Ecosystem Services 60 (2023) 101519

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Full Length Article

Cultural functional groups associated with birds relate closely to avian ecological functions and services

Kim C. Zoeller[a,b,c,*], Graeme S. Cumming[a,b]

[a] Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia
[b] Percy FitzPatrick Institute, University of Cape Town, Rondebosch, Cape Town 7701, South Africa
[c] CSIRO Land and Water, Black Mountain, Canberra, ACT, Australia North Road, Acton, Australian Capital Territory 2601, Australia

ARTICLE INFO

Keywords:
Cultural functional groups
Ecological functional groups
Birds
Cultural ecosystem services

ABSTRACT

The global rapid decline of ecological systems has highlighted the potential of ecosystem functions to drive conservation discourse. Ecosystem functions underpin important ecosystem services, and have been described for birds in South Africa based on measurable ecological traits (physiological, structural, behavioural, or phenological characteristics), as well as cultural functions (human preferences for morphological and behavioural traits). Understanding the spatial relationships between ecological and cultural functions can provide insight into the extent to which cultural services of birds are correlated with different ecological functions, and identify potential synergies in the distribution of cultural and ecological services. Here we show that when correcting for the effect of species richness and spatial autocorrelation on functional group richness, there is a clear correlation between avian cultural and ecological functional groups in South Africa ($r = 0.6$, $t = 32.20$, $df = 1936$, $p < 0.05$), suggesting that cultural functions are strongly correlated with ecologically relevant traits, despite their production being primarily mediated through human perception. This relationship was highly correlated in National Parks ($r = 0.75$, $t = 14.95$, $df = 182$, $p < 0.05$). For conservation initiatives that aim to maximise both ecosystem function and ecosystem service production, it is critical to identify and support synergies in the distribution of different functional groups to promote the production of multiple ecosystem services.

1. Introduction

Ecosystems have the capacity to provide a range of functions that contribute to human wellbeing by generating ecosystem services (Schuldt et al., 2018). Increasing demand for the sustainable provision of ecosystem services has highlighted the importance of identifying the functions that underpin ecosystem service production (De Bello et al., 2010). One approach for identifying these processes and clarifying the nature of ecosystem service production is to group species-specific functional traits into functional groups, improving our capacity to generalise, synthesise, and make predictions about complex ecological processes and structures (de Groot et al., 2002; Shipley et al., 2016). Linking species-specific functional traits with ecosystem services has also provided critical advancement in understanding the flow of ecosystem services from production in ecological systems to delivery of their benefits in social systems (Potschin-Young et al., 2018).

Ideas about functional classifications and their links to ecosystem services have typically been applied to those traits that relate directly to biophysical processes (De Bello et al., 2010). For example, plant structural traits such as leaf area were identified as critical biophysical mechanisms underpinning ecosystem service provision (Lavorel et al., 2011). Groupings of species using traits that relate to biophysical mechanisms or other critical elements of an organism's ecology are defined here as ecological functional groups (EFGs). They include physiological, structural, behavioural, or phenological characteristics (Verner, 1984; De Graaf et al., 1985; Cumming and Child, 2009; Diaz et al., 2011). The ecological groupings of traits, however, are not the only mechanism underpinning all ecosystem service production. It has recently been proposed that the functional group approach can also be usefully applied to understanding the cultural services that organisms provide. Cultural ecosystem services refer to the nonmaterial benefits people derive from ecosystem such as recreation and spirituality and consequently, are underpinned by preference and perception-based traits, rather than biophysical ones. Using birds as an example, Zoeller et al. (2020) have shown how the organismal traits that influence people's perceptions of organisms – and hence, the benefits that people

* Corresponding author at: Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia.
E-mail address: kim.zoeller@my.jcu.edu.au (K.C. Zoeller).

https://doi.org/10.1016/j.ecoser.2023.101519
Received 12 January 2022; Received in revised form 9 February 2023; Accepted 13 February 2023
Available online 20 February 2023

derive from seeing or interacting with them - can be measured, using interview data, to derive a consistent set of 'cultural functional groups' (CFGs) based on human preferences for such avian cultural traits as size, colour, and song. Cultural functional groups are 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, their existence is dependent on both the species themselves and the sociocultural systems that influence human perceptions and preferences, making them social-ecological groupings rather than purely ecological or social (Zoeller et al., 2021).

