural gradient, specifically city centres (n=26), just outside the city (n=16), city suburbs (n=44), farms (n=80), nature reserves (n=19), rural areas (n=92), towns (n=101), just outside towns (n=7) and townships (n=16).

Table 2.2 Summary of socio-demographic data collected during the 2016-2017 collection period and data from the 2011 South African census.

	2016-2017 Sample data (%)	2011 Census data (%)
Ethnicity		
Black African	32	79
Coloured	26	9
White	39	9
Gender		
Male	47	49
Female	53	51
Age		
0-14	1	29
15-64	90	65
64+	8	5

2.3.2 Interview design

Respondents were interviewed in person using an adaptation of Q-factor analysis (Stephenson, 1953) in which they were asked to rank a random selection of 30 bird species by arranging their photos on a scoreboard in alignment with their subjective evaluation i.e. how well they liked the species (see Fig. 2.2). The photo of the bird species was therefore used as a symbol of the species, with respondents citing their experiential knowledge to explain the species position on the scoreboard. This was especially useful when interviewing non-birders, who might have seen the species in their local environment but not have been familiar with the species name. The scoreboard consisted of 30 open blocks arranged in a normal distribution, where each block represented a value between one and 10. It was explained to respondents that a score of one indicates a negative response to the bird and 10 a positive response, with five and six indicating a neutral attitude toward it. Respondents were then asked to justify their score for each species by detailing the traits they as individuals perceived in that species. There was no limit to the number of traits a person could cite. After sampling 401 respondents, responses were inductively coded into 45 trait categories. An example of a response is as follows: “Karoo Prinia scores a 5 because it’s common and I see it often in fynbos habitats. I really like fynbos because it reminds me of hiking with my family. It also has a distinctive song although I don’t like the sound of it”. From this description, the following traits would have received a score: “common”, “positive habitat association” and “negative song”. Traits were scored as either present (1) or absent (0). This process was repeated for 30 bird species per respondent, with the length of interviews ranging between 1 to 2 hours.

Figure 2.2 Respondent sorting and scoring bird species.

Relevant socio-demographic characteristics were also obtained from each respondent during the interview process, allowing me to relate perceptions of bird traits to the socio-demographic characteristics of individual respondents. Drawing on published literature, I identified the following socio-demographic characteristics as potentially important in influencing perceptions of cultural functional groups in the context of South Africa: education, gender, language, race, residential location, coarse residential location and birding self-classification. The potential importance of these characteristics as influences on perceptions of cultural functional groups is outlined in Table 2.3. I included biogeographical variables to control for external factors that may influence people’s perceptions of cultural functional groups. These variables included biome and province, since local vegetation influences the distribution of bird communities (Belaire et al., 2015). I additionally included frequency of bird encounters (ranging from daily to yearly) as a control variable, since greater frequencies of interactions with birds may create a feedback loop in which more sightings of bird species increases the ability of individuals to perceive their cultural functions (Clergeau et al., 1998; Gaston et al., 2018).

Table 2.3 Socio-demographic characteristics of respondents, how they were measured and how these characteristics might influence perception of ecosystem services, with examples.

Socio-demographic characteristic	Measurement	Category	Mechanism and examples
Age	Years	Continuous	Age has been shown to be related to perceptions of ecosystem services (Daw et al. 2011), with related priorities, responsibility and entitlements shifting with age (Lau et al., 2019; Lapointe et al., 2020). For example, Lau et al. (2019) found that older respondents assigned higher ratings to fuelwood than younger respondents in Papua New Guinea.
Birding self-classification	Interest level	Non-birder Casual birder Enthusiastic birder Fanatical birder	Elements of identity directly related to the service at hand have been shown to influence perceptions of ecosystem services. For example, Hicks and Cinner (2014) found that the fishery benefits people perceived from coral reefs were directly related to their strength of identity as a fisher.
Race	Self-classified racial identity	Black Coloured White	In a South African context, race and language are key markers of a person’s identity (Ramutsindela, 2007). Since ecosystem services are co-constructed (Fischer and Eastwood, 2016), knowledge, experience and preferences for ecosystem services are likely to be influenced by race and language.
Languages	Self-identified home language	Afrikaans English Xhosa Other African languages	
Gender	Self-identified gender	Male Female	Normative gender roles have been shown to influence access to ecosystem services and the way these services are perceived (Lau et al., 2019; Yang et al., 2019). For example, Yang et al. (2018) suggested that women generally express stronger connections to cultural

			ecosystem services and have a greater awareness of the spiritual benefits of ecosystem services.
Years of formal education	Years of school completed	<Grade 10 Grade 10 to Grade 12 Diploma Degree Honours graduate Masters graduates PhD graduates	Perceptions of ecosystem services have been shown to be influenced by level of formal education as knowledge on ecological systems shift (Echeverri et al. 2019; Lau et al. 2019). For example, Hicks and Cinner (2014) found that years of education influenced how respondents perceived material benefits associated with ecosystem services in Madagascar and Tanzania.
Residential Location	Self-identified residential classification	City centre Just outside city City suburbs Town Just outside town Township Farm Nature Reserve Rural	Bird diversity decreases with urbanisation, suggesting that an individual's position along an urbanisation gradient, both at the residential level and coarse level (simple urban vs. rural contrasts), is likely to affect biodiversity-based perception of ecosystem services (Clergeau et al., 1998).
Coarse Location	Broad classification based on population, infrastructure and access to nature	Rural Urban	

2.3.3 Species sub-sample selection

The 30 bird species for each individual interview were selected to ensure that respondents were familiar – or could in theory be familiar – with the species they were evaluating. The selection of bird species required two stages: firstly, 30 species were randomly selected from the 491 species in the study. Secondly, the distribution of these species was determined from Sinclair (2012) and cross-referenced with the respondent's location. Where respondent location and species distribution did not coincide, that bird species was discarded and an alternative species selected.

2.4 Landscape data

2.4.1. Sampling

To determine the relationships between the subjective experiences of the birders, their bird-related observations and quantifiable biophysical attributes of the landscape, I used the dataset for bird counts and birder experiences described in Cumming and Maciejewski (2017). Data were collected along 293 routes from all 19 of South Africa's National Parks: Addo, Agulhas, Augrabies, Bontebok, Camdeboo, Garden Route, Golden Gate, Karoo, Kgalagadi, Kruger, Mapungubwe, Marakele, Mokala, Mountain Zebra, Namaqua, Richtersveld, Table Mountain, Tankwa-Karoo, and West Coast from 2016 to 2017 (Fig. 2.3) (Cumming and Maciejewski, 2017). To collect these data, amateur birders went birding twice a day for at least two hours over a minimum distance of 2 km while wearing a Garmin GPS Forerunner 310XT wristwatch. Amateur birders were selected through purposive sampling. After completing each route, the track was downloaded from the wristwatch. The amateur birders submitted a list of birds they saw and/or heard, and completed a satisfaction survey (see Section 2.4.2). In total, 101 people participated in this study. Most participants were experienced and well-established birders in South Africa, where the mean number of years of birding experience was 18.6 (±SD 12.3), and the mean number of South African birds seen by participants was 483 (±SD 201) (Cumming and Maciejewski, 2017). While there was an even divide of gender (50 female and 51 male), there was limited variability in socio-demographic characteristics of participants (specifically an over-representation of white participants), reflecting broader demographic patterns of national park visitors in South Africa (Scholtz et al., 2015).

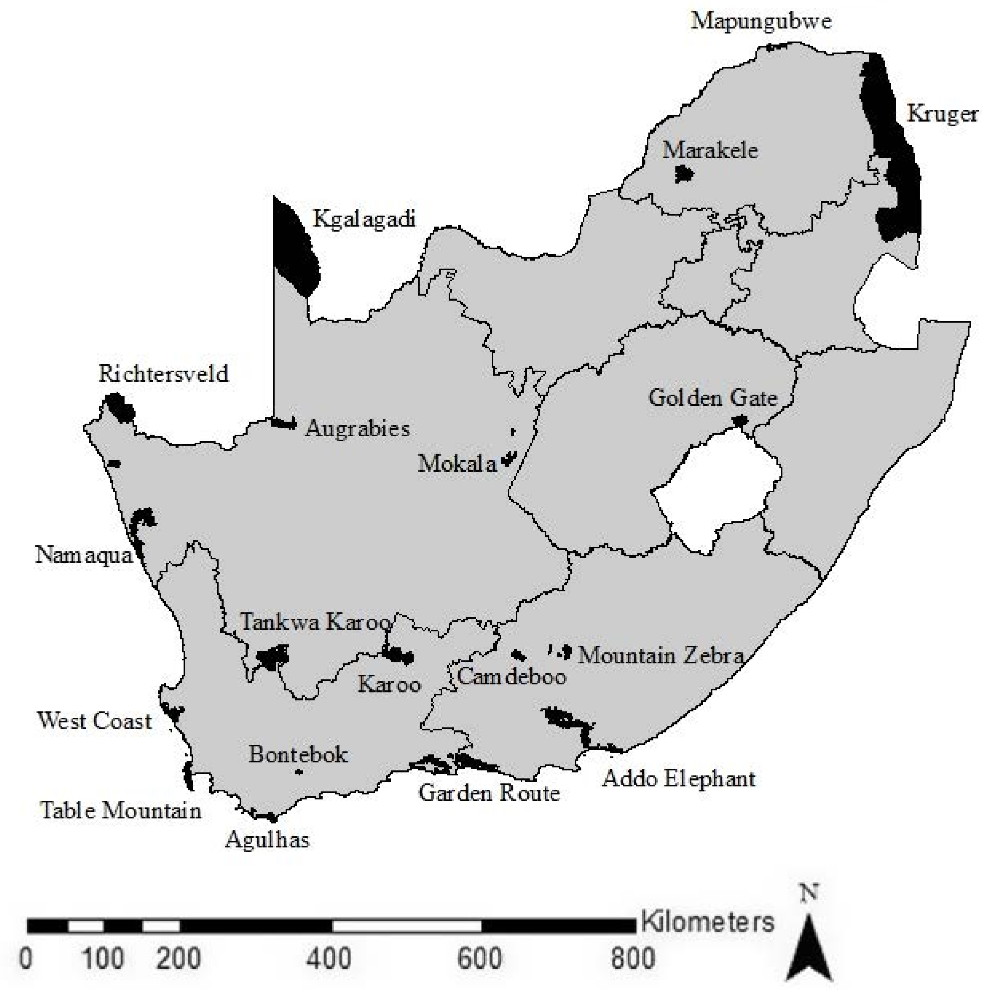


Figure 2.3 Map of study sites South African National Parks.

2.4.2 Survey design

The satisfaction surveys completed by amateur birders comprised a pre-trip and post-trip questionnaire. The pre-trip survey focused on their birding expectations. Longer surveys were conducted for the post-trip survey, in which respondents scored their birding experience using a Likert-type scale from 1-10 (i.e., terrible to excellent) to provide a single measurement of overall satisfaction of their birding experience. I term this 'birder benefit' (following Cumming and Maciejewski, 2017), recognising that it is likely to be a relatively coarse correlate of the actual psychological benefit received. Amateur participants also provided detailed explanations for the benefit scores that they assigned, defined as perception-based birding experiences. These were coded, using an inductive thematic analytical approach, into five summary categories: (1) subjective impressions of the overall number and nature of birds seen; (2) comfort variables, such as weather, company, and ease of movement along the route; (3) impressions directly related to the particular species seen, such as rare and endemic birds, and specific behavioural interactions (e.g., predation, competition, mating); (4) subjective landscape correlates of the experience, such as the beauty of the surroundings and general visibility; and (5) educational value of the experience, such as new birds learned. To determine which categories contributed to birder benefits, I excluded reasons that explained less than 5% of their variance, as determined by Cumming and Maciejewski (2017). The subsequent reasons included in the final analysis under the first four categories were: (1) perceived species richness, low diversity of species, and low abundance of species; (2) bad weather, good weather and unfavourable route; (3) unexpected sighting of a species and a good sighting of species; and (4) boring, monotonous landscape and interesting, diverse landscape (see Table 2.4 for further explanations of these variables).

2.4.3 Landscape Attribute Data

The parks in this study include an exceptionally diverse range of habitats, ranging from coastal to highland and forested to desert. To determine the contribution of biophysical attributes to amateur birder benefits, the birding route coordinates were converted into a shapefile and analysed in a Geographic Information System (GIS). I added a 5km buffer around each route to mirror the field of view of standard binoculars and account for biophysical attributes that participants might have encountered while birding, which could have included views across valleys or over the ocean. From existing maps of biophysical landscape attributes, I extracted data on features that have been shown to influence birder enjoyment: biome, elevation, roads, water bodies, vegetation type and land cover (see Table 2.4). Each of the variables within each buffer zone was measured for each route.

Table 2.4 Landscape characteristics and how these characteristics might influence perception of ecosystem services, with examples.

Landscape characteristics	Measurement	Mechanism and examples
Biome	Categorical	Biomes are defined by the dominant plant growth form and associated climatic thresholds (Conradi et al., 2020). From an ornithological perspective, biomes create specific conditions for which bird species are adapted (Steven et al., 2017). Specific plant growth forms in biomes may be associated with rare, endangered or common species (Chettri et al., 2005).
Elevation	Mean Variance	Variation in elevation produces different habitat types, contributing to high biodiversity of birds (Baral, 2018). Higher elevation has been correlated with low species richness (Graves et al. 2019). In addition, elevation might impede the field of view of birders, negatively affecting their birding experience.
Roads	Length Presence/absence Road type	The effect of roads on birding include higher rates of disturbance and disruption of bird activity
Water body	Presence/absence Water body type	The importance of water bodies for birdwatching has been well documented in ecosystem service literature (Raudsepp-Hearne et al., 2010). Bodies of water may also contribute positively to the aesthetic experience of birdwatching (Chettri et al. 2005).

Vegetation type	Categorical	Vegetation type is classified according to criteria including physiognomy, structure, plant functional traits and species composition (De Cáceres and Wiser, 2012). Local vegetation influences the distribution of bird communities through habitat heterogeneity and resource availability (Belaire et al. 2015).
Land cover	Categorical	Land cover is defined by environmental attributes (including landform, altitude, soil) and specific technical attributes (including cultivated areas) which influences the availability of habitats for birds and therefore the spatial distribution of bird communities (Chettri et al., 2005; Di Gregorio, 2005; Kolstoe et al., 2018).
Species richness Low diversity Low abundance	Count Count Count	Evidence has suggested that species richness, diversity and abundance of bird communities affects perceptions of birding experiences (Booth et al., 2011; Cumming and Maciejewski, 2017).
Unexpected species Good sighting of species	Perception Perception	Unexpected species refers to a bird species that, given the terrain, area or time, was unexpected, but nevertheless a pleasant surprise to the birder. Sightings of unexpected species or a good sighting of species (through e.g. clear observations or witnessing particular behaviours) are highly correlated with birder benefits since birders may become conditioned to cultural ecosystem service provision by the same species in different locations

		(Cumming and Maciejewski, 2017).
Good weather Bad weather Interesting, diverse landscape	Perception Perception Perception	External variables such as weather and perceptions of landscape has been shown to significantly influence birder benefits. For example, Cumming and Maciejewski (2017) found that incorporating these variables with biodiversity measures increased the percentage of variance explained in birder benefits from 27% to 57%.

2.5 Ecological data

2.5.1 Ecological functional groups

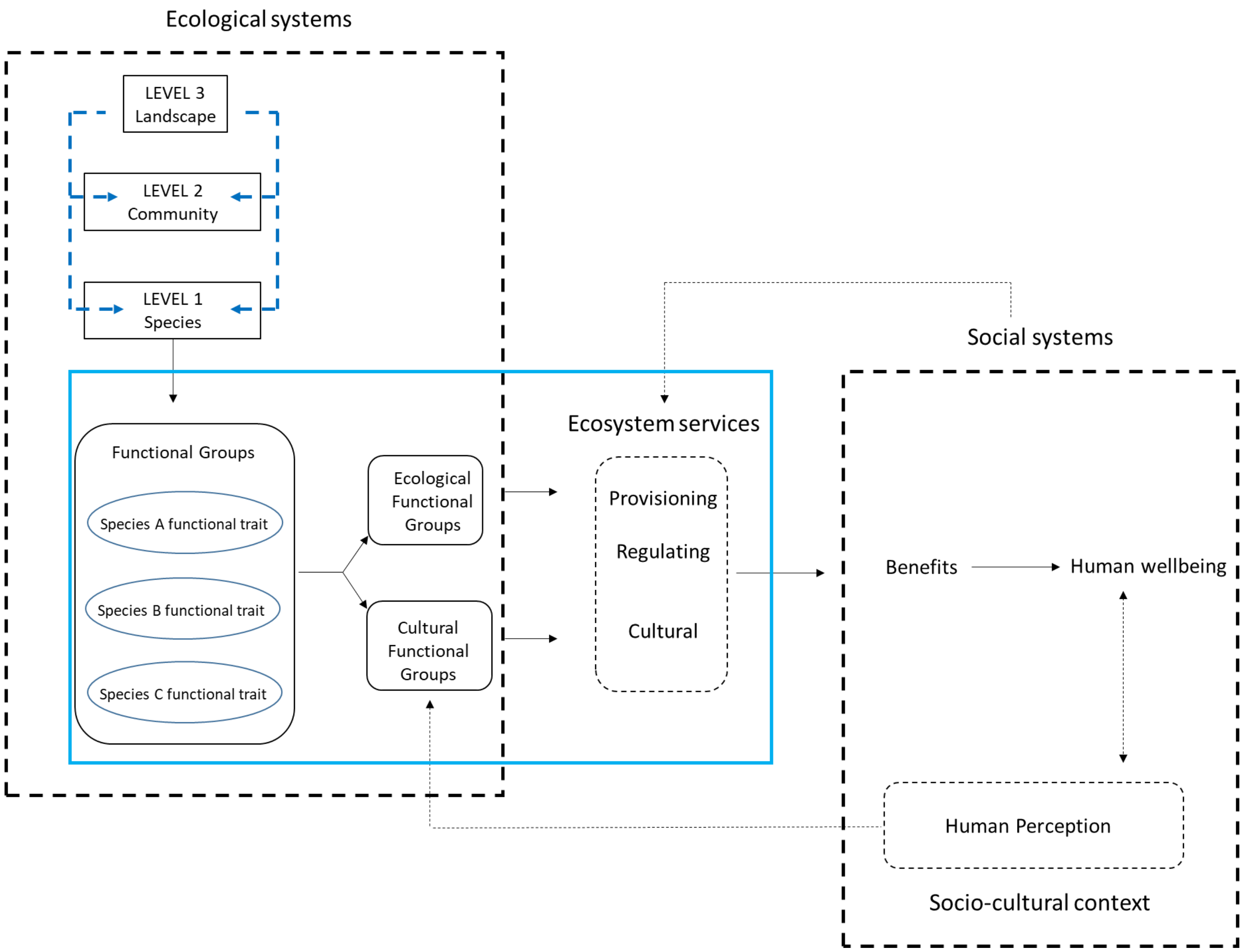
Birds provide a range of ecological functions that are critical for ecological processes. I adopted the ecological functional classification of South African birds developed by Cumming and Child (2009). It is based on Sekercioglu's (2006) classification of avian ecological functional groups, and uses detailed quantitative data on the foraging ecology and biology of Southern African birds (Hockey et al., 2005). The classification places 950 bird species into one or more of nine EFGs: Seed Dispersers, Pollinators, Nutrient Depositors, Grazers, Insectivores, Raptors, Scavengers, Ecosystem Engineers, and Granivores (Sekercioglu, 2006; Cumming and Child, 2009).

2.5.2 Distribution data

The second Southern African Bird Atlas Project (SABAP2) was established in 2007 to capture the distribution of bird species in the region (Underhill et al., 2017). Data for SABAP2 were collected via a minimum of 2-hour intensive bird surveys in defined locations by citizen birders. These locations were mapped within 0.25 degree grid cells (Underhill et al., 2017) and can be visualised online (http://sabap2.birdmap.africa; checked 7/09/2021).

3 Defining cultural functional groups based on perceived traits assigned to birds*

In my first data-based chapter, I use people's perceptions of bird traits to describe cultural functional groups. The next three data chapters build on these findings.



*Adapted from Zoeller, K.C., Gurney, G.G., Heydinger, J., Cumming, G.S., 2020. Defining cultural functional groups based on perceived traits assigned to birds. Ecosystem Services 44.

Contributions: I developed the research question, methodology, collected the data, performed the data analyses, and developed the figures and tables with the advice of G. Cumming and G. Gurney. I wrote the first draft of the paper which was revised with editorial input from G. Cumming, G. Gurney and J Heydinger.

3.1 Abstract

The sustainable delivery of ecosystem services relies on the functional traits that underpin ecosystem service production. Organisms that share functional traits can be grouped together, simplifying questions of management and providing insights into the external drivers that impact ecosystem service provision. Linkages between the functional traits of organisms and provisioning and regulating ecosystem services are well established, but the traits that underpin the benefits derived from cultural ecosystem services are not. To this end I interviewed 401 socio-economically diverse local ecosystem users in South Africa, selected using a mixture of convenience and purposive sampling, to elucidate peoples' perceptions of the traits associated with bird species. Subsequently, I used cluster analysis to examine whether these traits could provide a consistent typology of cultural functional groups. I identified six major cultural functional groups based on scores assigned to bird species: Visual Traits; Negative visual and Behavioural Traits; Movement and Ecological Traits; Place Association and Abundance Indicators; Common Traits; and Behavioural Traits. Significantly higher scores were assigned to birds with interesting movement and ecology, whereas bird species with perceived negative visual or behavioural traits scored poorly. I additionally show that there are potential synergies between positively perceived cultural functions and ecological functions. Grounding cultural functional traits in a broader typology of functional groups makes components of ecological complexity more interpretable and may be used to predict how the loss of functional traits within a system will impact cultural benefits experienced by local ecosystem users.

