

# The influence of landscape context on the production of cultural ecosystem services

Kim Christie Zoeller (✉ [kim.zoeller@my.jcu.edu.au](mailto:kim.zoeller@my.jcu.edu.au))

James Cook University <https://orcid.org/0000-0002-5064-5443>

Georgina G. Gurney

James Cook University

Graeme S. Cumming

James Cook University

---

## Research Article

**Keywords:** landscape variation, biophysical attributes, cultural ecosystem services, birds

**Posted Date:** April 2nd, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-310439/v1>

**License:** © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

**Version of Record:** A version of this preprint was published at Landscape Ecology on February 3rd, 2022.  
See the published version at <https://doi.org/10.1007/s10980-022-01412-0>.

# Abstract

**Context:** 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.

**Objectives:** To quantify the amount of variation in cultural ecosystem service provision by birds to birders that is due to landscape-level attributes.

**Methods:** We 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.

**Results:** Biophysical attributes (particularly biome, vegetation type, and variance in elevation) significantly increased the percentage of variance explained in birder benefits from 57–65%, demonstrating that birder benefits are derived from multi-level (birds to ecosystems) and multi-scale (site to landscape) social and ecological interactions.

**Conclusions:** 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.

## 1. 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. 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.

We explore the concept of multi-level and multi-scale organisation in the production of ecosystem services through a cultural ecosystem services lens (Fig. 1). Cultural ecosystem services are non-material benefits such as aesthetic values, spiritual fulfilment, tourism and recreation (Chan et al. 2012). They are coproduced 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. 1) (Fischer and Eastwood 2016). Ecological systems comprise multiple levels of ecological organisation. We focused particularly on three levels relating to the provision of cultural ecosystem services: species, community, and landscape (Fig. 1). While the relationship between scales and levels in ecological systems is complex, we 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).

We 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. We hypothesized 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 (Fig. 1) (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).

## 2. Methods

### 2.1 Bird Occurrence Data

To determine the relationships between the subjective experiences of the birders, their bird-related observations and quantifiable biophysical attributes of the landscape, we used the dataset for bird occurrences 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, Au-grabies, 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) (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. 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 Sect. 2.2).

### 2.2 Surveys

The satisfaction surveys completed by amateur birders comprised a pre-trip and post-trip questionnaire. The pre-trip questionnaire was a short survey 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. We 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, we 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.

### 2.3 Landscape Attribute Data

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). We 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, we extracted data on features that have been shown to influence birder enjoyment: biome, elevation, roads, water bodies, vegetation type and land cover (see Table 1). Each of the variables within each buffer zone was measured for each route.

Table 1

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

<b>Landscape characteristics</b>	<b>Measurement</b>	<b>Mechanism and examples</b>
Biome	Categorical	Biomes are characterised by distinct flora and fauna, which from an ornithological perspective, create specific conditions for which bird species are adapted (Steven et al. 2016). Specific vegetation types in biomes may be associated with rare, endangered or common species (Chettri et al. 2005).
Elevation	Mean Variance	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 (Finlayson et al. 2011; Raudsepp-Hearne et al. 2009). Bodies of water may also contribute positively to the aesthetic experience of birdwatching (Chettri et al. 2005).
Vegetation type	Categorical	Local vegetation influences the distribution of bird communities through habitat heterogeneity and resource availability (Belaire et al. 2015).
Land cover	Categorical	Land cover, including vegetation cover, water body types and transformed landscapes influences the availability of habitats for birds and therefore the spatial distribution of bird communities (Chettri et al. 2005; Kolstoe et al. 2018).
Species richness	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).
Low Diversity	Count	
Low Abundance	Count	
Unexpected Species	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 Sighting Of Species	Perception	
Good weather	Perception	External variables such as weather and perceptions of landscape has been shown to significantly influence birder

Landscape characteristics	Measurement	Mechanism and examples
Bad Weather	Perception	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 27–57%.
Interesting Diverse Landscape	Perception	

## 2.4 Data analysis

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

We 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, we used the continuous rating data of satisfaction scores (birder benefits) as our response variable, and perception-based and biophysical landscape attributes as predictors. To account for nested structure of our data (multiple birders in each National Park), we included location (National Park) as a random effect in the model.