Crucially, research on cultural ecosystem services and the benefits they deliver remains nascent, especially compared with scholarship focused on other services (Cheng et al., 2019). A primary reason for the underrepresentation of cultural services is the difficulty of evaluating nonmaterial contributions to human wellbeing, resulting in a limited understanding of the full range of services available in the landscape (Cheng et al., 2019). As a result, cultural ecosystem service assessments are at risk of minimising the extent to which people are central in driving the production of ecosystem services (Echeverri et al., 2019). Addressing these issues from a functional perspective 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 (Maciejewski et al. 2015; Clements and Cumming, 2017a; Clements and Cumming, 2017b). 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 (Maciejewski et al., 2015; Bartelet et al., 2022).

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, we might expect that ecological functions would correlate in some way with cultural functions.

Regardless of their possible adaptive value, with cultural services 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 we assume an 'umbrella effect', where conservation action that supports cultural service provision will also be sufficient to retain a full range of ecological functions?

We addressed these questions in a three-step process. First, we 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, we 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, we asked whether there was a relationship between the spatial distributions of particular ecological and cultural functional groups. By focusing on a specific taxon to explore complex socio-ecological interactions, our results provide valuable operational insights into the relationships between ecological functional and cultural service provision.

2. Methods

2.1. Describing functional groups

2.1.1. Ecological functional groups

Birds provide a range of ecological functions that are critical for ecological processes. We 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 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 ecological functional groups: Seed Dispersers, Pollinators, Nutrient Dispersers, Grazers, Insectivores, Raptors, Scavengers, Ecosystem Engineers, and Granivores (Sekercioglu, 2006; Cumming and Child, 2009). These groups recognise that birds impact ecosystems through what they eat, what they move, and how they alter physical structures. For example, nutrient dispersers (e.g., Grey Heron) move nutrients between aquatic and terrestrial ecosystems; and ecosystem engineers (e.g., Sociable Weaver, Cardinal Woodpecker) create habitat, such as tree hollows or massive nests, that is used by other organisms. Birds may fall into more than one functional group; so, for example, a granivore (e.g., Cape Sparrow) may also be a seed disperser, but not all seed dispersers are granivores (e.g., Knysna Turaco). Using independently defined ecological functional groups with assigned bird species enabled the relationship between ecological and cultural functional groups to be directly addressed.

2.1.2. Cultural functional groups

To describe cultural functional groups, perception data for 491 bird species from 401 respondents were used to identify morphological, behavioural and culturally significant functional traits (Zoeller et al., 2020). These data were collected between 2016 and 2017 using in-person interviews with individuals from a range of socio-demographic identities to enhance individual variation in human perception, selected using a mixture of convenience and purposive sampling (Zoeller et al., 2021). Each respondent was asked to score a random selection of 30 bird species (whose range coincided with that individual's geographic location) using an adaptation of Q-factor analysis which produced a Likert-scale ranking system. Respondents were specifically asked to rank 30 bird species by placing a photo (i.e. a representative symbol) of that species on a scoreboard. The scoreboard consisted of 30 blocks arranged in normal distribution, and each block represented a score ranging from one to 10. A score of one represented a negative response to that species, 10 a positive response and five and six a neutral response. Respondents were then asked to justify the species' score by describing reasons for its placement on the scoreboard (See Zoeller et al. 2020; 2021 for more detail). For example, one respondent scored an Orange-breasted Sunbird a nine because she has a positive reaction to its plumage, its song and its foraging behaviour. There were no limits to the number of reasons respondents could cite. Based on 401 interviews, the reasons respondent's cited were inductively coded into 41 traits (see Table S2). These traits were grouped using K-means cluster analysis, which allocated each of the identified traits into one of six clusters based on distance-based measures of similarity. The dominant traits in each cluster were incorporated into a typology of cultural functional groups as described in detail in Zoeller et al. (2020) and listed in Table S2. Each bird species could then be categorised into one or more of the six cultural functional groups: Visual Traits; Negative Visual and Behavioural Traits; Movement and Ecological Traits; Place Association and Abundance

Indicators; Common Traits; and Behavioural Traits.