3.2 Introduction

The sustainable delivery of ecosystem services relies on the functions that underpin ecosystem service production. Conserving functional diversity at the species level is imperative in ensuring the production of multiple ecosystem services and promoting the resilience of the system (Bellwood et al., 2019). Identifying species-specific functional traits enables the role that individual species play in driving ecosystem service production to be determined, and has been well documented, for example, in birds (Sekercioglu, 2006); soil microbes (Pommier et al., 2018) and plants (Lavorel and

Grigulis, 2012). Understanding the representation of functions by species in ecosystems is also the first step towards exploring portfolio effects (Schindler et al., 2015), response diversity (Elmqvist et al., 2003), and the degree to which the functions performed by one species can be substituted by another. Of particular interest is the capacity of different species with convergent functional traits to generate shared ecological processes and produce synergistic ecosystem functions (de Bello et al., 2010). Monitoring functional traits can also provide insight into the external drivers that impact functional trait selection within a system (Kahmen et al., 2002; de Arruda Almeida et al., 2018).

An important but seldom assessed driver of trait selection in anthropogenic landscapes is the preferences and perceptions of local human communities. Birds in particular have already received widespread attention for their contribution to ecosystem services that improve ecosystem resilience and integrity, such as pollination, pest control and waste decomposition (Sekercioglu, 2006; Morante-Filho and Faria, 2017). The contribution of birds to human wellbeing can also be negative (i.e. ecosystem disservice), resulting from aggressive or destructive behaviour, unpleasant noises and smells, disease transmission, and pollution of water supplies (Cox et al., 2018). People may manipulate habitat extensively to favour their preferred species. For example, urban gardens are often deliberately planted with bird-attracting plant species; bird feeders and nest boxes are used to attract desirable species; wetlands may be managed for duck hunting; and people may shoot or poison raptors that are perceived to impact favoured species such as grouse (Tenan et al., 2012; Tryjanowski et al., 2015). The relationships between people, bird species, and their perceived functional traits thus create feedbacks from people to nature and from nature to people. The identification of functional traits through a cultural lens is a potentially important element in understanding the processes that underlie social-ecological relationships. Further, by connecting ecosystem functions in the biophysical domain with ecosystem benefits in the social domain (Daniel et al., 2012), identifying functional elements through a cultural lens may promote understanding of the flow of cultural service production in an ecosystem cascade (see Fig. 3.1).

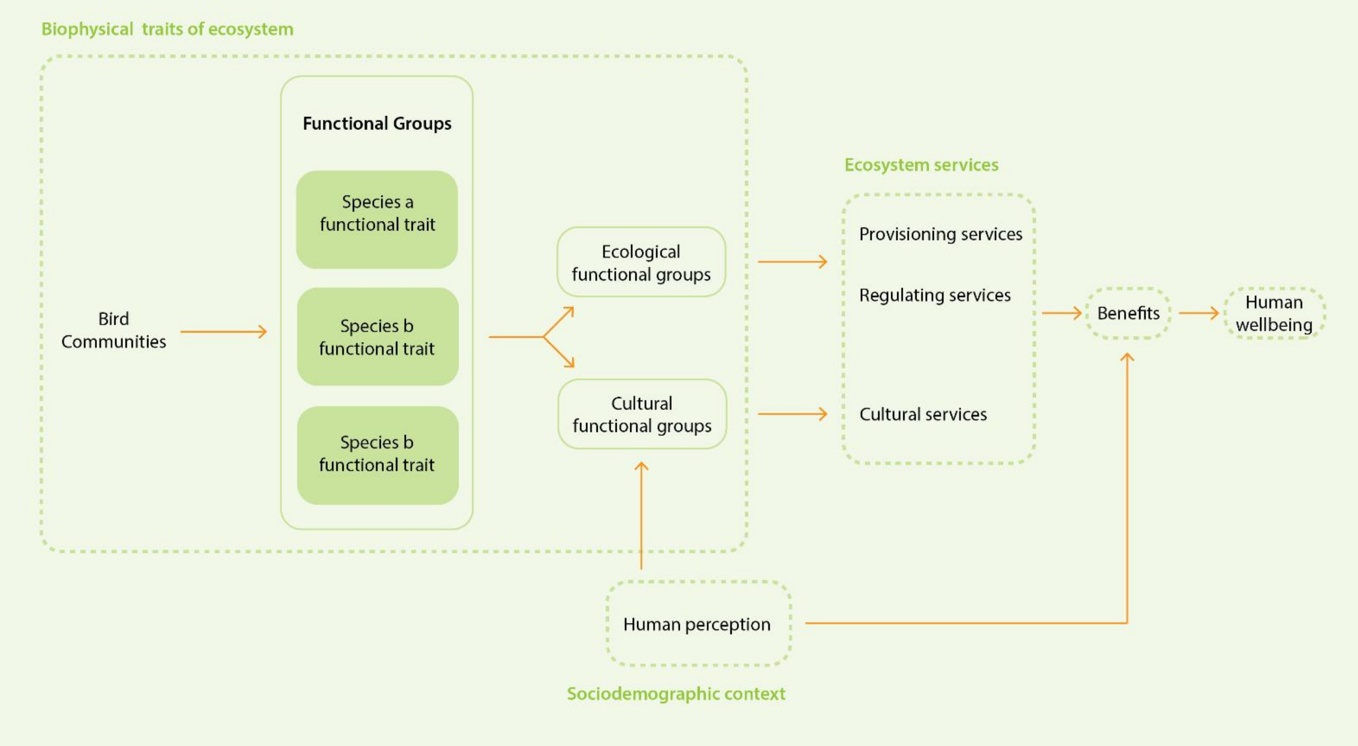


Figure 3.1 A simplified ecosystem service cascade model using a cultural perspective lens (adapted from de Groot et al. (2002) and Cumming and Maciejewski (2017)).

Individual species within communities possess convergent functional traits than can be grouped together to form functional groups (Fig. 3.1). Functional groups are produced from and embedded in the biophysical traits of ecosystems, creating interactions between ecosystems, communities and individual species traits. Functional groups in this model can be delineated into either ecological or cultural functional groups, although I specifically focus on cultural functional groups that underpin the production of cultural ecosystem services. Ecosystem services create benefits that contribute directly to human wellbeing by fulfilling the wants, needs and preferences of individuals. I focus primarily on the contribution of cultural functional traits to the benefits people derive from cultural ecosystem services, and not the ecosystem services themselves. These benefits include spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences (MA, 2005). I distinguish ecosystem services and benefits according to the framework proposed by Fisher and Turner (2008), who differentiate benefits from services through their direct and explicit contribution to changes in human wellbeing. In a cultural ecosystem service context, the benefits that people derive from cultural ecosystem services are co-produced through interactions between between people (social systems) and their environment (ecological systems), and co-constructed through the interaction between individual perception and society (socio-demographic context) (Fischer and Eastwood, 2016; Fish et al., 2016). Human perception also affects the organisation of cultural functional groups, since the co-construction of cultural functional groups is informed by individual's specific worldview resulting from their socio-demographic context.

Previous research has identified the importance of categorising bird traits to understand the processes underpinning cultural ecosystem services and disservices (Echeverri et al., 2019). Despite their potential to inform conservation and monitoring initiatives, however, most research has ignored the relationship between cultural functional traits and the benefits that people derive from cultural ecosystem services. Here I describe cultural functional traits as *the dominant characteristics of a species that affect local ecosystem users through their contribution to cultural ecosystem services or disservices*. Cultural ecosystem services provide non-material benefits, such as recreation, aesthetics, and spirituality to local users (MA, 2005; Chan et al., 2012). However, since the benefits associated with these services are intangible, they do not contribute directly to instrumental values and are consequently particularly challenging to measure and communicate to decision-makers (Gould et al., 2015). Considering cultural ecosystem services in management decision-making is critical. Indeed, discounting socio-cultural considerations has been shown to undermine the effectiveness of conservation initiatives (Villamor et al., 2014; Morante-Filho and Faria, 2017; Marshall et al., 2018). This is particularly apparent when there are synergies among multiple services that are underpinned by both biophysical and cultural functional traits, such as planting a cherry tree for both the fruit (provisioning service) and the flowers (aesthetic service). Delineating cultural functional traits into a typology of cultural functional groups based on perceptions of local ecosystem users will provide new insights that can inform the conservation of functional diversity and promote holistic, inclusive management strategies (Bellwood et al., 2019). Moreover, identifying the underlying drivers of cultural ecosystem services through a formal framework of cultural functional groups should enable decision-makers to better identify the links and feedbacks between people and nature, integrate local knowledge into conservation discourse, and promote local environmental stewardship (de Groot et al., 2002; Chan et al., 2012; Scholte et al., 2015).

To explore the validity of applying a cultural functional group approach to birds, I asked (1) Is there consistency in the way that people score birds? (2) Can the cultural functional traits identified by individuals that underpin cultural ecosystem services used to create justifiable cultural functional groups? (3) What is the relationship between perceived cultural functional traits of birds and their assigned scores?

3.3 Materials and methods

3.3.1 Dataset

To describe cultural functional groups, I used the trait dataset described in Chapter 2.

3.3.2 Analysis

I first calculated Cronbach's α (Cronbach, 1951) for the ranked scores of the bird species (n=491) to ensure that there was internal consistency in the scoring of birds. Cronbach's α measures how closely related a set of items are as a group on a scale from 0 to 1 (Streiner, 2003). A value close to one indicates high internal consistency. For my data its value was 0.88, indicating that the data have a shared co-variance and measure the same underlying concept.

I conducted a K-means cluster analysis on the 45 traits for each of the 491 bird species identified by respondents during interviews. The silhouette coefficient was calculated to determine how well the observations are clustered. The K-means cluster analysis allocated each of the 45 traits into a cluster. I then calculated the average number of times each trait occurred in each cluster, and clusters with the greatest number of occurrences of each trait were allocated that trait so that the dominant cultural functional traits of each cluster could be determined. The dominant traits in each cluster were then used to identify the fundamental attributes of each cluster; these were then treated as cultural functional groups.

To further explore the typology, I determined the dominant five species in each cluster by calculating the percentage contribution of each species to their cluster. This was achieved by calculating percentage occurrence of each bird species in each cluster. The cluster with the highest percentage of occurrence for each species was allocated that bird.

The average score per species was calculated to determine which cultural functional groups as indicated by species-specific traits were most well-regarded by respondents. A 2-way ANOVA and post-hoc Tukey test were performed on the average scores to determine whether there were significant differences in how these cultural functions were valued. The total number of species that had been assigned each cultural functional trait by respondents was also calculated to determine which cultural functions were most commonly considered.

3.4 Results

The optimum number of clusters based on the average silhouette width was six (Fig. 3.2). The K-means cluster analysis therefore identified six clusters from the 45 cultural functional traits inferred from interviews with respondents (Table 3.1.) Clusters with the highest count of each trait were allocated that trait, thus identifying the cultural functional traits that defined each cultural functional group (Table 3.1). I identified six cultural functional groups based on trait assignment: Visual Traits; Negative Visual and Behavioural Traits; Movement and Ecological Traits; Place Association and Abundance Indicators; Common Traits; and Behavioural Traits (Table 3.1).

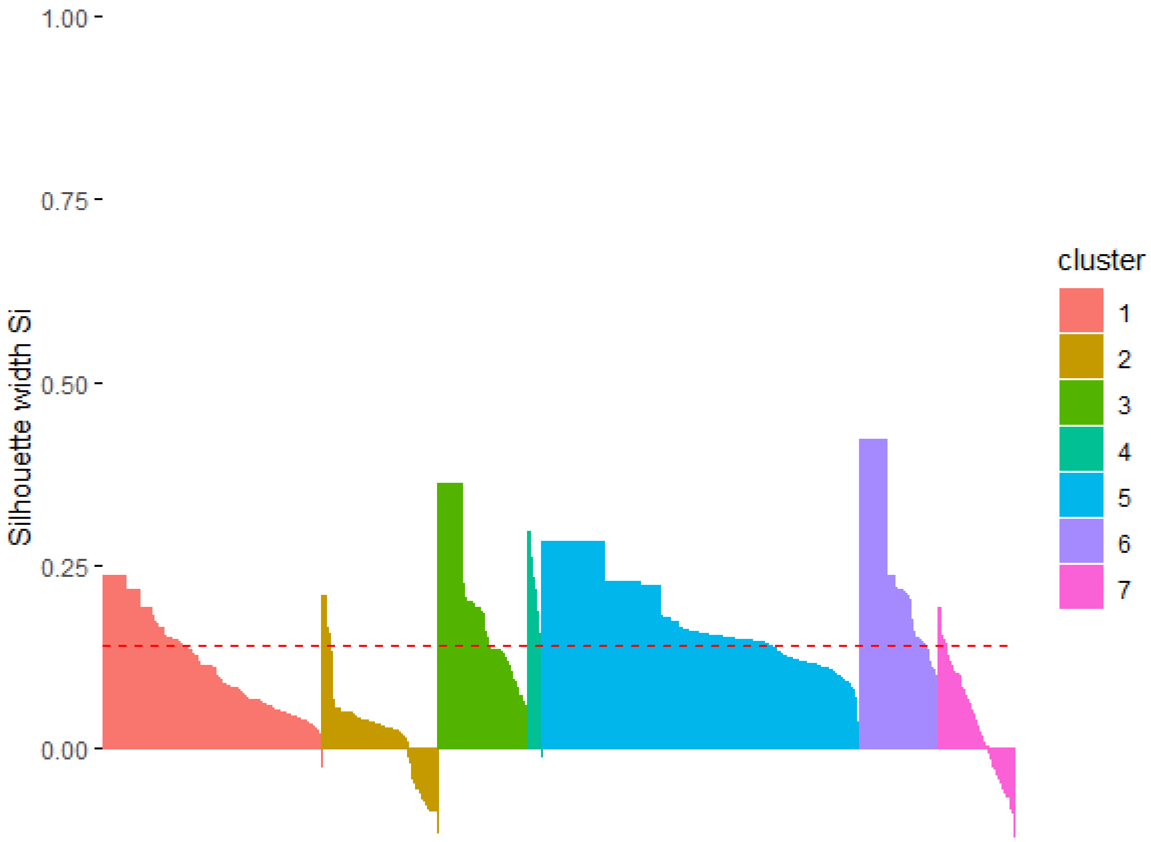


Figure 3.2 Silhouette plot indicating the optimum number of clusters based on silhouette width.

Table 3.1 Cultural functional traits of each cluster that characterise the cultural functional group.

Cluster number	Cultural functional group name	Cultural functional traits
C1	Visual Traits	Colourful/handsome plumage
		Positive response to the bird's name
		Small body
		Stance
		Shape
C2	Negative Visual and Negative Behavioural Traits	Dull/ugly plumage
		Negative song
		Negative habitat
		Difficult to identify
		Aversion for the bird at the family level
		Invasive/pest
		Negative symbology
		Boring/average behaviour
		Aggressive/territorial
C3	Movement and Ecological Traits	Interesting flight
		Interesting foraging behaviour
		Conspicuous
		Affinity for the bird at the family level
		Camouflage/adaptability
		Clever
		Endangered
		Strong/powerful
C4	Place Association and Abundance Indicators	Positive song
		Positive habitat
		Rare
		Migratory
		Few sightings of the species
		Breeding display
		Difficult to locate
		Indigenous/endemic
		Positive association with their sighting
		Positive symbology
		Easy to identify
C5	Common Traits	Common
		Many sightings of the species
		Confiding
C6	Behavioural Traits	Large body
		Interesting movement
		Parental care
		Flock size
		Source of food

The highest scoring species were predominantly concentrated in the Movement and Ecological cultural functional group. This suggests that species with cultural functional traits that include inter alia interesting flight, foraging behavior, camouflage and/or adaptability and perceived cleverness are highly regarded by ecosystem users (Table 3.1; Fig. 3.3). The Movement and Ecological Traits group received significantly higher scores than functional groups comprising Visual Traits, Place Association and Abundance Indicators, Common Traits and Behavioural Traits. In contrast, species exhibiting Negative Visual and Behavioural Traits received significantly lower scores, suggesting species with traits such as dull or ugly plumage, negatively perceived songs, negative cultural associations and those perceived as boring or average were discounted by South African communities (Fig. 3.3).

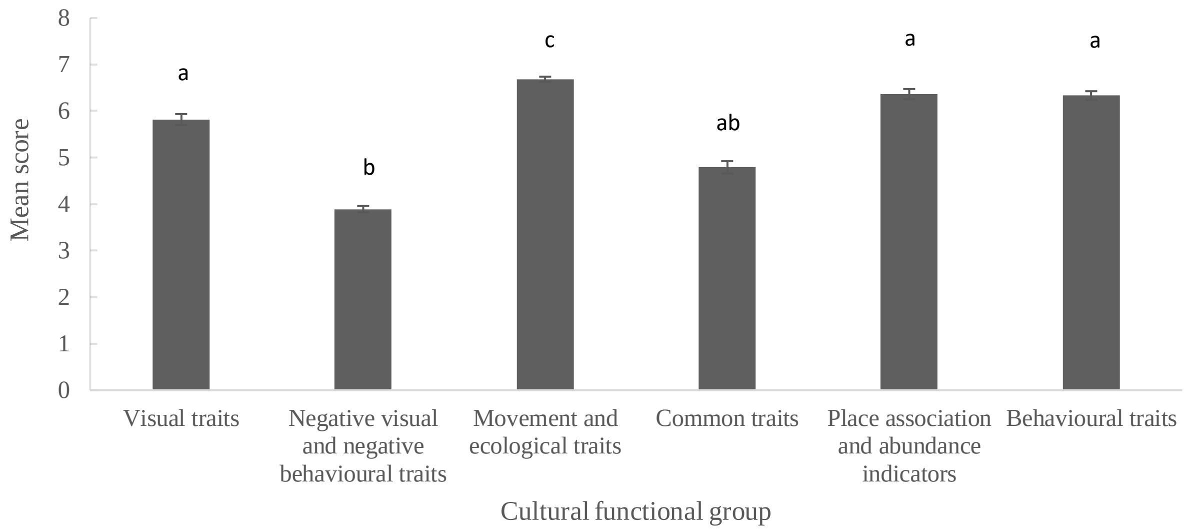


Figure 3.3 Average species score (± standard error) of the dominant species in each cluster. Clusters sharing a letter are not statistically different from each other ($p<0.05$).

The cultural functional group with the greatest number of species was Visual Traits. Negative Visual and Behavioural Traits received the second greatest number of species, whereas Common Traits were allocated comparatively few species (Fig. 3.4).

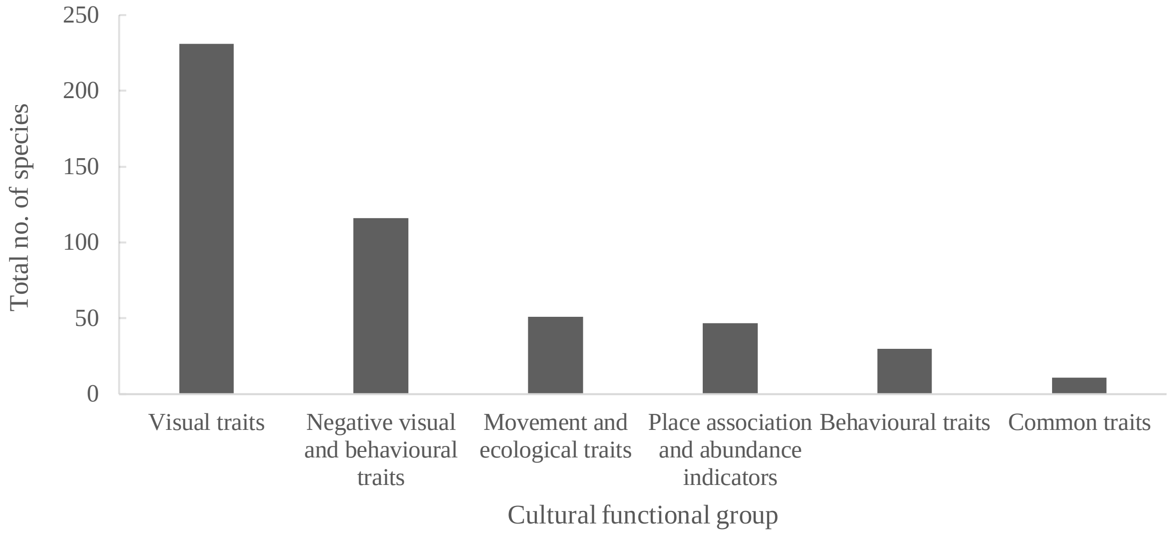


Figure 3.4 Total number of species in each cultural functional group.

The indicator species for each cultural functional group shared common ecological defining features (Table 3.2), specifically for Visual Traits: membership of the Passeriformes order, (although there is variation at the family level); a diet of terrestrial invertebrates using gleaning foraging behavior; and small bird sizes (<40 grams). There were broad ecological features for indicator species of the Negative Visual and Behavioural Trait functional groups, although indicator species tended to be South African residents that forage through gleaning. Indicator species for the Movement and Ecological Traits functional group were both predators and insectivores/nectarivore, and generally associated with specific habitat types. The insectivores/nectarivore in particular are found in fynbos or savanna biomes, whereas the predators were generally found in forested and woodland areas. The biggest similarity in species from the Place Association and Abundance Indicator group was habitat, with these species occurring primarily in wetlands and fynbos. Indicator species in the Common Traits primarily included Columbiformes and Galliformes. These species were South African residents with widespread distribution across the country. The Behavioural Traits group indicator species consisted of Charadriiformes which are generally located near wetlands and whose foraging behaviour consists of running, stopping and searching. This functional group also comprises Galliformes, which are large-bodied and prominent in woodland and savanna habitats.