We 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.

## 3. 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 ( $r^2 = 0.65$  AIC = 1012, deviance = 933.6,  $df = 273$ ) (Table 2). Adding landscape variables increased our 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.

Table 2

Summary table of estimates, standard error (SE), t-value and p-value of the multivariate linear model (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	4.612	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	
<i>Road type</i>	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	
<i>Water body type</i>	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	4.470527	-0.306	0.759912	
	River area	12.327655	89.917848	0.137	0.891054	

		Estimate	Std. Error	t value	Pr(> t )	
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	4.49E-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	***

The dominant biophysical attribute that explained variance in birder benefits in our model was biome, with all biome types being strong, positive predictors of route ranking (Table 2). 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 our 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. 3). 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.

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.

## 4. Discussion

Our 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. We 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 inclusion 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 measures of biophysical attributed added significant explanatory power to the model. The primary explanatory biophysical variables in this model were biome and vegetation type. The importance of biome 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 characterised by distinct flora and fauna, which from an ornithological perspective, create specific conditions to which bird species are adapted (Chettri 2005; Steven et al. 2017). 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). Since bird distributions are influenced by biome type and related ecological variables, landscape processes will strongly influence the provision of birder benefits at the species level (Filloy et al. 2019).

Birder benefits in the Succulent Karoo were not significantly different from other biome types. The Succulent Karoo, which features Tankwa Karoo vegetation, 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 conditions are fragile or require more specialised adaptations to inhabit, biodiversity-based cultural ecosystem services may be outweighed by spatially explicit attributes such as landscape composition (Cumming and Maciejewski 2017).

Aesthetic and cultural landscapes are amongst the most valued components of ecosystems (Orenstein et al. 2015), but are challenging to manage since aesthetic 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 our 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. Nuances in individual perception are challenging to capture, but must be considered since individuals 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).

The interactions between biodiversity and biophysical attributes that produce cultural benefits are poorly understood despite their role in creating areas with high potential for cultural ecosystem service production. Since the values people assign to particular areas are likely to vary significantly across socio-demographic and cultural characteristics (Zoeller et al. 2020), managing the provision of cultural ecosystem services equitably is challenging (Marshall et al. 2019). Avitourism tends to attract an older demographic with high enough income to afford travel and park entry fees (Steven et al. 2017). Indeed, typical visitors to National Parks in South Africa average 46 years old, are married, and possess higher education qualifications (Scholtz et al. 2015). Thus, our understanding of perceptions of ecosystem service benefits in National Parks exclude substantive subsets of society. Decisions around biodiversity conservation and landscape protection should ideally include the values associated with National Parks held by a wider spectrum of society.

We 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 explicitly accounting for seasonal shifts in bird assemblages and their impact on cultural benefits received from ecosystems. While we conducted sampling evenly throughout summer and winter (Cumming and Maciejewski 2017), we did not measure species-specific responses to seasonal changes and their influence on birder benefits (Graves et al. 2019). Similarly, we 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 benefits 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). We 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 cascade models, even where a cultural service is heavily linked to individual organisms. 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).

## Declarations

Funding: Funding was provided by the National Research Foundation (NRF) through a Blue Skies grant to GSC, by the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, and by James Cook University.