2.2. Distribution data

The second Southern African Bird Atlas Project (SABAP2) was established in 2007 to capture the distribution of bird species in the region (out of a possible 950 species) at an annual resolution (Underhill et al., 2017). Data for SABAP2 were collected via a minimum of two-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 (https://sabap2.birdmap.africa; checked 7/09/2021).

2.3. Data analysis

2.3.1. Functional group richness comparison

To facilitate the interpretability of the results we 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 and cultural functional groups across the whole of South Africa, each bird species was allocated to one or more cultural and ecological functional groups based on their functional traits. Functional group richness and the number of species present within each functional group could then be determined by counting bird species within each functional group inside each 0.25 × 0.25 degree grid cell. Since species were often allocated to more than one functional group, it was critical to account for grid cells that had multiple functional groups represented by single species. Both ecological and cultural classifications were strongly influenced by species richness, with richness potentially confounding our understanding of the relationships between cultural and ecological groupings. We corrected for this confounding relationship following methods outlined by Cumming and Child (2009). Specifically, we plotted functional group richness against taxonomic richness for each functional group (independently for cultural and ecological functional groups respectively), fitted a regression, and extracted the residuals. The residuals describe variance in each of the two functional groups that cannot be attributed to species richness (Cumming and Child, 2009). They were compared for cultural functional groups and ecological functional groups using correlations and mapped to illustrate divergence in spatial pattern between species richness and functional group richness. We ran the analysis again after removing potential outliers (i.e. observations with z-score less than −3 or greater than 3). All subsequent analyses involving cultural functional group and ecological functional group comparisons exclude those outliers. Overlap in the distribution of cultural functional groups and ecological functional groups were further visualised using a kernel density plot.

We additionally ran a correlation analysis on a sub-set of the data, focusing on cultural and ecological functional group richness in South Africa's 20 National Parks. National Parks are of particular interest as they represent areas with lower levels of anthropogenic disturbance, and can therefore help us understand the balance of ecological and cultural functional groups in the absence of human influence. Due to data quality concerns, we did not feel comfortable running the equivalent analysis on heavily impacted areas (citizen science bird counts in *peri*-urban areas of South Africa are restricted by safety concerns).

2.3.2. Functional group spatial relationship

To determine whether the spatial relationship between ecological and cultural functional groups were different from what might be expected if birds were assigned to cultural functional groups at random, we 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 and ecological functional richness, as described in section 2.3.1.

To determine whether assessing functional group relationships using residuals was sufficient to eliminate spatial autocorrelation (which we would expect in the untransformed data as a consequence of the autocorrelation in species richness that arises from broader-scale geographic patterns), we 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 our results indicated that $p < 0.05$ for both cultural and ecological functional groups, we 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 richness in one grid cell reflects functional richness in another. Distance was determined following the approach outlined by Stata (StataCorp. 2015). We initially generated a matrix of inverse distance weights. Pairs of points closer together are situated higher than points that are further apart. Coordinates for latitude and longitude for these points were treated as values on a plane rather than being treated as spherical. Once the distance matrix was created, we took the inverse of the matrix values where each off-diagonal entry [i, j] in the matrix is equal to 1/(distance between point i and point j).

The autocovariate model is determined through the following equation: $y = X\beta + \rho A + \varepsilon$, where β is a vector of coefficients for intercept and explanatory variables X (set to null in our model); and ρ is the coefficient of the autocovariate A (Dormann et al., 2007). The weighted sum of A can be calculated as:

$$A_i = \sum_{j \in k_i} W_{ij} Y_j$$

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

2.3.3. Individual functional groups association

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

3. Results

3.1. Functional group richness comparison

The analysis identified areas that are species rich but have low functional 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. 1). Functional group richness was correlated between cultural functional groups and ecological functional groups independently of species richness (i.e., based on comparison of residuals) for the whole country ($n = 1972$, Pearson's $r = 0.47$, $t = 24.14$, $df = 1970$, $p < 0.05$). After removing outliers, the strength of the species richness-independent relationship