Table 3.2 The most commonly occurring species (indicator species) in each cultural functional group (CFG) and their defining features according to Roberts' Birds of Southern Africa database.

CFG	Indicator species	Order and (family)	Ecological defining features
Visual Traits	African Paradise Flycatcher	Passeriformes (Monarchidae)	Intra-African migrant, main habitat is woodland, feed on terrestrial invertebrates, male body mass=14.6, distinguishable tail, foraging behaviour is perch and sally and gleaning
	Yellow-breasted Apalis	Passeriformes (Cisticolidae)	South African resident, main habitat is forests, feeds on terrestrial invertebrates, male body mass=8.5, foraging behaviour is gleaning
	European Roller	Coraciiformes (Coraciidae)	Intercontinental migrant, main habitat is savanna, feed on terrestrial invertebrates, brilliant blue colour, plumage dimorphism, foraging behaviour is perch and pounce
	Gorgeous Bushshrike	Passeriformes (Malaconotidae)	South African resident, main habitat is forest and woodland, feed on terrestrial invertebrates, male body mass=36.5, foraging behaviour is gleaning
	African Stonechat	Passeriformes (Muscicapidae)	South African resident, main habitat is grassland, feed on terrestrial invertebrates, male body mass=14.6, plumage dimorphism during breeding season, foraging behaviour is gleaning and probing
Negative Visual and Behavioural Traits	Barratt's Warbler	Passeriformes (Sylviidae)	South African resident, main habitat is wetlands, feeds on terrestrial invertebrates, male body mass= 19.5, foraging behaviour is gleaning
	Wing-snapping Cisticola	Passeriformes (Cisticolidae)	South African resident, main habitat is grassland, feeds on terrestrial invertebrates, male body

			mass= 9.6, foraging behaviour is gleaning
	African Cuckoo	Cuculiformes (Cuculidae)	Intra-African migrant, brood parasite, main habitat is savanna, feeds on terrestrial invertebrates, male body mass= 103, plumage dimorphism, foraging behaviour is gleaning
	Cape Crow	Passeriformes (Corvidae)	South African resident, main habitat is grassland, feeds on terrestrial invertebrates, male body mass= 9.6, foraging behaviour is gleaning
	Trumpeter Hornbill	Bucerotiformes (Bucerotidae)	South African resident, main habitat is forests, feeds on fruits, predates eggs, male body mass=721, foraging behaviour is gleaning and scavenging
Movement and Ecological Traits	Common Tern	Charadriiformes (Laridae)	Intercontinental, long-distance migrant, main habitat is open coasts and estuaries, feeds on fish, foraging behaviour is plunge diving.
	Woodland Kingfisher	Coraciiformes (Dacelonidae)	Intra-African migrant, main habitat is woodland, feeds on terrestrial invertebrates, male body mass=721, foraging behaviour is perch and pounce.
	Long-crested Eagle	Accipitriformes (Accipitridae)	South African resident, main habitat is forest, feeds on mammals, male body mass= 568, foraging behaviour is perch and pounce.
	Southern Double-collared Sunbird	Passeriformes (Nectariniidae)	South African resident, endemic main habitat is fynbos and karoo, feeds on nectar and terrestrial invertebrates, male body mass=8.7, plumage dimorphism, foraging behaviour is gleaning and probing.

	Malachite Sunbird	Passeriformes (Nectariniidae)	Nomad, main habitat is fynbos, feeds on nectar and terrestrial invertebrates, male body mass=19.4, plumage dimorphism, foraging behaviour is gleaning and probing.
	Amethyst Sunbird	Passeriformes (Nectariniidae)	South African resident, main habitat is savanna, feeds on nectar and terrestrial invertebrates, male body mass=14.7, plumage dimorphism, foraging behaviour is gleaning and probing.
Place Association and Abundance Indicators	African Swamphen	Gruiformes (Rallidae)	South African resident, main habitat is wetlands, feeds on plant parts, male body mass=636, foraging behaviour is perch and pounce.
	Gurney's Sugarbird	Passeriformes (Promeropidae)	Endemic South African resident, main habitat is fynbos, feeds on terrestrial invertebrates and nectar, male body mass=38.2, foraging behaviour is gleaning and probing.
	Swift Tern	Charadriiformes (Laridae)	Endemic South African resident, main habitat is lagoons, estuaries and coastal wetlands, feeds on fish, foraging behaviour is plunge diving.
	Cape Sugarbird	Passeriformes (Promeropidae)	Endemic South African resident, main habitat is fynbos, feeds on terrestrial invertebrates and nectar, male body mass=36.9, foraging behaviour is gleaning and probing.
	Grey Heron	Pelecaniformes (Ardeidae)	South African resident, main habitat is wetlands and estuaries, feeds on fish and aquatic invertebrates, male body mass= 1510, foraging behaviour is gleaning.
Common Traits	Speckled Pigeon	Columbiformes (Columbidae)	South African resident, main habitat is cliffs, feeds on seeds, male body mass= 358, foraging behaviour is gleaning.

	Crested Guineafowl	Galliformes (Numididae)	South African resident, main habitat is forest, feeds on seeds, male body mass=1149, foraging behaviour is gleaning.
	Red-eyed Dove	Columbiformes (Columbidae)	South African resident, main habitat is woodland, feeds on seeds, male body mass=241, foraging behaviour is gleaning.
	Cape Spurfowl	Galliformes (Phasianidae)	South African resident, main habitat is fynbos, feeds on terrestrial invertebrates, seeds and other plant parts, male body mass=977, foraging behaviour is gleaning.
	Lemon Dove	Columbiformes (Columbidae)	South African resident, main habitat is forests, feeds on seeds, male body mass= 152.8, foraging behaviour is gleaning.
Behavioural Traits	Common Ringed Plover	Charadriiformes (Charadriidae)	Intercontinental migrant, main habitat is lagoon, estuaries and coastal wetlands, feeds on freshwater and marine invertebrates, foraging behaviour is run, stop and search.
	Grey Plover	Charadriiformes (Charadriidae)	Intercontinental migrant, main habitat is lagoon, estuaries and coastal wetlands, feeds on marine invertebrates, foraging behaviour is gleaning.
	African Pied Wagtail	Passeriformes (Motacillidae)	South African resident, main habitat is agricultural land and wetlands, feeds on terrestrial invertebrates, male body mass= 27.3, foraging behaviour is gleaning.
	Helmeted Guineafowl	Galliformes (Numididae)	South African resident, main habitat is woodland and savanna, feeds on terrestrial invertebrates, seeds and other plant parts, male body mass= 1380, foraging behaviour is gleaning.

Crested Francolin	Galliformes (Phasianidae)	South African resident, main habitat is savanna, feeds on terrestrial invertebrates, male body mass= 382, foraging behaviour is gleaning.

3.5 Discussion

The results indicate that perceived traits of birds identified by ecosystem users can be applied to develop a typology of cultural functional groups. Traits associated with interesting movement and ecology had particular importance for the respondents in this study, as these species were assigned significantly higher scores than species in any other cultural functional group. Traits including foraging, flight, camouflage and/or adaptability therefore hold particular salience for ecosystem users. In contrast, species with traits that were perceived as visually or behaviourally negative were assigned significantly low scores. Interestingly, there was no correlation between trait preferences (based on species scores in each cluster) and trait awareness (based on species abundance in each cluster), suggesting that familiarity with species traits does not necessitate a positive response to that species. Given this disparity in trait awareness and trait preferences, prioritising research on cultural ecosystem services that are underpinned by prolific functional traits may underestimate the full range of cultural services present in a system (Marshall et al., 2018).

Species in the Common Traits cultural functional group did not produce significantly different scores to species underpinned by ostensibly negatively or positively perceived traits. Indeed, Columbiformes indicator species for this cultural functional group are ubiquitous across urban and rural landscapes, suggesting widespread familiarity with these species (Conole and Kirkpatrick, 2011). This result suggests that species that are commonly occurring, seen often and engaged with regularly do not elicit particularly strong reactions from ecosystem users.

The results show that cultural functional groups that were underpinned by positive traits (Visual Traits, Place Association and Abundance Indicators, Movement and Ecological Traits and Behavioural Traits) scored significantly higher and those that were underpinned by negative traits

(Negative Visual and Behavioural Traits). Although literature on ecosystem disservices as underpinned by negative functional traits is emergent, ecosystem disservices associated with birds have been documented in previous research (Whelan et al., 2015; Cox et al., 2018). In urban areas in England, for example, species associated with cultural disservices possess traits that include aggression, noisy and destructive behaviour and negative foraging (Cox et al., 2018). My results corroborate this evidence, as species with low scores exhibited similar negative visual/aural and behavioural traits, as well as negative habitat association, negative cultural associations, difficulty identifying them and invasive natures.

Indicator species for the Negative Visual and Behavioural Traits group exhibited behaviour that included brood parasitism (African Cuckoo), as well as species that contributed directly to human-animal conflict (Cape Crow). These species were identified by respondents for traits that include aggressive, territorial and/or pest behaviour, as well as general aversion at the family level. Crows in particular are known for negative impacts on the benefits associated with cultural ecosystem services in both urban and rural environments. For example, crows reduce biodiversity through predation, have unpleasant calls, and species from the Corvidae family affect livelihoods through their well-documented impact on sheep husbandry in farmlands (Houston, 1977; Gaertner et al., 2016). Similarly, the practice of brood parasitism in the African Cuckoo suppresses nesting success of the host, decreasing cultural ecosystem benefits to local communities through reduced biodiversity (Payne, 1977).

Despite the contribution of birds to cultural ecosystem disservices, indicator species for Negative Visual and Behavioural Traits functional groups fulfil vital ecological roles. The Trumpeter Hornbill and Cape Crow, for example, support healthy ecosystem functioning by scavenging their food sources, promoting carcass recycling and the flow of food web energy (Sekercioglu, 2006). Moreover, scavengers have been identified as providing non-material contributions to people (Aguilera-Alcalá et al., 2020). Since the benefits of these important ecosystem services may be overlooked by local communities when they are underpinned by negatively perceived cultural functional traits, it is important that trade-offs between bundles of ecosystem services and disservices be identified in future studies (Iniesta-Arandia et al., 2014; Aguilera-Alcalá et al., 2020)

Operationalising cultural functional roles has enabled me to identify commonality in cultural functional traits and their inherent ecological traits. Since membership of species in cultural functional groups were reinforced by similarities in their orders, habitat types and/or foraging behaviour, I can conclude that there are consistencies in cultural functional groups and ecological traits. For example, the indicator species for Movement and Ecological Traits cultural functional group were primarily sunbirds. These species were identified by respondents for distinct foraging behaviour, specialized morphology and conspicuous colouring. From an ecological perspective, these traits enable sunbirds to provide regulating ecosystem services through their capacity to pollinate, providing both biophysical benefits (fruit production) and cultural benefits (aesthetic pleasure) (Ollerton, 2017).

Predators were also prolific in the Movement and Ecological Traits cultural functional group. Cultural functional traits of predators that play a potentially important role in underpinning cultural ecosystem services include inter alia camouflage and/or adaptability, cleverness, interesting flight and strong/powerful nature. These species also share common ecological traits, and the ecological functions underpinning their ecosystem services have been rigorously explored (Sekercioglu, 2006; Whelan et al., 2008). The effects of avian predators on trophic cascades and ecosystem functioning is of particular relevance from an ecological perspective, and has been addressed in numerous frameworks, such as Food Web Theory (Finke and Denno, 2005). Here I provide new evidence that the position of avian predators in the trophic hierarchy not only has important implications on local ecology, but also provides a framework through which cultural functions of these species are perceived (Martín-López et al., 2012).These results suggest that cultural functions and ecological functions work synergistically (de Bello et al., 2010).

The benefits people derive from cultural services are essential for human wellbeing, and degradation of cultural services is likely to have devastating effects for local communities (Tengberg et al., 2012; Milcu et al., 2013a; Marshall et al., 2018). Despite their importance, empirical research on the cultural functional traits underpinning cultural ecosystem services is poorly understood. Challenges associated with capturing and measuring the contribution of cultural functional groups to human wellbeing has meant that their position on the ecosystem cascade has largely been overlooked (Hernández-Morcillo et al., 2013). As a result, the full range of cultural ecosystem services in an anthropogenic landscape may be discounted (Hernández-Morcillo et al., 2013). I argue here that an important and novel approach for understanding cultural ecosystem services is through empirical research on perceptions of the cultural functional traits that underpin their production.

Despite awareness of their cultural significance, the majority of research on bird species is concentrated on either their direct contribution to human wellbeing, or their ecological traits that underpin these services (Cumming and Child, 2009; Whelan et al., 2015; Echeverri et al., 2019). It is important to note, however, that deriving cultural functional groups from species traits is a complex process. As such, grouping multiple traits under one cultural function risks excluding more nuanced traits. Future studies would benefit from a methodological approach that incorporates quantification of the cultural service value of different species, which could be used in ecosystem accounting to improve our understating of the value end of the cultural ecosystem cascade model. Testing for collinearity in the traits identified by local communities may also need to be explored in future studies.

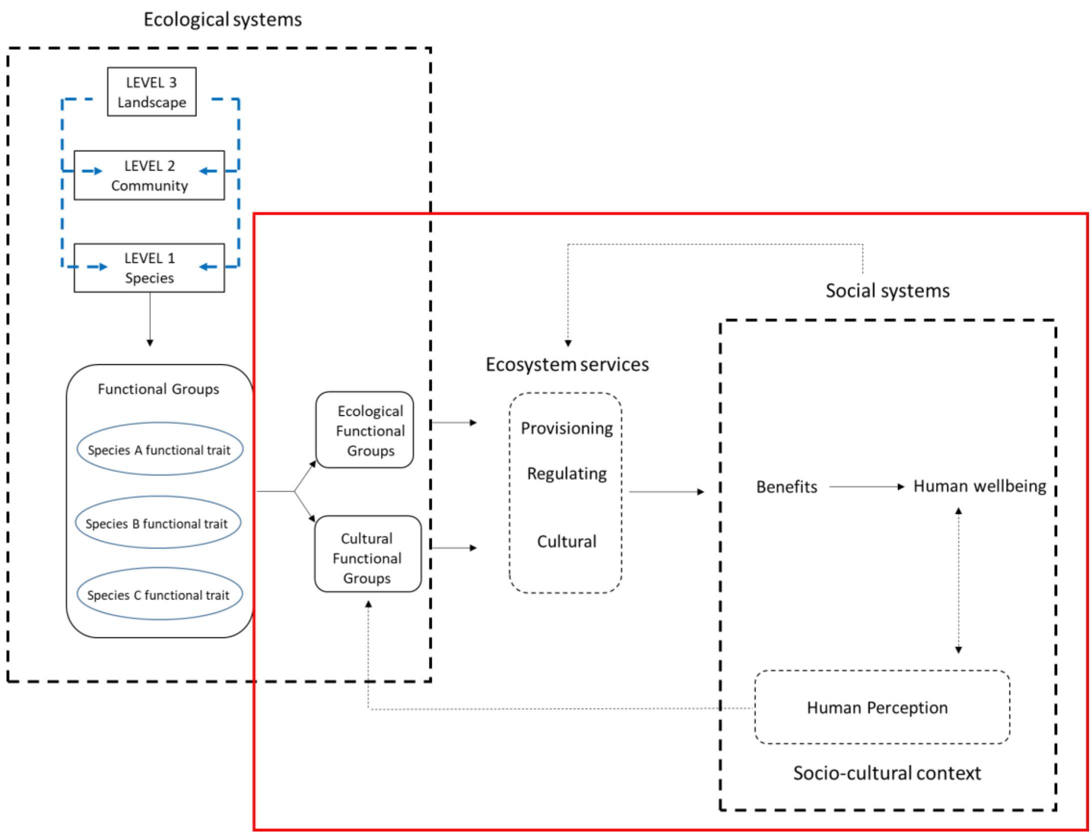
The next step in understanding the flow of ecosystem services from function to benefit is the valuation of species based on their traits. For example, the Place association and Abundance Indicator group comprised of traits that include positive habitat, positive song, rarity, migration and frequency of sighting. These traits are measurable through various techniques, such as Geographic Information Systems modelling (Keller et al., 2014), Acoustic Complexity Index (Buxton et al., 2016) and Soundscape Recording System (Celis-Murillo et al., 2009). However, using tools to quantify species traits is unlikely to accurately represent how their associated benefits are valued. This is particularly apparent when the importance of these benefits is weighted differently by respondents. Moreover, assigning value to intrinsically invaluable elements of nature may undermine conservation efforts by distracting from the ultimate goal of supporting biodiversity (Reyers, 2012).

Nevertheless, elucidating the value of species to local ecosystem users can be useful in supporting conservation strategies through potentially enhancing the support of local communities.

In this study, I have identified the functional traits that underpin the benefits derived from cultural ecosystem services provided by bird species. This is a novel attempt at simplifying cultural functional traits into functional groups to facilitate a better understanding of the flow of ecosystem services and establish the role of human perception in cultural functional trait selection. Despite the indication of Cronbach's α that socio-demographic characteristics account for a very small proportion of variance in perceptions in scores in this study, exploring the role individual characteristics in informing people's preferences for particular cultural functional groups is an important direction for future studies. In South Africa in particular, the interaction between characteristics such as race, age, gender and language, and the unequal distribution of access to ecosystem services in a historically unequal society are pertinent. Mapping cultural functional traits onto the production of cultural ecosystem services through ecosystem cascade models provides a vital missing link between ecosystems and people via functional cultural groups (de Groot et al., 2002; Cumming and Maciejewski, 2017). While my application of the functional groups approach has focused on cultural functional groups, similar grouping strategies may be potentially important in interpreting ecosystem services in other contexts, enabling a better understanding of how the loss of species within a system will impact benefits to local ecosystem users. This study has contributed to making ecological complexity more interpretable by exploring the functional end of the ecosystem cascade. I have shown here that understanding the mechanistic functions underlying cultural ecosystem services enables biophysical processes in nature to be linked to the related benefits experienced by people.

4 The role of socio demographic characteristics in mediating relationships between people and nature*

In the previous chapter, I described six distinct cultural functional groups associated with bird traits. In this chapter, I explore how individuals' socio-demographic characteristics mediate how people perceive these cultural functional groups.



*Adapted from Zoeller K.C., Gurney G.G., Marshall N., Cumming G.S., 2021. The role of socio-demographic characteristics in mediating relationships between people and nature. Ecology and Society 26(3).

Contributions: I developed the research question, methodology, collected the data, performed the data analyses, and developed the figures and tables with the advice of G. Cumming and G. Gurney. I wrote the first draft of the paper which was revised with editorial input from G. Cumming, G. Gurney and N Marshall.

4.1 Abstract

Research on ecosystem services has focused on their availability or supply and often takes a socially-aggregated approach that assumes a single human community of identical beneficiaries. However, people's ability to derive benefits from ecosystem services can differ strongly across societal groups. Access to ecosystem services can be related to socio-demographic characteristics such as material wealth, gender, education and age. Developing environmental management that does not have unequal impacts on different groups thus depends on taking a socially-disaggregated approach to assessing perceptions of ecosystem services. I explored how socio-demographic characteristics relate to cultural functional groups based on perceived bird traits. Using perception data on 491 bird species from 401 respondents along urban rural gradients in South Africa, I found that socio-demographic characteristics are strongly associated with cultural functional groups based on perceived bird traits. My results provide a starting point for understanding heterogeneity in the benefits from avian ecosystem services and how perceptions of cultural functional groups vary across societal groups.

4.2 Introduction

Delivery of ecosystem goods and services is critical for human wellbeing and has become an important objective for environmental governance and management (MA, 2005; Berbés-Blázquez et al., 2016). Although some ecosystem goods and services are unequivocally necessary for all people (e.g., breathable air and potable water), the importance of others is more subjective and hence more likely to be controversial (e.g. fish harvesting vs. tourism on coral reefs) (Lau et al., 2018). Understanding heterogeneity in how people perceive and experience elements of nature requires an understanding of the complex factors that mediate human-nature interactions, and remains a key challenge for environmental management (Lindemann-Matthies et al., 2014; Díaz et al., 2015; Milcu et al., 2015; Lau et al., 2018).

While ecosystem services research has tended to take a socially-aggregated approach that focuses on an average beneficiary (Daw et al. 2011), the ways in which people perceive and interact with their environment are not uniform (Scholte et al., 2015; Gurney et al., 2017). Individuals' perceptions of ecosystems are affected by a range of socio-demographic characteristics linked to key elements of identity, such as gender, ethnicity, and education, which influence how they use, value, and access ecosystem (Lau et al. 2018, 2019). For example, Lau et al. (2019) found that individuals' ratings of cultural ecosystem services were significantly influenced by gender, with men rating the service higher than women. Furthermore, perceptions of ecosystem services can be attributed to elements of identity that are specific to individual ecosystems; for instance, degree of identification as a fisher was strongly linked to how respondents rated a range of ecosystems services from coral reef fisheries (Hicks and Cinner et al. 2014). Perceptions of ecosystem services can also be influenced by where and how people live. Urban ecosystems, for example, are perceived as more limited in their capacity to produce services than rural ecosystems (Lapointe et al. 2019). As a result, the ability of people to access ecosystem services may be more restricted in urban areas. Given the rapid rates of urbanisation in the global South generally, and in Africa in particular, understanding how perceptions of ecosystem services change along an urban-rural gradient is important in ensuring the equitable management of ecosystems in developing countries (Elmqvist et al. 2013).