Conflicts of interest/Competing interests: Not applicable

Ethics approval (include appropriate approvals or waivers): This study was granted approval through the University of Cape Town, permit number SFREC 48\_2012

Consent to participate (include appropriate statements): Not applicable

Consent for publication (include appropriate statements): Not applicable

Availability of data and material (data transparency): Where storage will not compromise the anonymity of research participants, data will be deposited in the Dryad repository

Code availability (software application or custom code): Not applicable

Authors' contributions: K.C.Z. and G.H.C. designed research; K.C.Z. performed research; K.C.Z. analysed data; and K.C.Z, G.S.C and G.G.G wrote the paper.

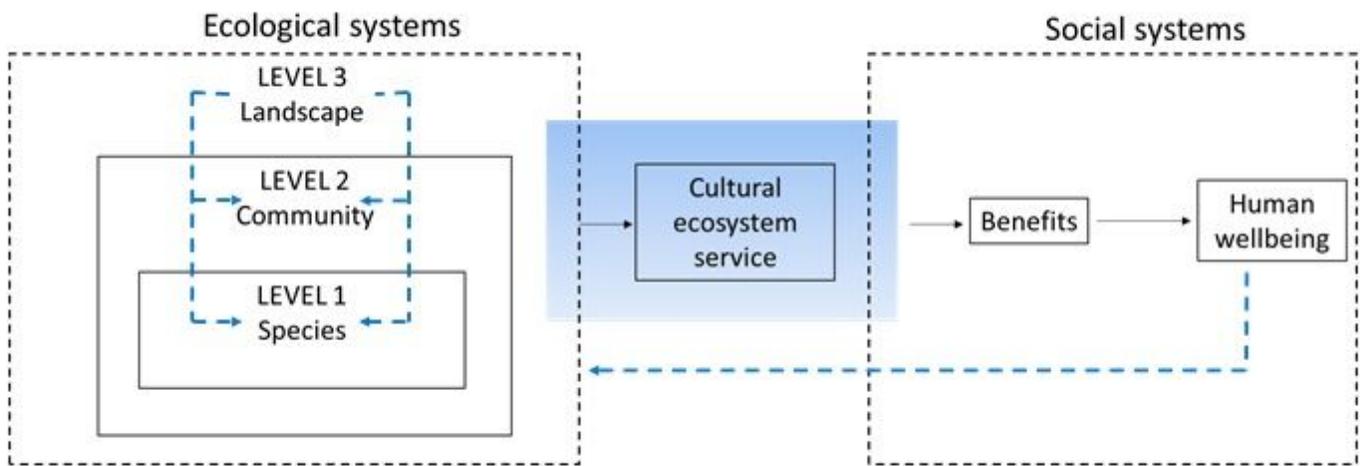
## References

- Aalders I, Stanik N (2019) Spatial units and scales for cultural ecosystem services: a comparison illustrated by cultural heritage and entertainment services in Scotland. *Landscape ecology* 34(7):1635-1651
- Allan TFHH, T. W. (1990) The confusion between scale-defined levels and conventional levels of organisation in ecology. *Journal of Vegetation Science* 1:5-12