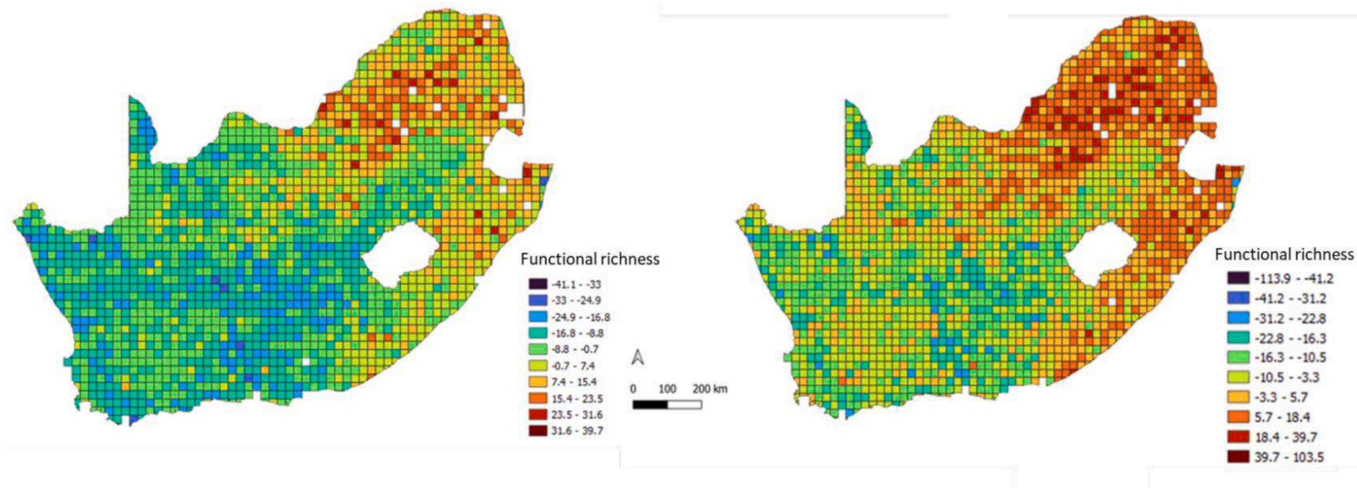

Fig. 1. Functional group richness of bird species in South Africa for ecological functional groups (a) and cultural functional groups (b). These distributions represent residuals of the relationship between functional group richness and taxonomic richness (i.e., they are corrected for species richness). Higher values indicate greater functional richness; blank grid cells were outliers.

between cultural and ecological functional groups increased slightly (n = 1938, Pearson's r = 0.49, t = 10.50, df = 1936, $p < 0.05$) (Figs. 2 and 3). Residuals for ecological functional group and cultural functional group richness were highly correlated in National Parks, whether including outliers (n = 186 Pearson's r r = 0.63, t = 11.11, df = 184, $p < 0.05$) or excluding them (n = 184, Pearson's r = 0.64, t = 11.37, df = 182, $p < 0.05$) (Figs. 4 and 5).