Taking a socially-disaggregated approach to perceptions of ecosystem services can clarify who experiences costs and benefits related to ecosystem change and management, and thus help ensure equitable outcomes from decision-making processes. Aggregated assessments of ecosystem services that ignore differences between people may obscure the preferences and interests of subgroups, potentially resulting in management decisions that lead to unequal access to ecosystem services within society. Differential access to ecosystem services has been highlighted as a major gap in ecosystem service research, particularly in areas where systemic inequalities, exclusion and segregation may result in conflict and violence (Lapointe et al. 2019). Examining heterogeneity in perceptions of ecosystem services is particularly important in post-colonial countries, since colonisation typically led to unequal access to ecosystem services, mirroring broader social and economic inequalities (Musavengane and Leonard 2019). Sustained unequal access to ecosystem services risks reinforcing existing social and economic inequalities (Daw et al., 2011;

Sikor, 2013). In South Africa, for example, formalised segregation based on “race” under apartheid has led to access to ecosystem services in South Africa historically being unevenly distributed, with management decisions largely informed by white and “upper class” priorities (Musavengane and Leonard, 2019). Despite progress in economic and social integration since the end of apartheid in 1994, South African society remains economically and socially divided along racial lines (Ramutsindela, 2007; Kepe, 2009; Amodio and Chiovelli, 2014). Therefore, to foster equitable and inclusive environmental management and governance in this context, it is critical to consider the legacy of apartheid by examining how human-nature relationships are related to race (Kepe, 2009; Martin et al., 2016).

I explored how socio-demographic characteristics relate to people’s perceptions of cultural ecosystem services provided by birds in South Africa. I used a functional group approach, grouping birds that shared similar behavioural and morphological traits that are relevant to cultural service provision. Functional approaches have a long history in avian ecology but are more typically applied to foraging guilds (e.g., insectivores, frugivores, raptors; Sekercioglu 2002). Since cultural ecosystem services are inherently intangible (Chan et al. 2012), developing a functional classification for cultural ecosystem services relies on capturing human perception. My previous chapter used an intensive analysis of people’s perceptions of birds to identify six cultural functional groups. Cultural functional groups are defined by the characteristics of bird species that people perceive as contributing to cultural ecosystem services or disservices (Zoeller et al. 2020, Chapter 3). The functional group approach reduces irrelevant between-species heterogeneity and facilitates the identification of external influences on functional groupings (Kahmen et al., 2002; de Arruda Almeida et al., 2018). It is particularly useful in establishing linkages between the functional traits of individual organisms and the production of ecosystem services (Sekercioglu 2002). Individual functional traits of organisms that underpin provisioning and regulating ecosystem services have been widely reported (Sekercioglu 2002; Cumming and Child 2009), but the functional traits that underpin cultural ecosystem services have received limited attention. In this paper I address this research gap by asking how socio-demographic characteristics influence perceptions of cultural functional groups of birds in South Africa. Extending research on cultural functional groups by understanding how socio-demographic characteristics shape human perceptions can elucidate where human-nature connections differ and how an individual's identity can inform this difference.

4.3 Materials and methods

4.3.1 Dataset

Data from the trait dataset for each respondent included: 1) socio-demographic characteristics; 2) bird ratings; and 3) score justifications. Traits elicited from the score justification process were grouped using K-means cluster analysis (a distance-based measurements of similarity), producing six distinct cultural functional groups composed of different birds (see Chapter 2). Given that the traits that define the six cultural functional groups are based on perceptions, they are associated with a suite of socio-demographic characteristics, representative of individual respondents who cited that specific trait during the interview process. Thus, I examined how socio-demographic characteristics are related to cultural functional groups (i.e. perceptions of bird traits).

4.3.2 Data analysis

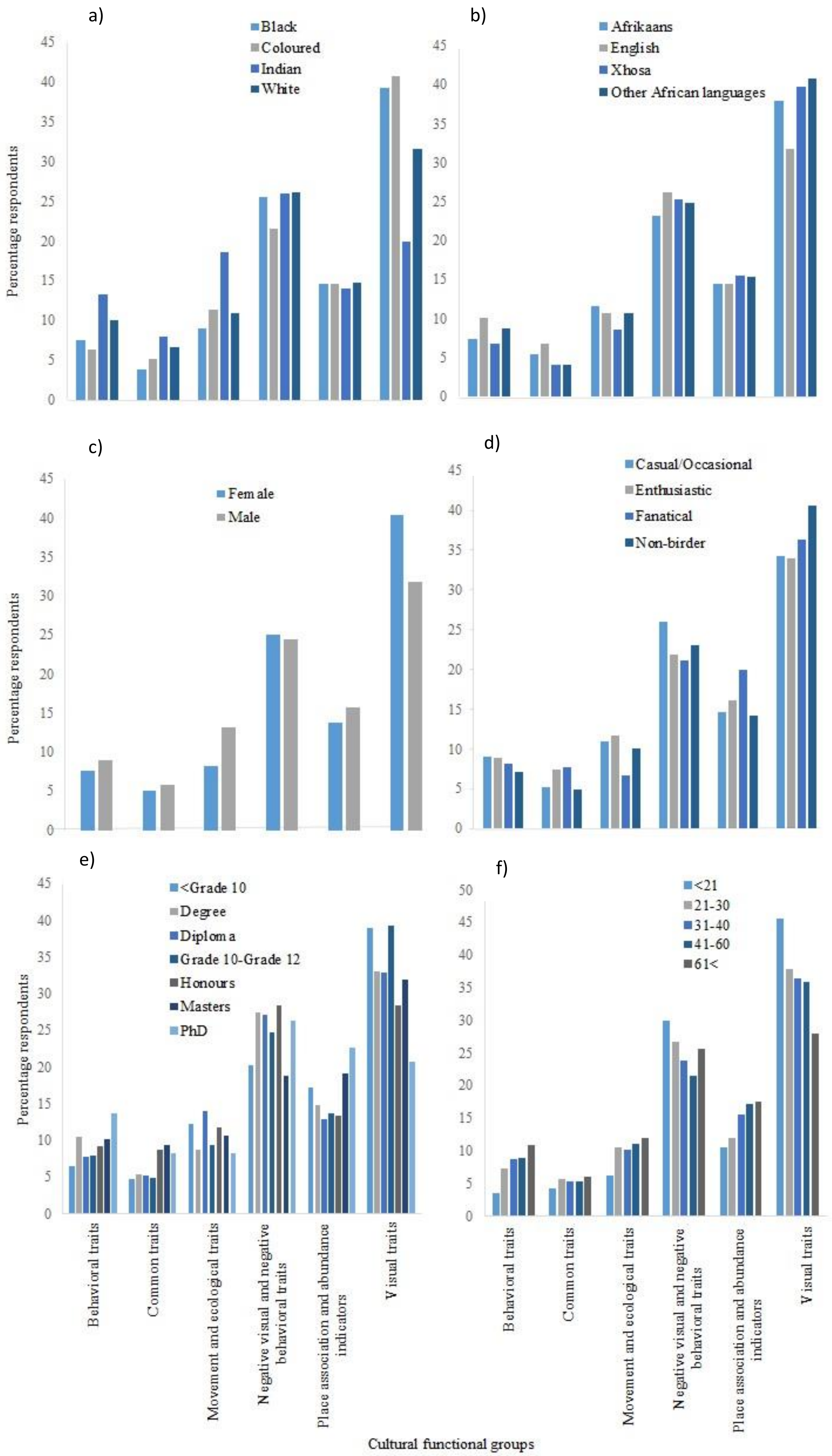
To determine whether socio-cultural characteristics were associated with cultural functional groups based on perceived bird traits, I first used χ^2 analyses to compare differences in the observed frequencies of socio-demographic characteristics between avian cultural functional groups. These analyses clarified the potential relevance of individual socio-demographic (explanatory) variables but were not able to provide estimates of the influence of a particular variable whilst controlling for the effects of the other explanatory variables.

I then used multinomial logistic regression (Upton, 2017) to explore the relative influences of socio-demographic characteristics on perceptions of cultural functional group in a way that incorporated the interactions between explanatory variables. Multinomial regression can be seen as an extension of logistic regression (i.e., with a response variable of 1 or 0) to consider more than two categories. The traditional assumptions of regression analysis need not be met to run a multinomial logistic regression, although it is important that observations are independent (Corona et al., 2008). I used multinomial analysis to determine the probability of respondents perceiving each of six cultural functional groups based on socio-demographic characteristics (i.e., I treated the socio-demographic variables as explanatory or X variables and the six cultural functional groups as a single categorical response or Y variable with six categories). I also included three variables representing biome, province and frequency of bird encounter as independent variables in order to control for key biogeographical factors thought to influence ecosystem service perceptions. I designated Movement and Ecological traits as the reference category for this model because this analysis produced the lowest AIC. One category for each independent variable was used as a reference category, with the model predicting the probability of respondents perceiving each cultural functional group against the socio-demographic reference category (Koster and McElreath, 2017). All analyses were conducted in R (version 4.1.3) using stats package v7.3-14 and nnet package v7.3-14.

To reduce the dimensionality of my data, I screened for redundancy by separately coding each independent variable as a set of individual categories and removing non-significant categories from the multinomial model. I reran the analysis three times, removing non-significant variables each time, to identify the model that best fit my data based on the lowest AIC value. As summarised in Table 4.1, the model with the lowest AIC included variables in the broader categories of age, gender, home language, education and race. All categories were z-score standardised.

4.4 Results

Results from χ2 tests suggested that socio-demographic factors were significantly associated with people's preferences for different avian cultural functional groups. Comparisons of human preferences across avian cultural functional groups differed significantly on all of the dimensions of socio-demographic characteristics that were measured: age (χ^2 5441.2, df = 20, p-value < 0.001), gender (χ^2 = 147.7, df = 5, p-value <0.001), race (χ^2 = 150.3, df = 30, p-value< 0.001), language (χ^2 = 108.4, df = 15, p-value < 0.05), education (χ^2 = 230.9, df = 6, p-value < 0.001), coarse location (χ^2 = 29.6, df = 5, p-value < 0.001), residential location (χ^2 = 208.4, df = 40, p-value < 0.001), and birding self-classification ($\chi^2 = 88.8$, df = 15, p-value < 0.001). A higher percentage of respondents across all socio-demographic characteristics reported perceiving Visual Traits than any other cultural functional group (Figure 4.1). In contrast, Common Traits and Behavioural Traits consistently had the lowest number of respondents, suggesting that individual people are more likely to perceive avian visual cues than traits pertaining to behaviour or observation frequency. (Fig. 4.1).


a)
Black
Coloured
Indian
White
Percentage respondents
b)
Afrikaans
English
Xhosa
Other African languages
c)
Female
Male
d)
Casual/Occasional
Enthusiastic
Fanatical
Non-birder
e)
<Grade 10
Degree
Diploma
Grade 10-Grade 12
Honours
Masters
PhD
f)
<21
21-30
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Behavioral traits
Common traits
Movement and ecological traits
Negative visual and negative behavioral traits
Place association and abundance indicators
Visual traits
Cultural functional groups

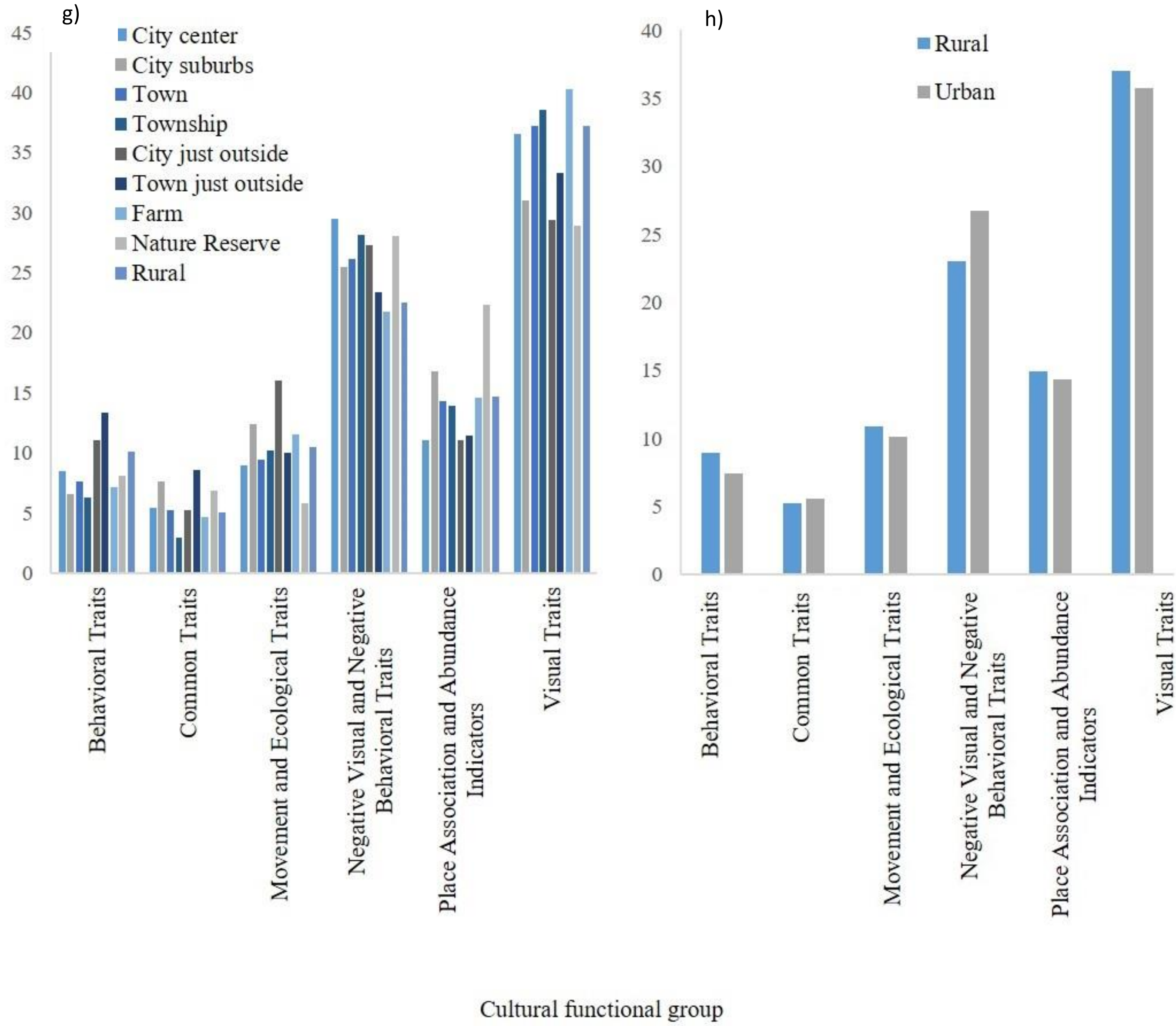


Figure 4.1 Percentage distribution of socio demographic characteristics between dimensions of cultural functional groups: (a) race, (b) language, (c) gender, (d) birding self-classification, (e), education, (f) age, (g) residential location and (h) coarse location.

The multinomial analysis supported the argument that socio-demographic characteristics are associated with perceptions of birds from all six cultural functional groups (Fig. 4.1; Table 4.1). Age, gender, race, language and education emerged as important socio-cultural characteristics influencing what people perceived about birds. The model explained 24% of the variance (AIC=37118.65, residual variance=36818.65, McFadden pseudo R^2 =0.24, $p<0.05$) (Table 4.1). Socio-demographic characteristics differed across cultural functional groups, both in the significance of the effect and whether it was negative or positive (Fig. 4.1; Table 4.1). Gender and education were consistently significant as explanatory variables across all avian cultural functional groups, suggesting these characteristics are strongly associated with human perceptions of birds. In contrast, home language was significant for Visual Traits, and race was significant for Behavioural Traits and Visual Traits, suggesting that perceptions of birds differ significantly for people of different races and languages. Once I reduced the dimensionality of my data, only one province was significant for Behavioural Traits (Western Cape) and three biomes for Place Association and Abundance Indicators and Visual Traits (Forest and Fynbos, Fynbos and Succulent Karoo).

Table 4.1 Regression coefficients (CF), standard error (SE), z-statistic, and p-value of the multinomial model between dimensions of socio-demographic characteristics and cultural functional groups. Socio-demographic characteristics missing p-values indicate non- significance (p > 0.05).Socio demographic characteristics missing p-values indicate non-significance.

Characteristics	Category	Behavioural Traits				Common Traits				Negative Visual and Negative Behavioural Traits				Place Association and Abundance Indicators				Visual Traits			
		CF	SE	z statistic	P-value	CF	SE	z statistic	P-value	CF	SE	z statistic	P-value	CF	SE	z statistic	P-value	CF	SE	z statistic	P-value
	(Intercept)	-1.66	0.52	-3.19	0.01	-3.54	0.77	-4.56	0.001	-0.29	0.33	-0.88		-2.30	0.48	-4.77	0.001	-3.26	0.53	-6.14	0.001
Age	Continuous	-0.013	0.0029	-4.61	0.001	-0.0017	0.0032	-0.52		-0.0027	0.0019	-1.40		0.0054	0.0025	2.18	0.05	0.014	0.0022	6.34	0.001
Gender	Male	0.41	0.08	5.47	0.001	0.41	0.09	4.55	0.001	0.21	0.05	4.07	0.001	0.69	0.07	9.99	0.001	0.35	0.06	5.82	0.001
Home language	English	0.09	0.12	0.72		0.16	0.15	1.07		0.05	0.09	0.53		0.04	0.12	0.35		0.05	0.11	0.46	
	Other African languages	0.17	0.33	0.52		0.93	0.63	1.46		-0.20	0.21	-0.92		0.16	0.33	0.48		0.99	0.40	2.45	0.05
	Xhosa	0.08	0.33	0.23		1.32	0.62	2.11	0.05	-0.13	0.21	-0.65		0.15	0.32	0.46		1.38	0.40	3.46	0.001
Education	<Grade 10	-0.92	0.30	-3.10	0.01	-1.19	0.32	-3.67	0.001	-0.63	0.21	-2.96	0.01	-0.45	0.28	-1.65		-0.65	0.24	-2.71	0.01
	Grade 10 - Grade 12	-0.79	0.27	-2.90	0.01	-1.05	0.30	-3.55	0.001	-0.47	0.20	-2.34	0.05	-0.56	0.26	-2.13	0.05	-0.83	0.23	-3.64	0.001
	Degree	-0.57	0.30	-1.92		-1.07	0.33	-3.25	0.05	-0.27	0.22	-1.24		-0.48	0.29	-1.68		-0.70	0.25	-2.81	0.01
	Diploma	-0.69	0.29	-2.39	0.05	-0.94	0.32	-2.96	0.05	-0.22	0.21	-1.03		-0.15	0.27	-0.54		-0.69	0.24	-2.86	0.01
	Honours	-0.68	0.33	-2.05	0.05	-0.43	0.35	-1.23		-0.06	0.24	-0.27		-0.10	0.31	-0.33		-0.48	0.28	-1.70	
	Masters	-0.62	0.33	-1.91		-0.36	0.35	-1.04		-0.66	0.25	-2.67	0.01	-0.46	0.31	-1.45		-0.11	0.27	-0.42	
	PhD	0.18	0.35	0.52		-0.30	0.39	-0.77		0.09	0.27	0.35		-0.17	0.36	-0.48		-0.01	0.30	-0.02	
Race	Coloured	-0.04	0.32	-0.13		1.51	0.62	2.45	0.05	-0.34	0.20	-1.66		0.26	0.32	0.83		1.19	0.39	3.03	0.01
	White	0.60	0.30	2.02	0.05	1.84	0.60	3.06	0.01	0.07	0.18	0.40		0.51	0.30	1.73		1.19	0.38	3.14	0.01

Gender was the only socio-demographic characteristic that significantly explained differences in what people perceived across all avian cultural functional groups. Men were more likely than women to perceive Behavioural Traits, Common Traits, Negative Visual and Behavioural Traits, Place Association and Abundance Indicators and Visual Traits, compared with the Movement and Ecological Traits Group. Increasing age was significantly positively related to perceiving the Place Association and Visual Traits functional groups (compared to the Movement and Ecological Traits group), and negatively related to the Behavioural Traits, Common Traits and Negative Visual and Behavioural Traits functional groups (although the relationship was not significant with regards the latter two). There were few significant relationships for home language, except that Xhosa speakers were significantly more likely than Afrikaans speakers to perceive bird species in the Common Traits and Visual Traits functional groups than in the Movement and Ecological Traits group. For race, there was only one significant difference between those who identified as coloured as opposed to black, whilst there were three significant differences between white and black respondents. Respondents identifying as white were significantly more likely than black respondents to perceive traits associated with the Behavioural Traits, Commons Traits, and Visual Traits functional groups as opposed to the Movement and Ecological Traits functional group.

4.5 Discussion

The results indicate that all socio-demographic characteristics were significantly related to perceptions of cultural functional groups, and hence with perceptions of bird traits and ultimately the receipt of cultural ecosystem services and benefits. Perceptions of avian cultural functional groups were not uniform across the range of socio-demographic characteristics that were measured, highlighting the importance of disaggregating the beneficiaries of ecosystem services. The association of age, gender, race, language and education with different avian cultural functional groups emerged as particularly significant, suggesting that these characteristics can be used to predict patterns in perceptions of cultural ecosystem services.

Heterogeneity in the ways people perceive birds may be indicative of individuals' differential abilities to access ecosystem services, where access is constructed through identification with particular socio-demographic characteristics (following Hicks and Cinner 2014). For example, language as an influence on perceptions of bird traits was significantly associated with Xhosa and other African language-speaking respondents. Contrasts between perceptions of birds according to racial and linguistic characteristics probably relate to forced segregation during apartheid, where black and coloured South Africans were relocated to rural areas (Butler, 2003; Musavengane and Leonard, 2019). In a South African context, identification with a specific race and social construction through a specific language are likely to mediate an individual's interaction with their environment and contribute to their ability to access ecosystem services (Kittinger et al., 2012; Hicks and Cinner, 2014; Musavengane and Leonard, 2019).