- Ament JM, Moore CA, Herbst M, Cumming GS (2017) Cultural Ecosystem Services in Protected Areas: Understanding Bundles, Trade-Offs, and Synergies. *Conservation Letters* 10(4):440-450
- Andersson E, McPhearson T, Kremer P et al (2015) Scale and context dependence of ecosystem service providing units. *Ecosystem Services* 12:157-164
- Bachi L, Ribeiro SC, Hermes J, Saadi A (2020) Cultural Ecosystem Services (CES) in landscapes with a tourist vocation: Mapping and modeling the physical landscape components that bring benefits to people in a mountain tourist destination in southeastern Brazil. *Tourism Management* 77:104017
- Booth JE, Gaston KJ, Evans KL, Armsworth PR (2011) The value of species rarity in biodiversity recreation: A birdwatching example. *Biological Conservation* 144(11):2728-2732
- Bruley E, Locatelli B, Lavorel S (2021) Nature's contributions to people: Coproducing quality of life from multifunctional landscapes. *Ecology and Society* 26(1): 12
- Chan KMA, Satterfield T, Goldstein J (2012) Rethinking ecosystem services to better address and navigate cultural values. *Ecological Economics* 74:8-18
- Chettri NCD, Debes; Sharma, Eklabya; Jackson, Rodney (2005) The relationship between bird communities and habitat. *Mountain Research and Development* 25(3):235–243
- Cumming GS, Maciejewski K (2017) Reconciling community ecology and ecosystem services: Cultural services and benefits from birds in South African National Parks. *Ecosystem Services* 28:219-227
- Filloy J, Zurita GA, Bellocq MI (2019) Bird diversity in urban ecosystems: the role of the biome and land use along urbanization gradients. *Ecosystems* 22(1):213-227
- Fischer A, Eastwood A (2016) Coproduction of ecosystem services as human–nature interactions—An analytical framework. *Land Use Policy* 52:41-50
- Fish R, Church A, Winter M (2016) Conceptualising cultural ecosystem services: A novel framework for research and critical engagement. *Ecosystem Services* 21:208-217
- Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf BO (2014) The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology* 87(6):782-795
- Graves RA, Pearson SM, Turner MG (2019) Effects of bird community dynamics on the seasonal distribution of cultural ecosystem services. *Ambio* 48(3):280-292
- Katz-Gerro T, Orenstein DE (2015) Environmental tastes, opinions and behaviors: social sciences in the service of cultural ecosystem service assessment. *Ecology and Society* 20(3)