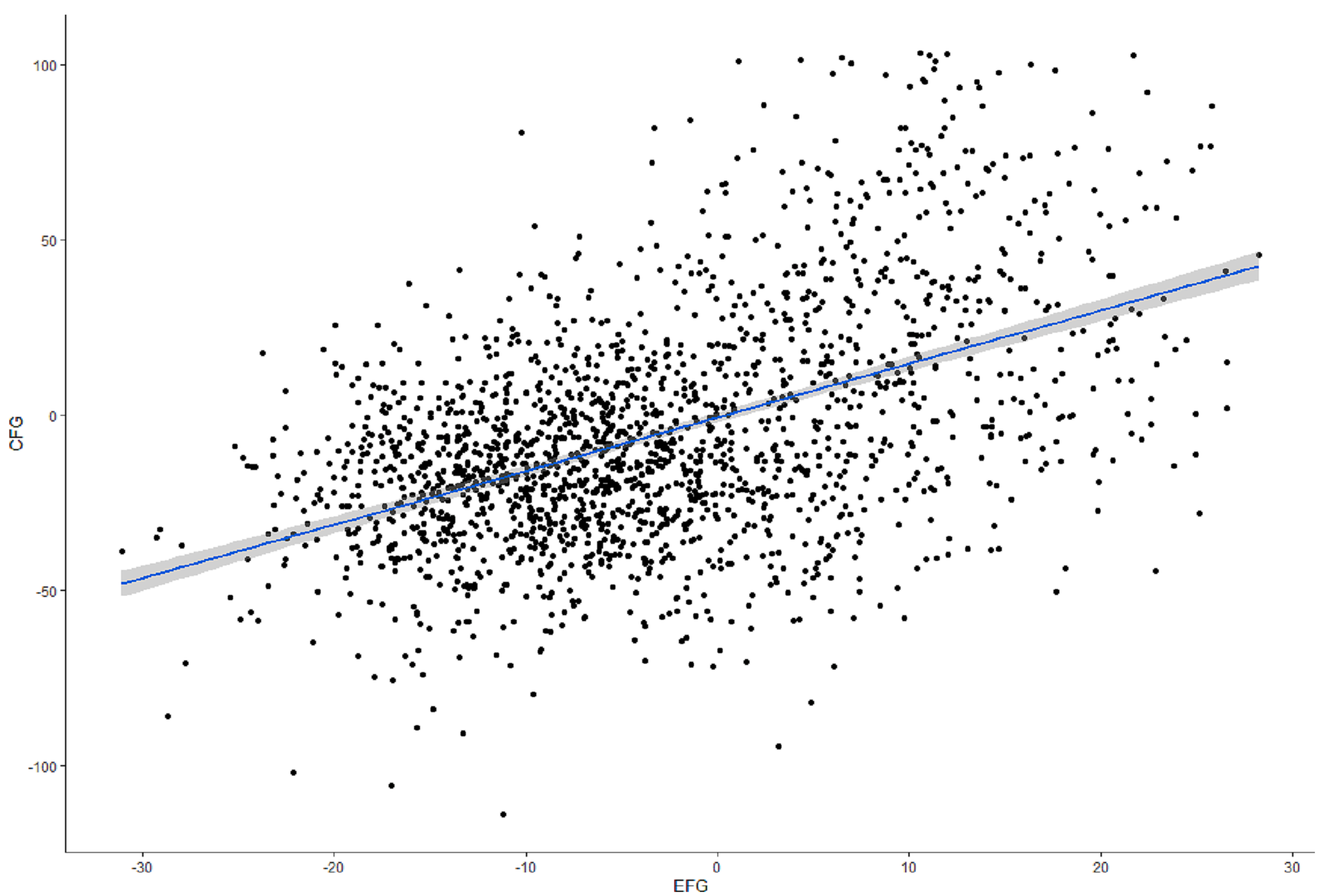

Fig. 2. Regression of the residuals of cultural functional group (CFG) on the residuals of ecological functional group (EFG) (n = 1938, Pearson's r = 0.49, t = 10.50, df = 1936, $p < 0.05$). This figure shows the relationship between CFG and EFG after correction for the shared influence of species richness and with outliers removed. Note that it is not corrected for spatial autocorrelation.