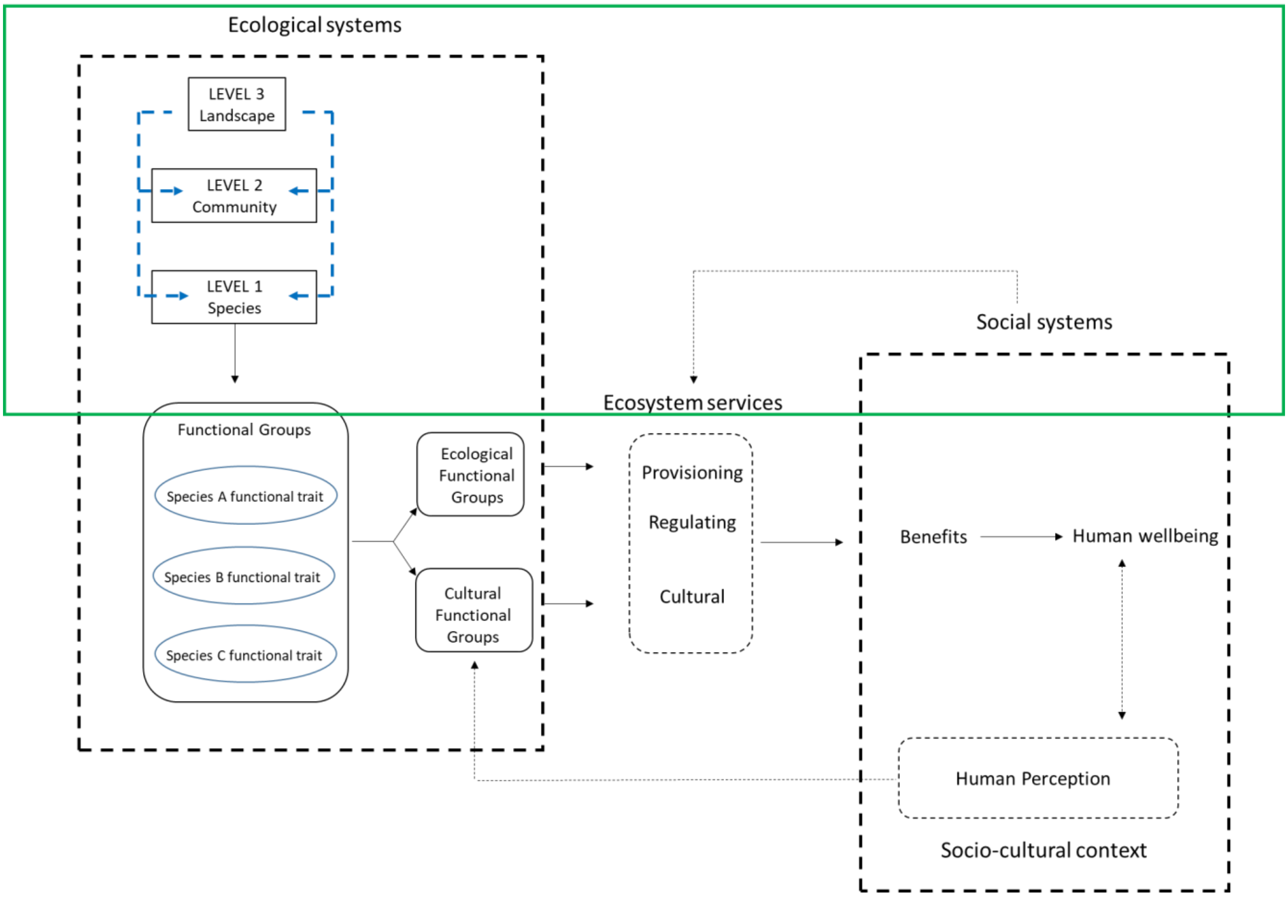
My results suggest that urbanisation does not affect perceptions of cultural functional groups. Despite there being significant differences between respondents living in different locations in the Chi-square tests, residential and coarse location were not significantly associated with particular avian cultural functional groups in the presence of other socio-demographic variables in the multinomial regression. Since research has indicated that bird diversity decreases with urbanisation (Suri et al., 2017), it was expected that an individual person's position along an urbanisation gradient would affect their perception of ecosystem services (Clergeau et al. 1998), particularly since others have found that species traits may be filtered in urban environments (Croci et al., 2008). Indeed, urban dwellers more frequently report limitations to ecosystem services benefits than rural dwellers (Lapointe et al. 2019). However, the relationships between how people interact with their environment and where they live are still connected in potentially important ways in South Africa. Due to forced segregation based on race for most of South Africa's colonial history, many urban households of historically disenfranchised communities in South Africa still maintain strong links to their traditional rural homes (Smit, 1998; Hamann et al., 2016). Rural-urban linkages are reinforced by circular migration and migrant labour between rural and urban households (Smit 1998). This may explain why perceptions of cultural functional groups still appear to be more strongly linked within shared social constructs that span urban and rural communities in South Africa.

Establishing where differences occur between people in their perceptions of avian cultural functional groups facilitates identification of potential barriers to ecosystem service access (Mensah et al., 2017). In countries where unequal access to resources has previously been institutionalised, understanding the underlying drivers of differential perceptions of ecosystem service is important in promoting distributive justice with respect to ecosystem services across previously disenfranchised communities (Musavengane and Leonard 2019). Indeed, in other contexts, research shows that ecosystem degradation and ecosystem service loss disproportionally affect marginalised groups, such as the poor, women, and indigenous communities (Sievers-Glotzbach, 2013). However, the challenges associated with capturing the complex socio-demographic factors that constrain access to ecosystem services (and subsequently result in diverse ecosystem service perceptions) have resulted in limited inclusion of diverse stakeholder preferences in ecosystem management (Kittinger et al., 2012; Iniesta-Arandia et al., 2014; Gurney et al., 2015). Incorporating diverse perceptions in ecosystem service management is particularly important in areas with social inequality, as the linkages between conservation, human wellbeing and the socio-demography of ecosystem users are often not explicitly discussed in the equitable management discourse (Kepe, 2009; Musavengane and Leonard, 2019). Management initiatives that seek to maintain ecosystem service delivery must therefore tailor their approach to match locally-specific preferences. This requires heterogeneity in ecosystem service perceptions to be incorporated into environmental management decisions (Lau et al. 2018), since I have shown that focusing only on specific cultural functional groups risks discounting the preferences of local ecosystem users.

I have demonstrated that exploring the drivers of perceptions of avian cultural functional groups, defined by the traits that people care about in birds, can promote an understanding of the causes of heterogeneity in people's relationships with their environment. Differences in perceptions of cultural functional groups were significant across all socio-demographic characteristics, implying that socio-demographic characteristics inform how people experience bird-related ecosystem services and their benefits. Notably, age, gender, race, language and education were shown to significantly affect perceptions of cultural services from birds. Further research on how different societal groups perceive and experience ecosystem services will be critical for resolving inequities in the distribution of ecosystem service benefits across socially heterogeneous communities (Kepe 2009; Sievers-Glotzbach 2013) and ensuring just and equitable management of ecosystems.

5 The influence of landscape context on the production of cultural ecosystem services*

In this Chapter, I determined the extent to which landscape attributes contribute to the cultural benefits people experience from birding.



*Adapted from Zoeller, K.C., Gurney, G.G., Cumming, G.S., 2022. The influence of landscape context on the production of cultural ecosystem services. Landscape Ecology. https://doi.org/10.1007/s10980-022-01412-0.

Contributions: I developed the research question, methodology, collected the data, performed the data analyses, and developed the figures and tables with the advice of G. Cumming and G. Gurney. I wrote the first draft of the paper which was revised with editorial input from G. Cumming and G. Gurney.

5.1 Abstract

Recent efforts to apply sustainability concepts to entire landscapes have seen increasing interest in approaches that connect socioeconomic and biophysical aspects of landscape change. Evaluating these connections through a cultural ecosystem services lens clarifies how different spatiotemporal scales and levels of organisation influence the production of cultural benefits. Currently, however, the effects of multi-level and multi-scale ecological variation on the production of cultural benefits have not yet been disentangled. I used data from 293 birding routes and 101 different birders in South African National Parks to explore the general relationships between birder responses to bird species and environmental conditions, bird-related observations, the biophysical attributes of the landscape and their effect on bird-related cultural benefits. Here I show that biophysical attributes (particularly biome, vegetation type, and variance in elevation) significantly increased the percentage of variance explained in birder benefits from 57% to 65%, demonstrating that birder benefits are derived from multi-level (birds to ecosystems) and multi-scale (site to landscape) social and ecological interactions. Landscape attributes influence people's perceptions of cultural ecosystem service provision by individual species. Recognition of the complex, localised and inextricable linkage of cultural ecosystem services to biophysical attributes can improve our understanding of the landscape characteristics that affect the supply and demand of cultural ecosystem services.

5.2 Introduction

Recent efforts to apply sustainability concepts to entire landscapes have seen increasing interest in approaches that connect socioeconomic and biophysical aspects of landscape change (Mao et al. 2020). One widely used approach for thinking about landscape sustainability is the ecosystem services framework, which focuses on the linkages between people and nature and specifically on the capacity of ecosystems to deliver essential benefits to people (Bachi et al. 2020; Bruley et al. 2021; MA 2005). The interaction between ecological systems and social systems in the production of ecosystem services forms a critical feedback loop in landscape management, where landscape condition is shaped by perception-based preference for particular ecosystem services that contribute to human wellbeing (Fig. 5.1) (Tengberg et al. 2012).

While the role of biophysical factors in driving ecosystem service production (such as sequestration capacity of a peat bog or timber production in a forest) has been well established across a range of different scales, the role of human social factors in the receipt of ecosystem benefits at different levels (organisms to ecosystems) and scales (site to landscape) has received limited attention (Bruley et al. 2021). Framing ecosystem services through people's connection to the environment is not a novel concept (Fish et al. 2016; Tew et al. 2019), but the effects of multi-level and multi-scale ecological variation on the production of cultural benefits have not yet been disentangled. It thus remains unclear how people experience ecosystem benefits that are produced over multiple scales and levels of organization and which kinds of benefit depend primarily on interactions with individual organisms, populations, communities, ecosystems, or landscapes respectively.

I explore the concept of multi-level and multi-scale organisation in the production of ecosystem services through a cultural ecosystem services lens (Fig. 5.1). Cultural ecosystem services are non-material benefits such as aesthetic values, spiritual fulfilment, tourism and recreation (Chan et al. 2012). They are co-produced through the interactions between people (in social systems) and their environment (ecological systems) (Fish et al. 2016), delivering benefits that have direct contributions to changes in human wellbeing (Fig. 5.1) (Fischer and Eastwood 2016). Ecological systems comprise multiple levels of ecological organisation. I focused particularly on three levels relating to the provision of cultural ecosystem services: species, community, and landscape (Fig. 5.1). While the relationship between scales and levels in ecological systems is complex, I use conventional levels of ecological organisation that should exhibit a hierarchical relationship to ecological processes and associated spatial and temporal scales (Allan 1990). Thus, species and communities are nested within landscapes since it is landscape-level biophysical attributes that support species propagation through the provision of resources like food and habitat (Aalders and Stanik 2019).

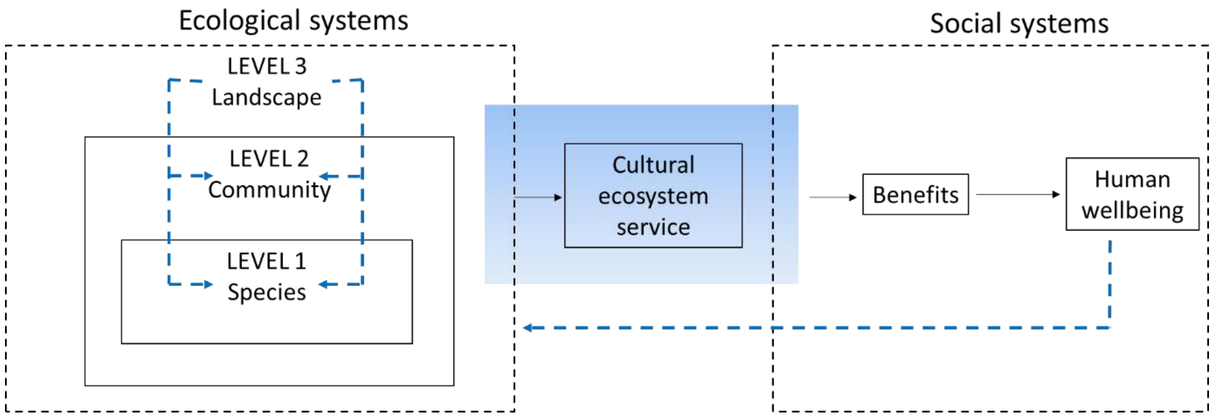


Figure 5.1 The flow of cultural ecosystem service benefits from ecological systems to social systems using a simplified ecosystem cascade model.

I used the cultural service of bird-watching as an accessible case study from which to explore how multi-level and multi-scale interactions are related to ecosystem service production. The distributions of birds vary in geographic space, and the benefits associated with birdwatching are well-established and globally pervasive (Graves et al. 2019; Sekercioglu 2002; Whelan et al. 2015). Bird-watching by its nature appears to focus on the level of individual organisms of different species. However, previous research has suggested that there may be a vital link missing in our understanding of the relationship between landscape-level processes and the benefits associated with birdwatching (Cumming and Maciejewski 2017). Benefits related to species observations alone accounted for only 27% of variance in birder benefits, while including birder expectations and responses to environmental conditions increased the proportion of variance explained to 57% (Cumming and Maciejewski 2017). Some previous research has identified aesthetic benefits associated with birding through elements of nature, such as water bodies or complex terrain (Andersson et al. 2015; Chettri 2005). The extent to which variation in landscape-level attributes supports the provision of birder benefits remain unclear, however, and has not been previously quantified relative to the direct benefits derived from seeing birds. I hypothesised that a significant proportion of the remaining 43% of unexplained variation might be explained by factors at a landscape level, particularly biophysical attributes such as elevation that might contribute to the benefits associated with birding (Booth et al. 2011; Chettri 2005). Connecting birder benefits with the biophysical attributes of landscapes provides important insights into how perceptions of cultural ecosystem services (and thus, benefits experienced) by people are mediated by the multi-level and multi-scale structure of ecological systems (Plieninger et al. 2013).

5.3 Methods

5.3.1 Dataset

To determine the extent to which landscape level attributes contributed to birder benefits, I used the landscape dataset described in Chapter 2.

5.3.2 Data analysis

First, to reduce the dimensionality of my data, I screened for redundancy in the landscape attribute data with over 40 categories (i.e., vegetation type and land cover). This was achieved by separately coding each independent variable (i.e. landscape attributes) as a set of individual categories and removing non-significant categories from the multivariate model. I reran the analysis three times, removing non-significant variables each time in a stepwise process, to identify the model that best fitted my data based on the lowest AIC value.

I tested for a relationship between birder benefits and landscape characteristics using multivariate linear models to take account of covariance effects within the data. For these models, I used the continuous rating data of satisfaction scores (birder benefits) as my response variable, and perception-based birding experiences and biophysical landscape attributes as predictors. To account for nested structure of my data (multiple birders in each national park), I included location (national park) as a random effect in the model. I also ran ANOVAs to determine whether there were differences in birder benefits and species richness according to biome, and post-hoc Tukey tests to see where those differences occurred.

5.4 Results

The multivariate analysis indicated that 65% of variance in birder benefits was explained by a combination of subjective responses by participants at the species scale (“bird species responses”), perception-based responses at the landscape scale (“environmental responses”) and biophysical attributes, specifically biome, vegetation type and variance in elevation ($r2=0.65$ AIC=1012, deviance=933.6, df=273) (Table 5.1). Adding landscape variables increased my ability to predict cultural service provisioning by a significant 38% relative to models that only included bird responses, and 8% relative to models that included bird responses and perception-based responses at the landscape scale.

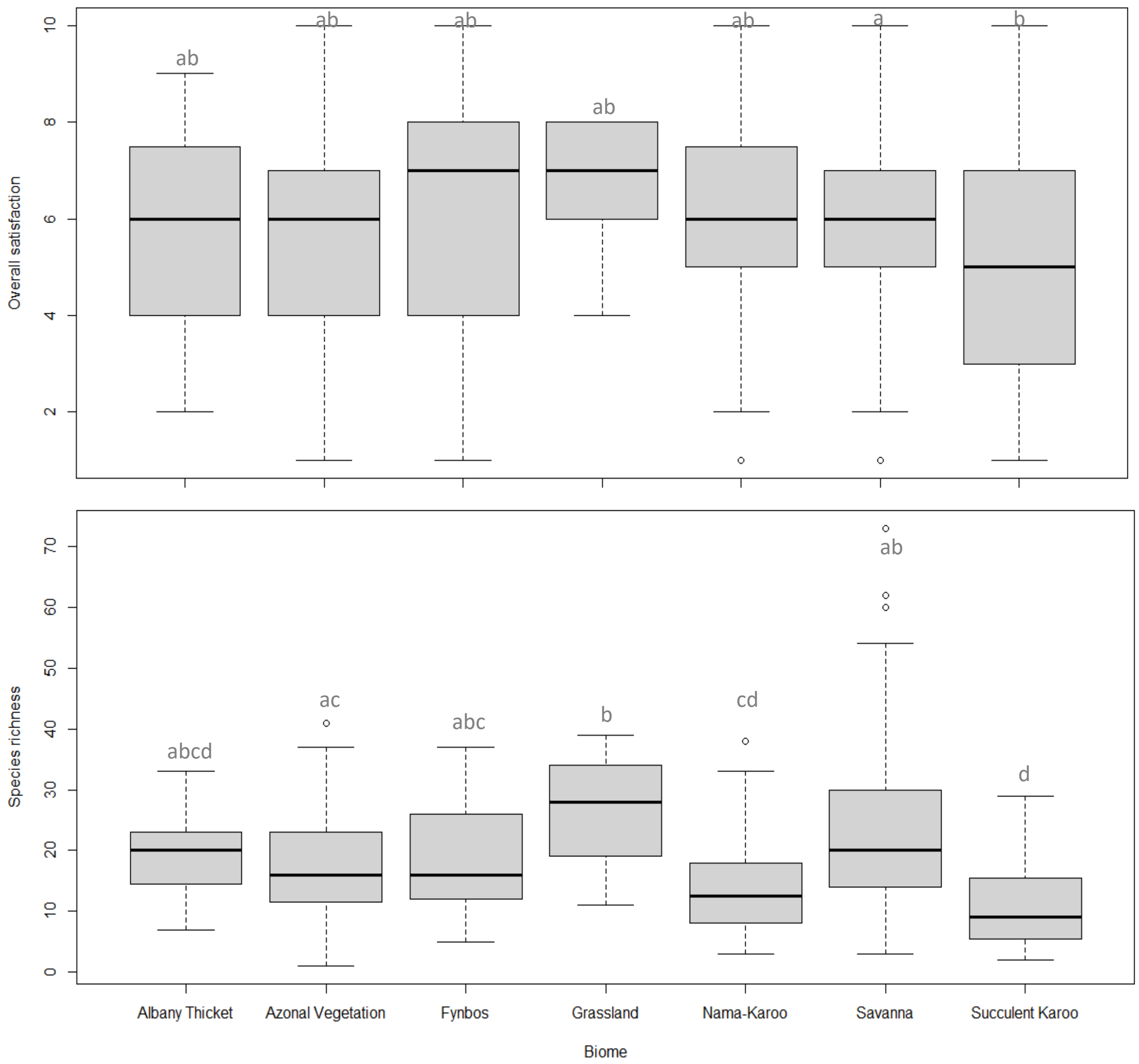


Figure 5.2 Comparison by biome of amateur overall satisfaction score with birding routes (top panel) and number of bird species seen (lower panel). Clusters sharing a letter are not statistically different from each other (p<0.05).

The dominant biophysical attribute that explained variance in birder benefits in my model was biome, with biome types being strong, positive predictors of route ranking (Table 5.1). Based on birder benefit averages (overall satisfaction), routes in Grassland and Fynbos biomes were favoured by participants. Gabbro Grassy Bushveld and Tankwa Karoo emerged as significant vegetation types in my multivariate model. These vegetation types are characteristic of Savanna and Succulent Karoo biomes respectively. On average, birders in Succulent Karoo reported lower benefits than all other biomes, although this difference was only significant when compared to routes in Savanna biomes (df=6, F-value=2.161, p =0.047) (Fig. 5.2). Differences in species richness according to biome were also significant (df=6, F-value=10.01, p=5.72e-10), specifically between Grassland and Azonal Vegetation and Nama Karoo; Nama Karoo and Savanna; and between Succulent Karoo and Azonal Vegetation, Fynbos, Grassland and Savanna (p<0.05). On average, species richness was greatest in Grasslands and lowest in Succulent Karoo. In addition to biome and vegetation, variance in elevation had a significant positive effect on route ranking, suggesting that routes with more complex terrain were preferred by birders. Despite the expectation that additional biophysical attributes would account for variance in the model, roads, water bodies and land cover types (keeping in mind that all surveys were undertaken in protected areas in 'natural' habitats) did not have a significant effect on benefits.