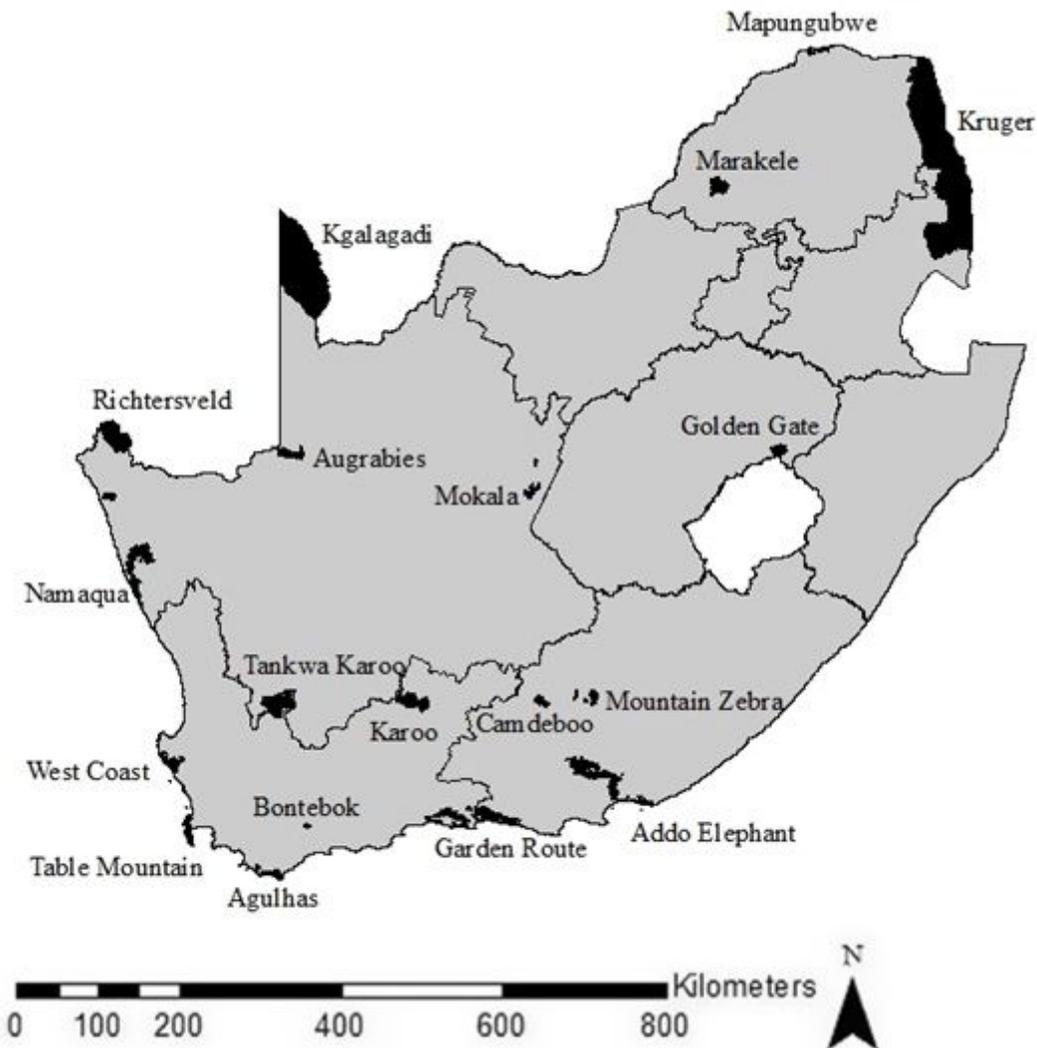
- MA (2005) Millennium Ecosystem Assessment. Ecosystems and human well-being: Synthesis. Island Press, Washington, D.C
- Mao D, Ma Q, Zhou B-B (2020) Sustainability of human–environment systems through the lens of landscape. Springer,
- Marshall N, Adger WN, Benham C et al (2019) Reef Grief: investigating the relationship between place meanings and place change on the Great Barrier Reef, Australia. *Sustainability Science* 14(3):579-587
- Orenstein DE, Zimroni H, Eizenberg E (2015) The immersive visualization theater: A new tool for ecosystem assessment and landscape planning. *Computers, Environment and Urban Systems* 54:347-355
- Plieninger T, Dijks S, Oteros-Rozas E, Bieling C (2013) Assessing, mapping, and quantifying cultural ecosystem services at community level. *Land Use Policy* 33:118-129
- Potschin M, Potschin M, Haines-Young R, Haines-Young R (2013) Landscapes, sustainability and the place-based analysis of ecosystem services. *Landscape Ecology* 28(6):1053-1065
- Schaich H, Bieling C, Plieninger T (2010) Linking ecosystem services with cultural landscape research. *Gaia-Ecological Perspectives for Science and Society* 19(4):269-277
- Scholtz M, Kruger M, Saayman M (2015) Determinants of visitor length of stay at three coastal national parks in South Africa. *Journal of ecotourism* 14(1):21-47
- Sekercioglu CH (2002) Impacts of birdwatching on human and avian communities. *Environmental Conservation* 29(3):282-289
- Steven R, Smart JCR, Morrison C, Castley JG (2017) Using a choice experiment and birder preferences to guide bird-conservation funding. *Conserv Biol* 31(4):818-827
- Tengberg A, Fredholm S, Eliasson I et al (2012) Cultural ecosystem services provided by landscapes: Assessment of heritage values and identity. *Ecosystem Services* 2:14-26
- Tew ER, Simmons BI, Sutherland WJ (2019) Quantifying cultural ecosystem services: Disentangling the effects of management from landscape features. *People and Nature* 1(1):70-86
- Whelan CJ, Şekerciöğlü ÇH, Wenny DG (2015) Why birds matter: from economic ornithology to ecosystem services. *Journal of Ornithology* 156(S1):227-238
- Zoeller KC, Gurney GG, Heydinger J, Cumming GS (2020) Defining cultural functional groups based on perceived traits assigned to birds. *Ecosystem Services* 44