*Table 5.1 Summary table of estimates, standard error (SE), t-value and p-value of the multivariate linear mode (n=273). Predictor variables were assigned significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

		Estimate	Std. Error	t value	Pr(>|t|)	
	(Intercept)	2.148926	1.010512	2.127	0.034353	*
Biome	Forest	2.429732	0.748238	3.247	0.001311	**
	Fynbos	3.068522	0.580547	5.286	2.57E-07	***
	Grassland	3.694464	1.047803	3.526	0.000495	***
	Nama-Karoo	3.069363	0.554283	5.538	7.21E-08	***
	Savanna	3.214063	0.553506	5.807	1.77E-08	***
	Succulent Karoo	2.474237	0.536446	5.612	6.13E-06	***
Elevation	Mean	-0.067674	0.057398	-1.179	0.239412	
	Variance	0.323834	0.084162	3.848	0.000148	***
Roads	Road Length	0.137437	0.537389	0.256	0.798337	

	Presence/Absence	-0.064289	0.84461	-0.076	0.939382	
Road type	Primary	-0.438707	0.429158	-1.022	0.307567	
	Secondary	-0.25979	0.348555	-0.745	0.45671	
	Service	-0.822557	1.394558	-0.59	0.55579	
	Tertiary	0.334996	0.476005	0.704	0.482179	
	Track	-0.520123	0.689357	-0.755	0.451196	
	Trunk	-0.018427	0.439869	-0.042	0.966615	
	Unclassified	-0.212259	0.333307	-0.637	0.524771	
	Unsurfaced	0.621175	1.033431	0.601	0.548285	
Water bodies	Water Presence	-0.011871	0.220424	-0.054	0.957091	
Water body type	Dry	-0.597705	0.83542	-0.715	0.47494	
	Non-Perennial	-0.16865	0.431912	-0.39	0.696491	
	Perennial	0.023209	0.493382	0.047	0.962515	
	Unknown	-0.501586	0.522773	-0.959	0.33817	
	River length	-1.367543	5.470527	-0.306	0.759912	
	River area	12.327655	89.917848	0.137	0.891054	
Vegetation type	Gabbro Grassy Bushveld	1.993262	0.684651	2.911	0.003896	**
	Kimberley Thornveld	0.905013	0.587533	1.54	0.124631	
	Tanqua Karoo	1.819932	0.475425	3.828	0.00016	***
Land cover	Low Shrubland (Nama Karoo)	-0.766333	0.451225	-1.698	0.090583	
Bird species responses	Richness	0.06887	0.009509	7.243	5.49E-12	***
	Low Diversity	-0.525371	0.103976	-5.053	7.98E-07	***
	Low Abundance	-0.321921	0.099448	-3.237	0.001357	**
	Unexpected Species	0.350256	0.107758	3.25	0.001297	**
	Good Sighting Of Species	0.33692	0.094402	3.569	0.000423	***
Environmental responses	Good Weather	0.210489	0.134004	1.571	0.117394	
	Bad Weather	-0.358387	0.090605	-3.955	9.74E-05	***
	Interesting Diverse Landscape	0.421013	0.103034	4.086	5.77E-05	***

With the exception of ‘good weather’, responses by participants to observations of bird species and biophysical attributes were dominant and consistently significant in predicting amateur birder rankings of birding routes. Perceptions of the diversity and abundance of birds observed had a significant effect on reported benefits.

5.5 Discussion

My results show that birder benefits were related to biome, vegetation type and perceptions of the bird population observed, the landscape, and the weather. Including biophysical attributes with perception-based birding experiences increased the percentage of variance explained in birder benefits from 57% (Cumming and Maciejewski, 2017) to 65%, supporting the hypothesis that a small but significant proportion of birder benefit is produced from multi-level and multi-scale social-ecological interactions. I would expect the influence of the surrounding landscape to increase in areas that are more heavily impacted by people (e.g., agricultural landscapes and urban areas) than national parks. These results provide support for the consideration of landscape-level attributes in addition to species observations, even in cases where cultural service provision appears to be highly dependent on individual organisms, to more accurately reflect the processes that result in the co-production of cultural ecosystem service benefits.

Despite their contribution to variance explained in birder benefits, only three biophysical attributes added significant explanatory power to the model. The primary explanatory biophysical variables in this model were biome and vegetation type. The importance of biomes in accounting for variance in birder benefits highlights potential connections between individual-level and landscape-level social-ecological interactions (typically occurring at fine and broad scales respectively). Biomes are defined by the dominant plant growth form and associated climatic thresholds (Conradi et al., 2020) which create specific conditions to which bird species are adapted (Chettri, 2005; Steven et al., 2017; Filloy et al. 2019). In the case of habitat specialists, specialised adaptations enable certain bird species to survive under specific conditions (e.g. cutaneous evaporation in desert birds) (Gerson et al., 2014). Landscape-level processes influencing biome distribution thus also contribute to the receipt of birder benefits at the species level.

Birder benefits in the Succulent Karoo were not significantly different from other biome types. The Succulent Karoo, which features the Tankwa Karoo vegetation type, is located in a biodiversity hotspot (CEPF 2001) that is characterised by fragile drylands that are highly susceptible to disturbance (Ament et al., 2017). Although species diversity was low in the Succulent Karoo, birder benefits did not generally differ compared to more speciose biomes (Cumming and Maciejewski, 2017). These results suggest that birder benefits were not reduced in low diversity biomes, implying in turn that birders may adjust their expectations to fit specific landscapes (Cumming and

Maciejewski, 2017). In areas where the environment is harsh and organisms require more specialised adaptations to survive (e.g., deserts, mountain-tops), cultural ecosystem services associated with species and communities may be outweighed by landscape level attributes such as biome and vegetation type (Cumming and Maciejewski, 2017).

Cultural ecosystem services are amongst the most valued products of ecosystems (Orenstein et al., 2015), but are challenging to manage since cultural values are subjective (Tew et al., 2019). Linking quantifiable landscape attributes with perception-based measures of the landscape may provide insight into the biophysical drivers of people's perceptions which can help prioritise landscape management decisions. For example, "interesting, diverse landscape" was a significant explanatory variable in my model. The attributes of a landscape that promote the perception of an interesting and diverse landscape can be linked to biome, vegetation type and variation in elevation since these biophysical attributes were also significant. Assessing cultural ecosystem services by considering all levels of ecological organization can provide insight into people's preferences and perceptions that drive the co-production of ecosystem services (Katz-Gerro and Orenstein, 2015).

However, it is important to note that individual perception is not uniform across a given population. For example, amateur birders have been found to be generally more interested in non-birding components of a birding experience than experts (Hvenegaard, 2002). (Katz-Gerro and Orenstein, 2015). Different social groups may preferentially engage with different levels of ecological organization to the extent that attributes that contribute to an "interesting, diverse landscape" could differ between ecosystem users (Katz-Gerro and Orenstein, 2015). Previous research has shown that perceptions of cultural ecosystem services associated with birds are likely to vary significantly across socio-demographic characteristics, such as age, gender, race language and education (Zoeller et al., 2021). For example, in South Africa, Xhosa-speakers were shown to perceive visual traits of birds (including *inter alia* plumage colour and body size) more frequently than English-speakers (Zoeller et al., 2020; Zoeller et al., 2021). Avitourism tends to attract an older demographic with high enough income to afford travel and park entry fees (Steven et al., 2017). Indeed, as reflected for my respondents, typical visitors to national parks in South Africa average 46 years old, speak either English or Afrikaans, are married, and possess higher education qualifications (Scholtz et al., 2015). Understanding how variation in birders' identity relates to perceptions of birder benefits and their multi-level biophysical drivers provides an important avenue for future research (Tengberg et al., 2012). Many birders fall into a relatively influential and empowered demographic; equitable decisions around biodiversity conservation and landscape protection will ultimately require inclusion of the values and preferences held by the full spectrum of society (Lau et al., 2018).

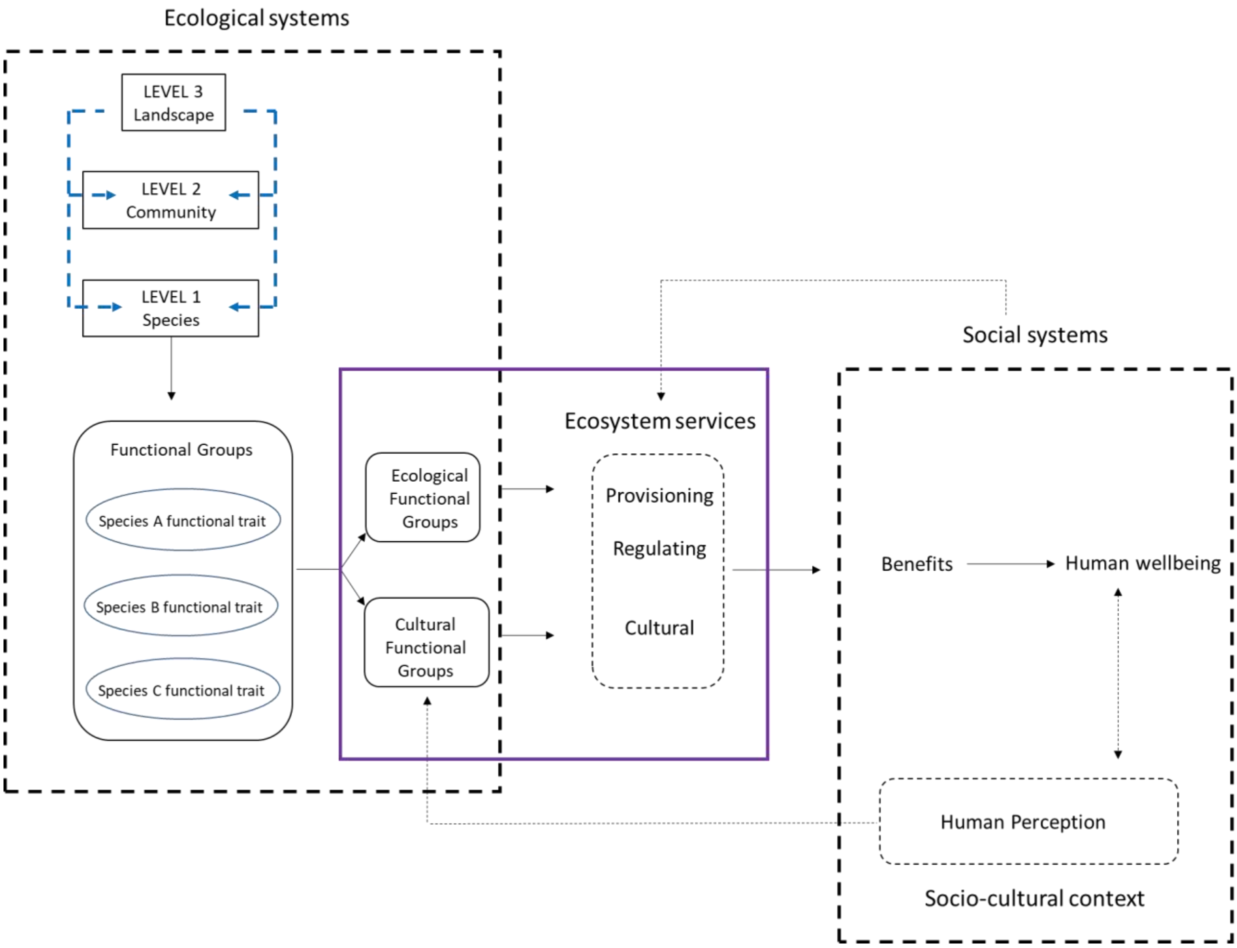
Understanding the influence of landscape characteristics on birder benefits requires consideration of the nested relationship between species, communities and landscape. While this study disentangled the individual effects of different levels of ecological organisation to better understand their contribution to birder benefits, components of ecological systems are not independent of each other (Suarez-Rubio and Thomlinson, 2009; Filloy et al., 2019). For instance, while the results suggested that biome, vegetation type and variance in elevation were significantly related to birder benefits, these biophysical attributes also affect the assemblage of bird communities through hierarchical relationships at different scales and levels (Aalders and Stanik, 2019). In addition, social systems exert a critical selective pressure on ecological systems (Tengberg et al., 2012), suggesting that the provision of birder benefits also depends on demand from birders. Consequently, the cultural benefits derived from birdwatching are produced from complex social-ecological interactions that occur at multiple levels and scales even when cultural services are ostensibly delivered at the species level.

I have provided evidence for the existence of significant, measurable, multi-level spatial influences on cultural ecosystem services associated with birding. An important consideration going forward would be to explicitly account for seasonal shifts in bird assemblages and their impact on cultural benefits received from ecosystems, particularly in relation to migratory species. While I conducted sampling evenly throughout summer and winter (Cumming and Maciejewski, 2017), I did not measure species-specific responses to seasonal changes and their influence on birder benefits (Graves et al., 2019). Similarly, I did not explore how seasonal shifts may impact benefits associated with landscape-level responses. For example, perceptions of birder benefits may be lower during dry periods than flowering seasons, through the formation of concentrations of nectarivorous birds and changes in vegetation-related aesthetics (Chettri, 2005). Exploring temporal variation in conjunction with spatial contexts may therefore provide further insight into birder benefits.

Understanding cultural ecosystem services at the landscape-level and implementing conservation measures to protect valuable biophysical attributes can mitigate against potential threats to ecosystem service delivery (Schaich et al., 2010). Although ecosystem services are generated within the landscape, there is little understanding of landscape-ecosystem service connections (Andersson et al., 2015). I found that biophysical attributes of the landscape influence the perception of cultural ecosystem service provision at the species scale and thus need to be explicitly considered in ecosystem service assessments, even where a cultural service is heavily linked to individual organisms. Components of landscapes interact with one another, resulting in a landscape mosaic comprising a composite of different attributes (Daniels, 1994). Landscapes are often perceived as a whole rather than the sum of individual biophysical attributes (Fagerholm et al., 2019). Safeguarding the provision of birder benefits therefore requires supporting variation in spatial contexts and across multiple scales (Graves et al., 2019). Recognition of the complex, localised and inextricable linkage of cultural ecosystem services to landscape features can also improve our understanding of landscape characteristics that affect the supply and demand of cultural ecosystem services (Potschin et al., 2013; Keller and Backhaus, 2019) .

6 Cultural ecosystem services from birds relate closely to avian ecological functions*

In this Chapter, I explored the spatial relationship between cultural and ecological functional group richness.



*Adapted from Zoeller, K.C. and Cumming, G.G., 2022. The relationship between cultural ecosystem services and ecological functions. Ecosystem Services. *Under review*.

Contributions: I developed the research question, methodology, collected the data, performed the data analyses, and developed the figures and tables with the advice of G. Cumming. I wrote the first draft of the paper which was revised with editorial input from G. Cumming.

6.1 Abstract

The rapid decline of ecological systems, globally and locally, has highlighted the potential of ecosystem functions to drive conservation discourse. Ecosystem functions have been described for birds in South Africa based on measurable ecological functional traits (physiological, structural, behavioural, or phenological characteristics), as well as cultural functional traits (human preferences for morphological and behavioural traits). Understanding the spatial relationships between ecological functional groups and cultural functional groups can clarify the extent to which cultural services are produced by organisms with different ecological functions, and identify potential trade-offs between cultural and ecological services. Here I show that when correcting for the effect of species richness and spatial autocorrelation on functional group richness, there is a clear but nuanced relationship between avian cultural and ecological functional groups ($r=0.6$, $t=33.26$, $df=1956$, $p< 2.2e-16$). This relationship was highly correlated in national parks ($r=0.8$, $t=18.27$, $df=190$, $p< 2.2e-16$), suggesting that ecological functional groups and cultural functional groups are particularly associated in areas with limited capacity for human selection of functional traits. Even though cultural ecosystem services are often considered to be primarily produced through human perception, they are strongly correlated with ecologically relevant traits. For conservation initiatives that aim to maximise both ecosystem function and ecosystem service production, it appears that human impacts on ecosystems have created trade-offs between cultural and other ecosystem services by altering the natural balance of cultural and ecological functions.

6.2 Introduction

Ecosystems have the capacity to simultaneously provide a range of functions that contribute to human wellbeing by generating ecosystem services (Schuldt et al., 2018). The rapid decline of ecological systems, globally and locally, has highlighted the potential of ecosystem functions to drive conservation discourse (Bellwood et al., 2019), in part, by enabling generality, synthesis, and predictive relationships to be identified in complex ecological processes and structures (de Groot et al., 2002; Shipley et al., 2016). Ideas about functional ecology, and functional classifications, have consequently been applied to a broad group of organisms, ranging from plants (Garnier and Navas,

2012) to fish (Villéger et al., 2017) and birds (Sekercioglu, 2002). Ecological functional groups describe groups of species according to their role in ecosystems. They are defined by measurable ecological traits, such as physiological, structural, behavioural, or phenological characteristics (Verner, 1984; De Graaf et al., 1985; Cumming and Child, 2009; Diaz et al., 2011).

It has recently been proposed that the functional group approach can be usefully applied to understanding the cultural services that organisms provide. Using birds as an example, I have shown in Chapter 3 how the organismal traits that influence people's perceptions of organisms (i.e. cultural functional traits) – and hence, the benefits that people derive from seeing or interacting with them - can be measured, using interview data, to derive a consistent set of 'cultural functional groups' based on human preferences for such avian traits as size, colour, and song. Cultural functional groups are thus defined as the dominant characteristics of a species that affect people through their contribution to cultural ecosystem services or disservices (Zoeller et al., 2020). Since cultural functional groups are based upon subjective human response to species traits (Zoeller et al., 2021, Chapter 4), their existence is dependent on both the species themselves and the socio-cultural systems that influence human perceptions and preferences, making them social-ecological groupings rather than purely ecological or social (Zoeller et al., 2021, Chapter 4).

Analysis of cultural functional groups has the potential to provide insights into how and why people interact with nature in particular ways and how these interactions influence human impacts on ecosystems. The provision of cultural ecosystem services has become an important factor underlying the social licence and funding support for conservation. Research increasingly shows benefits to human health and reductions in stress from time spent in nature (Donald and Gregory, 2019; White et al., 2019); and for many people, their willingness to support conservation actions that carry opportunity costs – such as creating protected areas or introducing no-take fishing zones – is tightly connected to their personal enjoyment of nature and the personal benefits they receive from such activities as bird-watching, hiking, or snorkelling.

In addition to the direct relationship between cultural services and support for conservation, there is evidence that some cultural and religious responses to nature may have arisen as adaptations that benefit the communities adopting them (Berkes, 2008). For example, groves of sacred forests in Madagascar that are used in burial ceremonies provide an additional ecological function by helping to maintain plant populations and associated pollination services (Tengö and von Heland, 2013). It is unclear whether, or to what degree, the preferences of people for particular species have evolved because they carry some value for individual or community survival. But if this were the case, I might expect that ecological functions would correlate in some way with cultural functions.

Regardless of their possible adaptive value, with cultural services and access to natural habitats acting as major influences on conservation actions, the question of whether cultural preferences align with ecological functions is critically important. Provision of the majority of ecosystem goods and services depends on ecosystem functions (e.g., carbon storage depends on hydrology and water cycling; freshwater quality and quantity relates closely to nutrient cycling). If pressure for conservation is based heavily on people's desire to obtain cultural services, do management decisions that are based on cultural service provision also enhance ecological function? Can I assume an 'umbrella effect', where conservation action that supports cultural service provision will also be sufficient to retain a full range of ecological functions?

I addressed these questions in a three-step process. First, I used bird atlas data to quantify and compare the richness of ecological and cultural functional groups across the whole of South Africa and specifically within South African National Parks. This analysis provided information about existing spatial patterns, their relationships to each other, and their dependence on individual species richness. Second, I tested for any additional structural relationships using a randomisation analysis to ask whether the spatial relations between ecological and cultural functional groups were in any way different from what might be expected if birds were assigned to cultural functional groups at random. Lastly, I asked whether there was a relationship between the distribution of particular ecological and cultural functional groups. My results provide valuable insights into the relationships between ecological functional and cultural service provision.

6.3 Methods

6.3.1 Datasets

To determine the relationship between cultural services and ecological functional groups, I compared Cumming and Child (2009) classification of ecological functional groups (see Chapter 2) to the description of cultural functional groups outlined in Chapter 3. Specifically, Cumming and Child's (2009) classification places 950 bird species into one or more of nine ecological functional groups: Seed Dispersers, Pollinators, Nutrient Depositors, Grazers, Insectivores, Raptors, Scavengers, Ecosystem Engineers, and Granivores (Sekercioglu, 2006; Cumming and Child, 2009). The cultural functional groups described in Chapter 3 grouped 45 traits into one of six functional groups based on distance-based measures of similarity: Visual Traits; Negative Visual and Behavioural Traits; Movement and Ecological Traits; Place Association and Abundance Indicators; Common Traits; and Behavioural Traits. In addition, I used distribution data from the second Southern African Bird Atlas Project (SABAP2) to determine the distribution of functional groups.

6.3.2 Data analysis

6.3.2.1 Functional group richness comparison

To facilitate the interpretability of the results I applied a conventional definition of functional richness (i.e. the number of species sharing the same functional traits (Blondel, 2003)), while recognising that methods and indices used to measure functional richness are complex (Legras et al., 2018; Bellwood et al., 2019).

To quantify and compare the richness of ecological functional groups and cultural functional groups across the whole of South Africa, each bird species was allocated to one or more ecological and cultural functional groups based on their functional traits. To account for grid cells that had multiple functional groups represented by single species, I corrected for the influence of species richness on relationships between functional groups. This was achieved by plotting functional group richness against taxonomic richness for each functional group per ecological functional group and cultural functional group. The residuals of this relationship (hereafter, 'residuals') were summed for ecological functional group and cultural functional group richness and mapped to illustrate divergence in spatial pattern between species richness and functional group richness. The summed residuals were correlated for ecological functional groups and cultural functional groups to determine whether there was a relationship between functional group richness. Overlap in the distribution of ecological functional groups and cultural functional groups were further visualised using a kernel density plot.

I additionally ran a correlation analysis focusing on ecological functional group and cultural functional groups richness in South Africa’s 20 national parks. National parks are of particular interest as they represent areas that have had limited anthropogenic disturbances, and can therefore help to understand the balance of ecological and cultural functional groups in the absence of human influence.

6.3.2.2 Functional group spatial relationship

To determine whether the spatial relationship between ecological functional groups and cultural functional groups were different from what might be expected if birds were assigned to cultural functional groups at random, I randomised the residuals of cultural functional groups by spatial location. The randomised residuals of cultural functional richness were correlated with unmodified residuals of ecological functional richness. The randomisation process was repeated 100 times. The mean correlation coefficient and its standard deviation were then determined, and compared against the correlation coefficient for the observed residuals of cultural functional richness and ecological functional richness, as described in section 6.3.2.1.

To determine whether assessing functional group relationships using residuals was sufficient to eliminate spatial autocorrelation (which I would expect in the untransformed data as a consequence of the autocorrelation in species richness that arises from broader-scale geographic patterns), I calculated Moran’s I (Moran, 1948) using the sp package in R (version 3.1.3). Spatial autocorrelation would indicate that species distribution data is more similar in locations that are closer to each other than those that are further apart, violating key assumptions of independent and identically distributed residuals (Dormann et al., 2007). Spatial autocorrelation is present when Moran's I standard deviate is statistically significant. Since my results indicated that $p<0.05$ for both cultural and ecological functional groups, I ran an autocovariate model to account for spatial autocorrelation. By adding a distance-weighted function of neighbouring functional richness to the model's explanatory variables (Dormann et al., 2007), the autocovariate model estimated the extent to which functional group richness in one grid cell reflects functional group richness in another. The autocovariate model is determined through the following equation: $y=X\beta+\rho+\varepsilon$, where β is a vector of coefficients for intercept and explanatory variables X; and ρ is the coefficient of the autocovariate A (Dormann et al., 2007). The weighted sum of A can be calculated as:

$$A_{\mathbf{i}} = \sum_{\mathbf{j}\in\mathbf{k_i}} \mathbf{W_{ij}}\mathbf{Y_j}$$

I ran separate autocovariate models on the residuals of both ecological functional groups and cultural functional groups. The autocorrelation-corrected residuals for ecological functional groups and cultural functional groups were correlated to determine whether the relationship between functional group richness was still apparent in the absence of spatial autocorrelation.

6.3.2.3 Individual functional groups association

To determine whether there was co-variation in the distribution of individual ecological functional groups and cultural functional groups, I ran a correlation analysis across all individual ecological functional groups and cultural functional groups. For this correlation, I used the residuals of the relationship between functional group diversity and taxonomic diversity to account for grid cells that had multiple functional groups represented by single species.

6.4 Results

6.4.1 Functional group richness comparison

The analysis identified areas that are species rich but have low functional group richness (high residuals), particularly in the north eastern region of South Africa. This pattern appears similar for both ecological functional groups and cultural functional groups (Fig. 6.1). Functional group richness was correlated between residuals of ecological functional groups and cultural functional groups (Figs. 6.2 and 6.3; Pearson's r=047, t =24.14, df= 956, p<2.2e-16). Residuals for ecological functional group and cultural functional group richness were highly correlated in national parks (Figs. 6.4 and 6.5, Pearson's r r=0.63, t=11.11, df= 184, p < 2.2e-16).

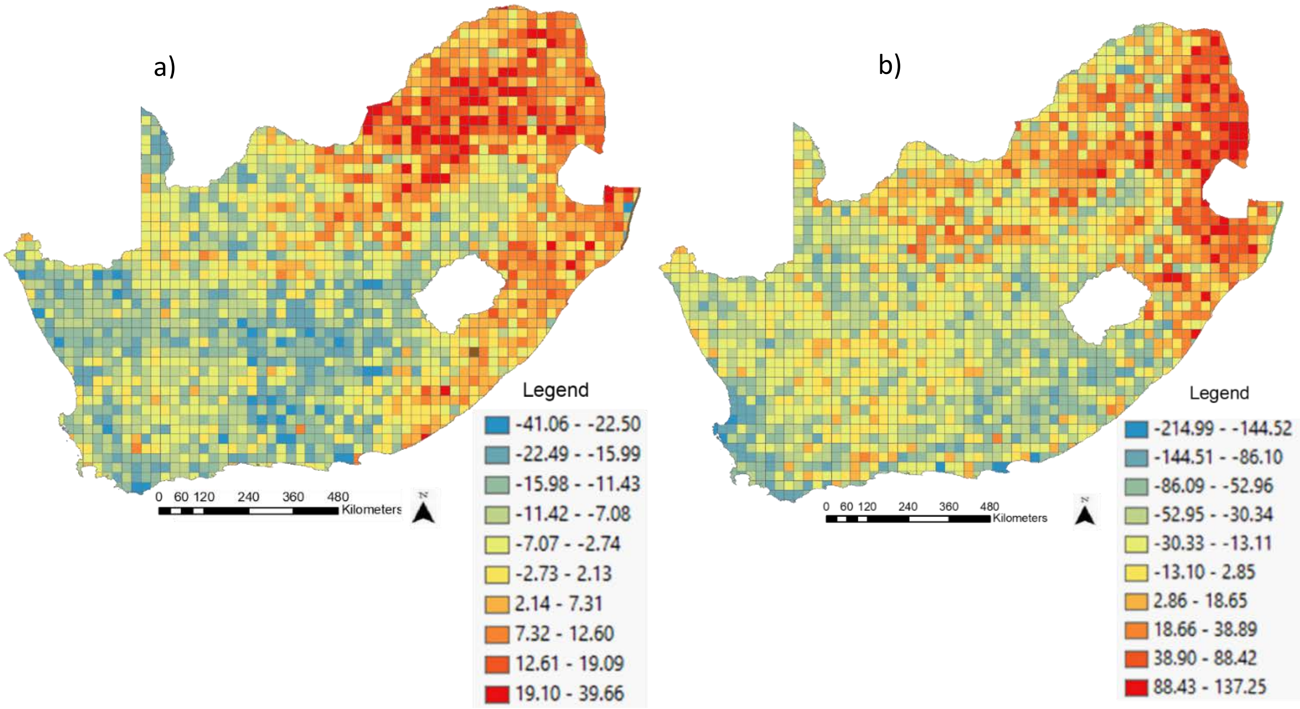


Figure 6.1 Functional group richness of bird species in South Africa for ecological functional groups (a) and cultural functional groups (b). These distributions represent residuals of the relationship between functional group richness and taxonomic richness.

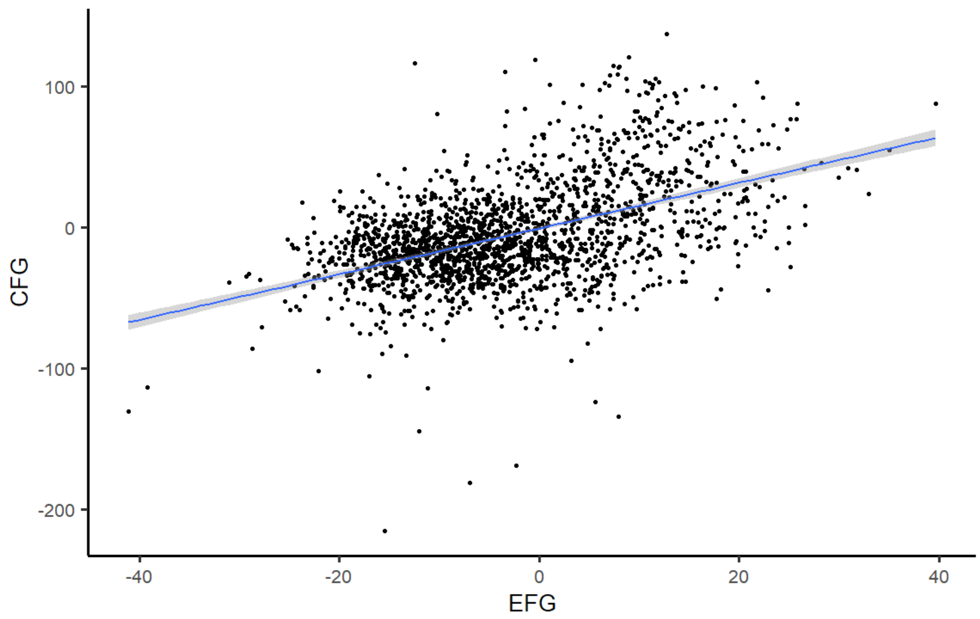


Figure 6.2 Correlation between the residuals of ecological functional groups (EFG) and cultural functional groups (CFG) distribution (r=0.47). The correlation between ecological functional groups and cultural functional groups represent residuals that are corrected for species richness, but not for spatial autocorrelation.

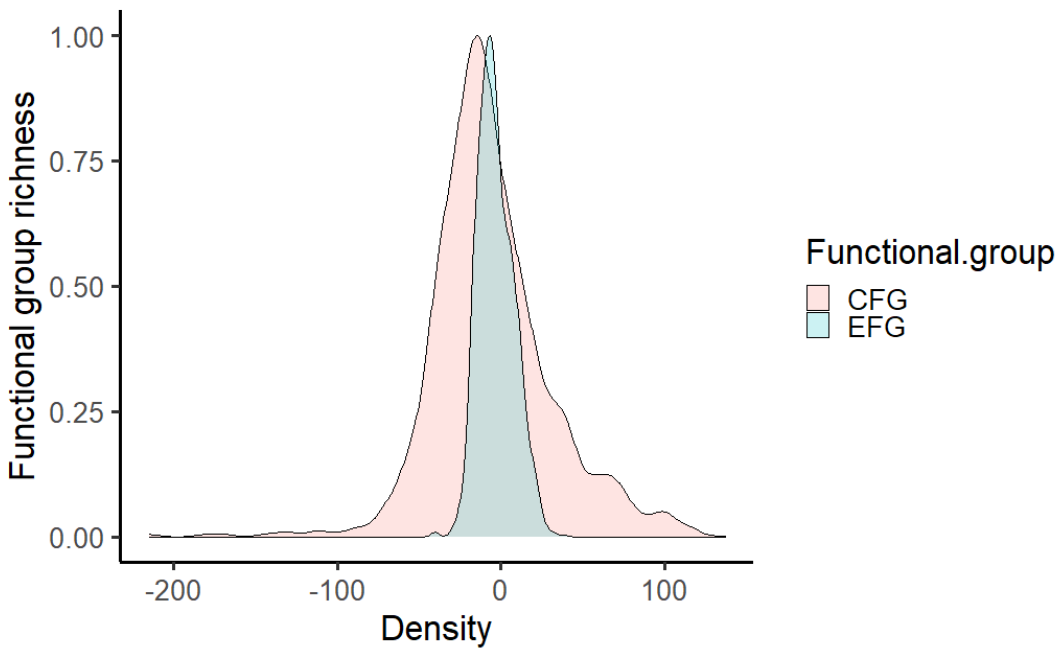


Figure 6.3 Density plot illustrating the distribution of ecological functional groups (EFG) and cultural functional groups (CFG) when corrected for species richness.

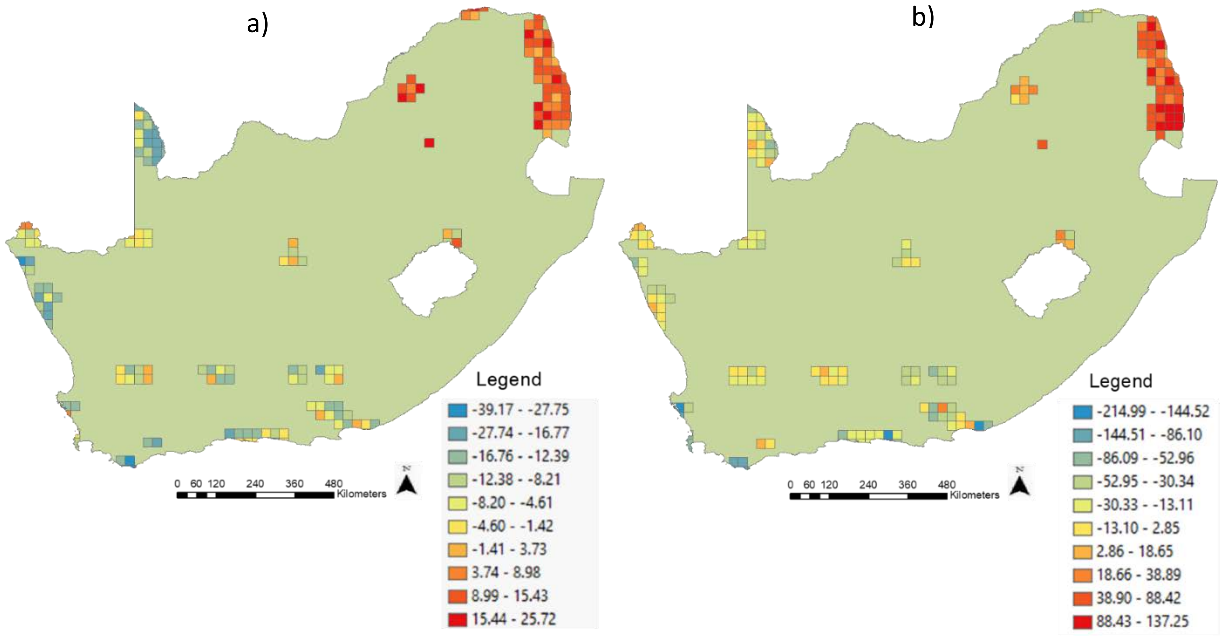


Figure 6.4 Functional group richness of bird species in South African National Parks for ecological functional groups (a) and cultural functional groups (b). These distributions represent residuals of the relationship between functional group richness and taxonomic richness.

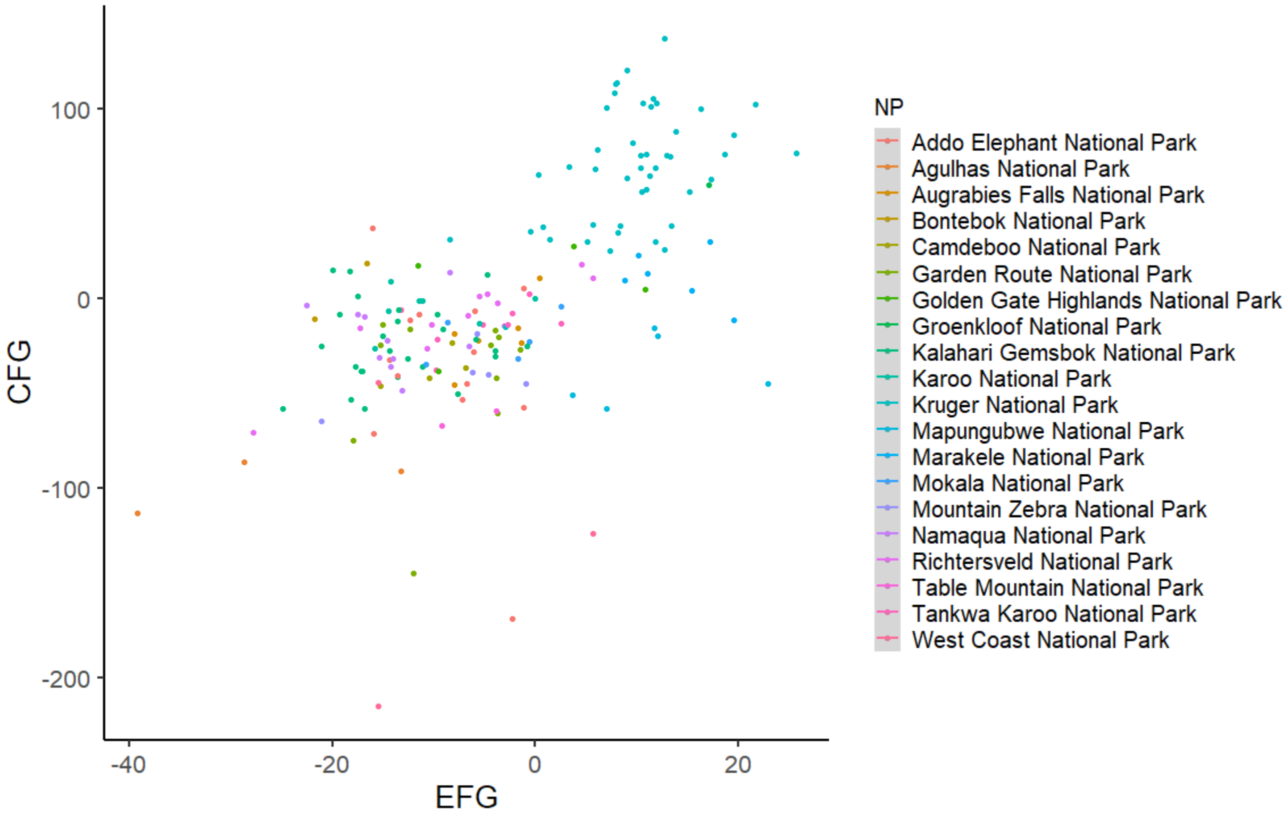


Figure 6.5 Correlation between the residuals of ecological functional group (EFG) and cultural functional group (CFG) distribution in South Africa's National Parks (NP) (r=0.63). The correlation between ecological functional groups and cultural functional groups is calculated from residuals that are corrected for species richness.

6.4.2 Functional group spatial relationship

The randomisation analysis showed that the association between randomised cultural functional group richness and ecological functional group richness was weak (r=0.002±0.02) compared to the association between observed cultural functional group and ecological functional group richness data (r=0.47). This association was similarly reflected in national parks, where the correlation coefficient was significantly lower for the randomised data (r=0.006±0.07) compared to the observed data (r=0.63), indicating an actual relationship between ecological and cultural functional groups.

Moran's I indicated significant spatial autocorrelation for ecological functional group richness (Moran's I standard deviate=282.68, variance =0.0000007, p<0.05) and cultural functional group richness (Moran's I standard deviate= 198.25, variance=0.0000007, p<0.05). These results imply that there is another spatially structured environmental variable that the analysis does not account for, leading to spatially dependent residuals (Dormann et al., 2007).

After correcting for spatial autocorrelation using the adjusted values from the autocovariate model, the relationship between ecological functional groups and cultural functional groups remained highly correlated across South Africa (r=0.6, t=33.26, df = 1956, p< 2.2e-16), and in national parks (r=0.8, t=18.27, df = 190, p< 2.2e-16). The correlation between ecological functional groups and cultural functional groups thus strengthened with autocorrelation-corrected residuals.

6.4.3 Individual functional groups association

Results of the correlation between all ecological and cultural functional groups indicated strong positive associations between Visual Traits and Seed Dispersers (r=0.6, t=32.79, df = 1956, p< 2.2e-16), Granivores (r=0.59, t = 32.31, df = 1956, p< 2.2e-16) and Ecosystem Engineers (r=0.55, t = 29.0, df = 1956, p< 2.2e-16) (Fig. 6.6). Movement and Ecological Traits had a similarly strong relationship with Seed Dispersers (r=0.41, t = 19.83, df=1956, p <2.2e-16) and Granivores (r=0.47, t = 23.64, df = 1956, p< 2.2e-16), while Place Association and Abundance Indicators had a positive relationship with Seed Dispersers (r=0.4, t=19.03, df=1956, p < 2.2e-16). Behavioural Traits did not have particularly strong associations with any ecological functional groups, but there was evidence of a positive relationship with Raptors (r=0.37, t=16.80, df=1956, p<2.2e-16). Negative Visual and Behavioural Traits had a positive association with Insectivores (r=0.45, t=22.50, df=1956, p< 2.2e-16). These positive associations suggest that in areas with high functional richness for these cultural functional groups one would also expect to find the associated ecological functional groups. In contrast, negative associations were evident between Nutrient Depositors and Visual Traits (r=-0.44, t=21.41, df=1956, p<2.2e-16), Movement and Ecological Traits (r=-0.38, t=18.09, df=1956, p< 2.2e-16), and Negative Visual and Behavioural Traits (r=-0.48, t= 3.95, df=1956, p< 2.2e-16), suggesting areas of high richness with Nutrient Depositors would have limited representation of these cultural functional groups.

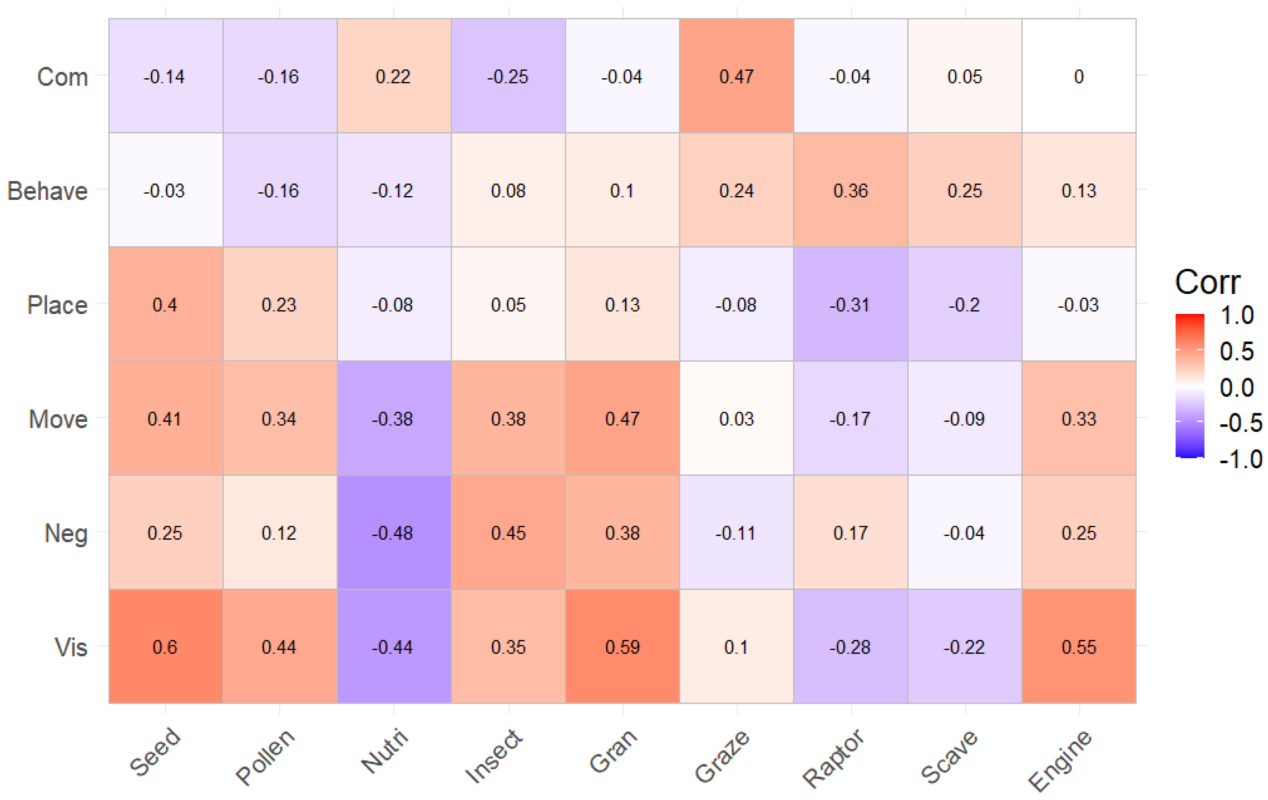


Figure 6.6 Correlation coefficients indicating the association between functional group richness for individual ecological functional groups (Seed Dispersers, Pollinators, Nutrient Depositors, Insectivores, Granivores, Grazers, Raptors, Scavengers and Ecosystem Engineers), and individual cultural functional groups (Common Traits, Behavioural Traits, Place Association and Abundance Indicators, Movement and Ecological Traits Negative Visual and Behavioural Traits and Visual Traits). The correlation coefficients between individual functional groups represent residuals that are corrected for species richness, but not for spatial autocorrelation.