## Figures



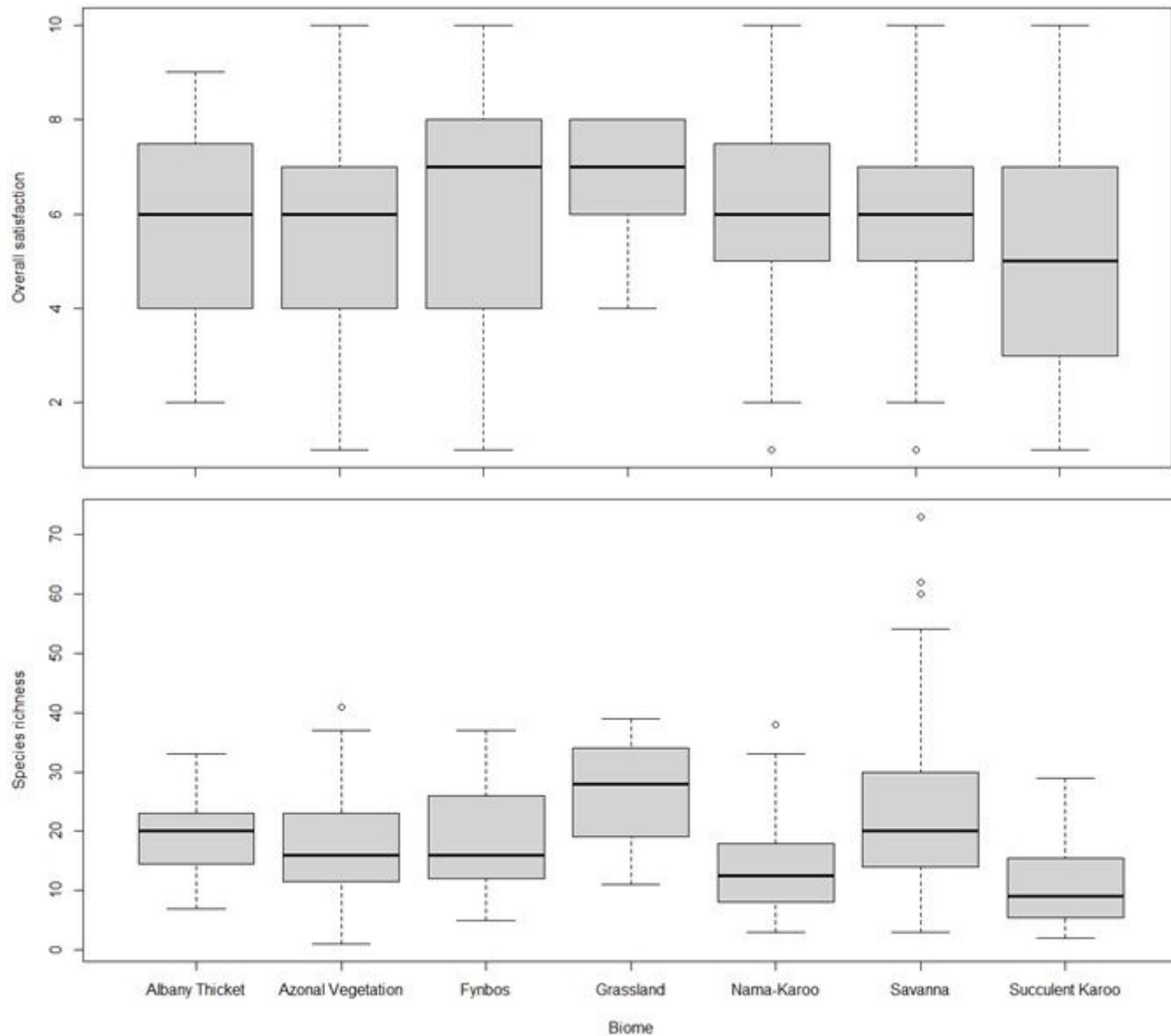
**Figure 1**

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



**Figure 2**

Map of study sites South African National Parks



**Figure 3**

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 ( $p < 0.05$ ).