6.5 Discussion

The results demonstrate a clear but nuanced relationship between avian ecological functional groups and cultural functional groups. The significant relationship between ecological functional group and cultural functional group richness at the extent of the entire country highlights the dependence of cultural service provision on ecological functional richness. This relationship was apparent when correcting both for the number of species present per functional group and spatial autocorrelation.

The relationship between ecological functional groups and cultural functional groups was particularly strong in national parks.

Understanding the overlap between ecological functional groups and cultural functional groups can elucidate the extent to which human preferences for bird species were grounded in ecological processes. Visual Traits, for example, demonstrated a high degree of correlation with four ecological functional groups (Seed Dispersers, Pollinators, Granivores and Ecosystem Engineers). Systems rich in species that provide cultural services associated with Visual Traits are therefore also likely to provide services associated with these ecological functions. The association between ecological functional groups and cultural functional groups can also help identify human perceptions of ecological functions. For example, Insectivores were associated with the Negative Visual and Behavioural functional group, traits of which included dull plumage, negative symbology and aggressive behaviour. Given evidence of this relationship, Insectivores are not likely to be favoured by ecosystem users, even though Insectivores provide a vital ecological function by limiting the effect of herbivore damage on plants (Sekercioglu, 2006). Despite these negative associations, Insectivores were positively correlated with all cultural functional groups, indicating that negatively perceived ecological functions still have the capacity to effect the production of cultural services.

The results also indicated that the relationship between ecological functional groups and cultural functional groups was weaker at the country scale than in national parks. This has important implications as national parks represent areas with limited capacity for human selection of functional traits, and thus provide insight into the balance of cultural functional traits and ecological functional traits when human preference is not the primary selective pressure. The results thus suggests that the balance of ecological and cultural functional groups changes between areas with human influence (altered balance) and areas without (natural balance). As a result, I can infer that human-induced effects on the environment reduces the natural balance of ecological functional groups and cultural functional groups. Understanding the relationship between ecological functions and cultural services would further benefit from deconstructing their relationship along an urban-rural gradient. Since the dependency of individuals on ecological services increases from urban to rural locations

(Martín-López et al., 2012), understanding whether the strength of the relationship between ecological functional groups and cultural functional groups changes along an urban-rural gradient could offer insight into the environmental parameters that shifts dependency from ecological services to cultural services.

Previously, spatial approaches have been applied to understand how complex processes at the landscape scale interact to produce a specific variety of co-occurring ecosystem service (Bennett et al., 2009; Ament et al., 2017). Identifying co-occurring ecosystem services has important implications for conservation targets that aim to maximise ecosystem service production (Bennett et al., 2009), and importantly, provides insight into how landscapes changes that ostensibly effect one service can have cascade effects on others (Cumming and Peterson, 2005). Identifying patterns of spatial concordance between individual ecological functional groups and cultural functional groups can further enhance my understanding of ecosystem service production, particularly when conservation decisions aim to promote ecosystem service hotspots. Establishing co-occurring functional groups can enable strategic decisions to be made that avoid risking trade-offs of ecological functions for cultural ones.

While this study has provided a foundation for linking cultural services with ecological functions, further research is needed to establish the generality of patterns identified here. Determining whether human preferences create bundles of ecological functional groups and cultural functional groups is a crucial next step in understanding synergies and trade-offs between ecosystem services (Martín-López et al., 2012). To do so, people's social identify and its influence on preferences for cultural services and ecological functions need to be identified to account for the effect of socio-demographic characteristics on perceptions of ecosystem services (Zoeller et al., 2021). Identifying bundles of functional groups and mapping their distribution can enable high value ecosystems to be identified (Yang et al., 2019), and provide insight into the degree to which human preferences for cultural services promotes ecological functions.

Efforts to understand the provision of ecosystem services have often overlooked the capacity of a system to produce multiple ecosystem services that interact in complex ways (Bennett et al., 2009).

Preference for one type of service (e.g. timber) may have cascade effects on others (e.g. soil stability and aesthetic pleasure), resulting in a decline of the full range of ecosystem services present in the landscape (Bennett et al., 2009). Consequently, a key objective for ecosystem service research should be to understand the association between ecological functional groups and cultural functional groups to identify trade-offs between ecological and cultural services (Kremen, 2005). My results have suggested that mapping ecosystem services that are generated by two distinct underlying processes (i.e. cultural and ecological) offers crucial insight into the capacity of a system to produce multiple ecosystem services and the selective pressures that inform their distribution (Martínez-Harms and Balvanera, 2012). The strong association between ecological functional groups and cultural functional groups, particularly when corrected for spatial autocorrelation, indicated that even though cultural ecosystem services are often considered to be primarily produced through human perception, they are strongly correlated with ecologically relevant traits (Belaire et al., 2015; Zoeller et al., 2022). For conservation initiatives that aim to maximise both ecosystem function and ecosystem service production, it appears that human impacts on ecosystems have created tradeoffs between cultural and other ecosystem services by altering the natural balance of ecological functional groups and cultural functional groups (Marshall et al., 2018).

7 General discussion

Overall, the work that I have presented in this thesis presents a nuanced analysis of the cultural services provided by birds. I have explored the degree to which these services depend on the perceptions of beneficiaries and are consistent between them; the dependence of cultural ecosystem service provision on landscape attributes at broader scales; and the relationships between ecological and cultural functions. The analyses that I have presented simultaneously support, challenge, and extend different elements of the current body of knowledge about ecosystem service provision, as discussed below.

7.1 Key findings

In **Chapter 3**, I explored the concept of functional groups through a cultural ecosystem services lens to determine if cultural functional traits of birds identified by individuals can be used to create cultural functional groups (Objective 1). I found that the cultural functional traits people perceived in birds could be grouped together to form six distinct cultural functional groups: Visual Traits; Negative Visual and Behavioural Traits; Movement and Ecological Traits; Place Association and Abundance Indicators; Common Traits; and Behavioural Traits. Cultural functional traits associated with Movement and Ecological Traits were particularly important for people since species in this functional group were assigned significantly higher scores than the other functional groups. This chapter demonstrates that people's perceptions of birds are consistent enough to form the basis for cultural functional groups; and moreover, that certain functional groups are preferentially engaged with by ecosystem users.

In **Chapter 4**, I asked how the cultural functional groups identified in Chapter 3 were related to an individual's socio-demographic characteristics. My objective in Chapter 4 was to understand if the ways in which people perceive cultural functional groups are related to people's social identity, as described by their socio-demographic characteristics and residential location (Objective 2). I was able to determine that human socio-demographic characteristics are critical for explaining how avian cultural functional groups are co-produced and co-constructed by people. Age, gender, race, language and education contributed significantly to differences in perceptions of cultural functional groups. By contrast, the location of respondents along a rural-urban spectrum did not influence how people perceived cultural functional groups. This research builds upon previous studies that have examined how cultural ecosystem services are related to socio-demographic characteristics by taking a socially disaggregated approach to cultural functional groups (Hicks and Cinner, 2014; Lau et al., 2018), and direct comparisons of ecosystem service preferences between urban and rural locations (Lapointe et al., 2019; Lapointe et al., 2020).

In **Chapter 5**, I analysed how complexity in ecological organization influences the production of cultural ecosystem services. I was particularly interested in understanding how cultural ecosystem services that are perceived at the level of individual organisms are filtered through multi-level and multi-scale social and ecological interactions. My objective for Chapter 5 was thus to understand how landscape attributes contribute to the cultural benefits people experience from birding (Objective 3). I found that biophysical attributes (particularly biome, vegetation type, and variance in elevation) significantly contributed to the cultural benefits associated with birding, demonstrating that birder benefits are derived from multi-level (birds to ecosystems) and multi-scale (site to landscape) social and ecological interactions. While landscape characteristics had a significant effect on birding benefits, people's perceptions of the environment and their subjective responses to the bird community remained important contributors to the cultural services associated with birding. Incorporating the broader context of the surrounding landscape on the production of cultural ecosystem services has highlighted the importance of evaluating cultural ecosystem services at different levels and scales. This finding may be particularly pertinent to cultural services associated with birdwatching, since although the aesthetic benefits of birdwatching appear to be linked to individual species or communities, the way that a person experiences a bird is embedded in the context in which that bird lives (Clergeau et al., 1998).

Finally, in **Chapter 6**, I analysed the spatial relationship between the cultural functional groups established in Chapter 3 and previously defined ecological functional groups associated with birds. My objective in Chapter 6 was thus to determine whether cultural services are produced by birds with different ecological functions (Objective 4). I found that there was a clear relationship between ecological functional groups and cultural functional groups associated with birds, and this relationship was particularly apparent when accounting for spatial autocorrelation. Consequently, ecological functions have the capacity to affect production of cultural services. Since the relationship between ecological functional groups and cultural functional groups were particularly significant in national parks, I additionally found that human impacts on ecosystems have affected the natural balance between cultural and ecological traits.

7.2 Summary of contributions to ecosystem services literature

7.2.1 Cultural functional groups

Ecosystem functions have traditionally been described as innate biophysical interactions that are produced regardless of human selection for ecosystem benefits (Costanza et al., 2017; de Groot et al., 2017). As a result, ecosystem functions have been viewed as being rooted exclusively in ecological systems (de Groot et al., 2002). However, focusing on the ecological processes that contribute to ecosystem functions risks minimizing the extent to which social processes, including people's preferences, contributes to the production of ecosystem services and the organization of functional groups. In Chapter 3, I found that ecological and social systems interact to generate cultural functional groups. Cultural functional groups are produced from subjective human response to traits of birds. By identifying species traits that contribute to cultural services and organising these traits into robust, statistically sound cultural functional groups, I have contributed to advancing our understanding of the production of cultural services, including the important influence that social systems exert on their formation. At the time of conception, this was the first approach to classifying avian cultural functional groups (although the relationship between functional traits and cultural ecosystem services has been since explored by Echeverrri et al. 2019). Nevertheless, the novel methods and analyses used in this thesis to describe cultural functional groups provide an important and replicable basis for future research on the important topic of cultural functional groups.

7.2.2 Disaggregating ecosystem values

Understanding how different views, traditions and culture affect the individual receipt of ecosystem service benefits has been a persistent gap in ecosystem service assessments (Daw et al., 2011). These assessments generally adopt a socially-aggregated approach, where people with different values are grouped together and assumed to have a fixed response to ecosystems services and their contribution to human wellbeing (Milcu et al., 2015). As a result, management decisions resulting from these assessments may not account for the values held by the wide spectrum of society (Lau et al., 2018). Using novel methods to capture individual perception and statistical tools to disaggregate perception according to socio-demographic characteristics, I demonstrated the importance of incorporating a broad range of socio-demographic characteristics to better understand how cultural functional groups are perceived. These findings offered greater insight into the role of social identity in the co-construction and co-production of cultural functional groups and contributes to understanding heterogeneity in demand and use as described in Fig 1.1 (Balvanera et al., 2022).

7.2.3 Landscape characteristics and cultural benefits

Despite the potential influence of landscape variation on the production of ecosystem services, there has been limited integration of cultural ecosystem services in landscape-level empirical assessments (Bagstad et al., 2016). In particular, the effect of variation in multi-level and multi-scale landscape characteristics on cultural ecosystem services has not been explored (Bruley et al., 2021). The production of cultural benefits at the landscape scale is thus poorly understood, and management decisions that aim to conserve cultural benefits may be overlooking important landscape characteristics that promote the production of cultural services (Graves et al., 2019). In Chapter 5, I demonstrated the importance of incorporating multi-level and multi-scale interactions on cultural benefits that have previously been linked exclusively to species and communities. The findings in Chapter 5 provided conclusive evidence that landscape processes influence cultural benefits experienced at the species level, and moreover, suggest that landscape-level management decisions have a cascade effect on the cultural benefits received from individual species.

7.2.4 Linkages between ecological functions and cultural services

Ecosystem functions are underpinned by complex interactions between biotic and abiotic processes, which cascade to produce ecologically, economically and culturally valuable services (de Groot et al. 2002; Mace et al. 2012). Ecosystem functions interact in complex ways, such that the production of one function may affect the availability of others, which in turn affects the delivery of ecosystem services (van Oudenhoven et al. 2010). In Chapter 3, I provided the first account of cultural functional groups associated with birds, and demonstrated the importance of cultural functions in ecosystem service production. A critically important next step was thus to understand the spatial relationship between avian ecological functional groups and cultural functional groups to demonstrate the dependence of cultural services on ecological functions. Determining the extent to which the cultural services of birds align with their ecological functions is a vital contribution to the ecosystem services literature since I was able to demonstrate that the production of cultural ecosystem services from cultural functions is also strongly correlated with ecologically relevant traits (Chapter 6). These findings have important implications for management initiatives that seek to maximise functional diversity in the landscape, and understand the drivers behind the distribution of cultural and ecological functions.

7.2.5 Cascade model

The ecosystem service cascade model was originally developed to provide a conceptual framework for linking ecosystem function and human wellbeing (Haines-Young and Potschin, 2010). Since its conception, iterations of the model have been developed to further understand the "production chain" that supplies ecosystem services (Potschin and Haines-Young, 2011). However, current cascade models often focus on the end value of the production chain, thereby overlooking important interactions at each step of the cascade that promote the co-production of ecosystem services (Bruley et al., 2021). To address these gaps, I developed a novel, more inclusive model that explores vital interactions between social and ecological systems in the production of cultural ecosystem services. By exploring cultural services through the lens of this cascade model, I have provided a practical framework for exploring relationships between different levels of ecological organization and the contribution of social systems to cultural service production.

7.3 Limitations and caveats

The main caveat of my research that may prevent further generalization is the focus of this thesis on the cultural services provided by specific taxa in a specific country. This case study approach may limit the potential of my findings to be extrapolated to broader scales. While I showed that socio-demographic characteristics are related to cultural functional groups, the exact contribution of different socio-demographic characteristics are likely to change in different socio-cultural contexts. The historical context specific to South Africa may have obscured the findings relative to studies conducted in other countries, specifically as it relates to similar perceptions of cultural functional groups between urban and rural environments. There is a common consensus in ecosystem service research that cultural ecosystem services are more highly valued in urban settings (Kremer et al., 2016), suggesting that there should be significant differences in how urban and rural inhabitants perceive cultural ecosystem services. However, previous research has also demonstrated similarly consistent valuation of cultural services between urban and rural respondents in the Solomon Islands (Lapointe et al., 2020), although research on other such direct comparisons is largely lacking in the global North. Nevertheless, the findings presented in this thesis would benefit from being evaluated against different contexts to validate their generality.

Secondly, the model developed in this thesis may not capture the full range of interactions in the production of cultural ecosystem services. While I expanded on traditional cascade models to incorporate additional linkages in ecological and social systems (e.g. multi-level and multi-scale variation and socio-demographic context respectively), the cascade model remains inherently rooted in westernized worldviews (Cook et al., 2020). As such, an additional caveat is the limitations I may have inadvertently imposed on the study through my own worldview. While I attempted to emphasize important social processes in the cascade of cultural ecosystem services from ecological systems to social systems, the model was still based on a western scientific epistemology.

Finally, the premise of this thesis is informed largely by ecosystem service literature. The approaches outlined by this literature are characterized by quantitative analysis of ecosystem values, even when these values are underpinned by socio-cultural determinants. Consequently, a potential limitation in this study was the paucity of qualitative social science methodology which may have provided a richer narrative and more depth in understanding with regards to the cultural ecosystem services arising from birds. Moreover, employing such methodology may have enabled me to better contextualise the results within the relevant social systems.

7.4 Future research needs

7.4.1 Specific needs

I suggest three avenues for specific future research. First, more research needs to be conducted on the relationship between ecological functions and cultural services. In particular, I suggest a deeper analysis of the distribution of ecological functional groups and cultural functional groups along an urban-rural gradient to further understand the social and environmental parameters that drive demand for particular services. While I have provided evidence that humans alter the natural balance of ecological functional groups and cultural functional groups (Chapter 6), the data suggest that people's perceptions of cultural functional groups do not change according to their location (Chapter 4). Incorporating deeper complexity into comparisons of rural-urban perceptions by including ecological functional groups would benefit future research by enabling the relative dependency of people on cultural and ecological services to be determined (Martín-López et al., 2012). Linking these findings to people's location along an urban-rural gradient would add to the growing body of research on urbanisation and the shifting relationship between people and nature (Lapointe et al., 2020).

Second, I suggest extrapolating on the methods introduced in this thesis to include other categories of ecosystem services. While provisioning and regulating services have traditionally been measured through economic and ecological metrics, evidence suggests that socio-cultural approaches are of critical importance in capturing the values of these ecosystem services (Asah et al., 2014). The individual-specific, socio-cultural values people ascribe ecosystem services inform society's compliance with environmental management and its uptake in policy agendas (Asah et al., 2014). Consequently, capturing the value of provisioning and regulating services using perception-based valuations described in this thesis can improve our understanding of the full range of benefits people receive from birds and moreover, further elucidate the extent to which different ecosystem services co-occur to create ecosystem service hotspots.

Lastly, an interesting avenue for future research would be to explore the applicability of my findings to sustainable management practices. Since the ecosystem services framework promotes the uptake of ecosystem service research in policy agendas, applying my findings could benefit governmental decisions on environmental management (Gómez-Baggethun et al., 2010). My findings present a concrete understanding of how socio-demographic characteristics mediate people's relationship with the environment; integrating these findings into policy could promote equitable environmental management and promote distributive justice with respect to ecosystem services across different communities (Musavengane and Leonard, 2019).

7.4.2 General needs

I have presented conclusive evidence of the importance of disaggregating ecosystem users by their socio-demographic characteristics to understand how cultural ecosystem services are perceived. However, an individual's identification with specific measures of socio-demographic characteristics may not remain static over time. For example, as someone gets older, do their perceptions of cultural ecosystem services differ? Most studies on ecosystem services and how their benefits are perceived are informed by a snapshot of time. To properly understand how changes to an individual's socio-demographic identity might shift their perceptions, it is important to incorporate interdisciplinary and cross-sectoral collaboration that will offer greater insight into how reframing an individual's sense of self through their social identity influences how they perceive cultural ecosystem services. (Abson et al., 2014; Arts et al., 2017). This approach is important for future research as it could offer insight into potential conflicts that may emerge between conservation, urbanisation and globalisation, and furthermore, highlights the need to explore context-specific factors in understanding social-ecological interactions.

7.5 Conclusion

Over the last fifteen years, ecosystem services have become the dominant paradigm for evaluating people's relationship with nature. In my thesis, I aimed to contribute to knowledge on ecosystem service research by addressing important research gaps related specifically to cultural ecosystem services. I have shown that perceptions of bird species traits can be grouped to form a broader typology of cultural functional groups, simplifying questions of management and promoting the sustainable delivery of cultural ecosystem services. To gain deeper insight into cultural ecosystem services, I addressed their production and delivery in ecological and social systems. From an ecological perspective, I found that cultural services associated with birds are produced from different levels and scales, highlighting the importance of the broader ecological context in informing the benefits people derive from birdwatching. Addressing cultural service production from a social systems perspective, I determined that perceptions of cultural functional groups are informed by an individual's socio-demographic characteristics. Thus, my research shows that social and ecological systems cannot be decoupled when exploring cultural ecosystem services.

Despite the importance of recognising and incorporating linkages between people, society and the environment into ecosystem assessment frameworks and valuations, much of the discourse in ecosystem service research still centers on the availability of ecosystem services (ecological attributes), and not the local socio-cultural attributes that drive demand for these services. My adaption of the cascade model provides a practical framework through which social-ecological linkages can be explored. Under this model, ecosystem services are contextualised within a dynamic social-ecological space that considers various processes, subsystems and components that interact to produce cultural ecosystem services (Cumming, 2011). In sum, the findings presented in this thesis provide an important theoretical and practical approach to better understand how cultural ecosystem services are produced through the interaction of social and ecological processes, the underlying social-ecological mechanisms that contribute to human wellbeing and the critical role that different perceptions of cultural ecosystem services play in their co-production.

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