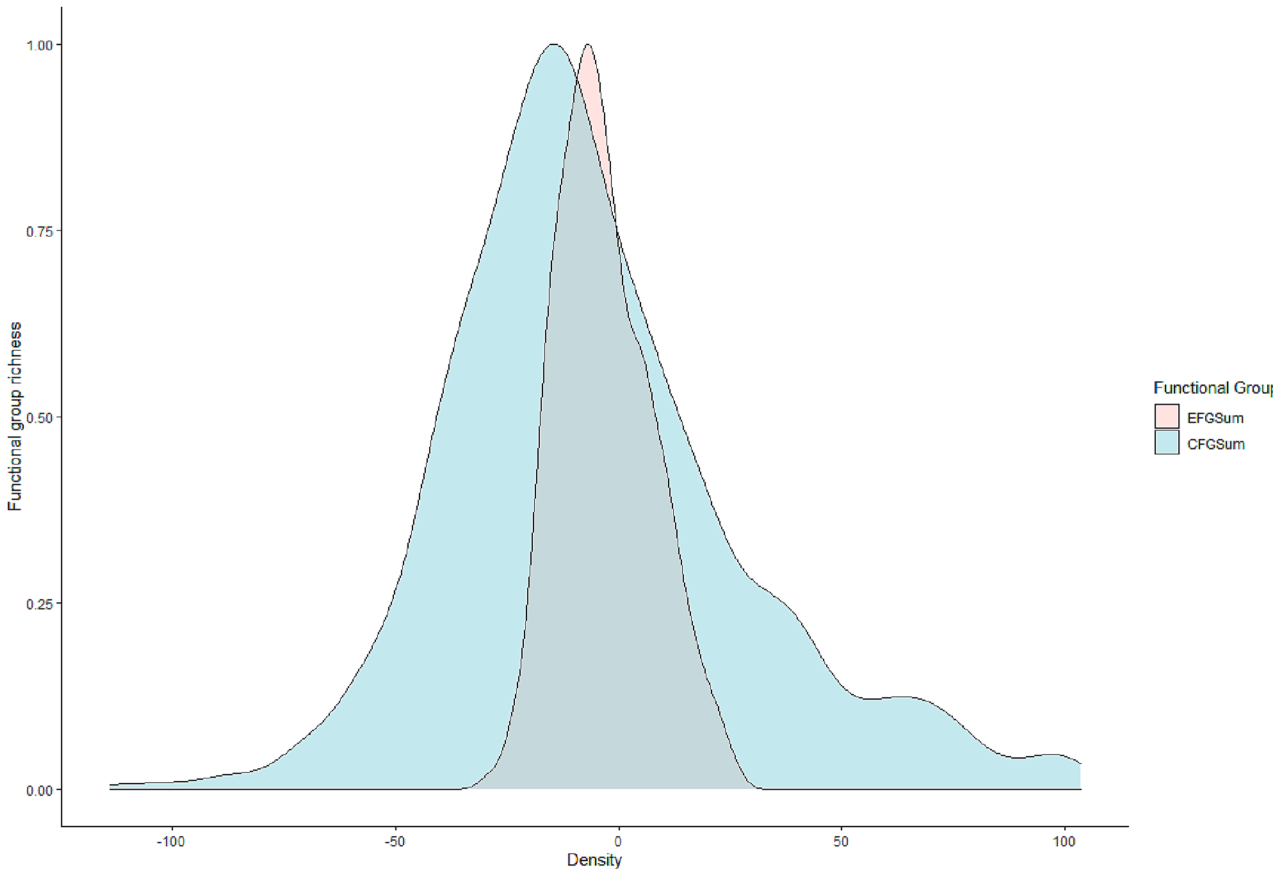

Fig. 3. Density plot illustrating the distribution of cultural functional groups (CFGSum) and ecological functional groups (EFGSum) when corrected for species richness using residuals and with outliers removed. Areas of overlap indicate shared probability of overlap in distribution between cultural functional and ecological functional groups. This figure shows how the cultural grouping corresponds closely to the ecological grouping for the same bird community, but exhibits greater variance.

3.2. Functional group spatial relationship

The randomisation analysis showed that the association between randomised cultural functional group richness and ecological functional group richness was weak ($r = 0.002 \pm 0.02$) 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 ($r = 0.006 \pm 0.07$) compared to the observed data ($r = 0.63$), indicating a clear relationship between functional groups.

Moran's I indicated significant spatial autocorrelation for cultural functional group richness (Moran's I index = 0.17, Moran's I standard deviate = 192.43, variance = 0.0000007, $p < 0.05$) and ecological functional group richness (Moran's I Index = 0.24, Moran's I standard deviate = 278.74, 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 cultural and ecological functional groups remained highly correlated across South Africa ($r = 0.6$, $t = 32.20$, $df = 1936$, $p < 0.05$), and in National Parks ($r = 0.75$, $t = 14.95$, $df = 182$, $p < 0.05$). The correlation between cultural and ecological functional groups thus strengthened with autocorrelation-corrected residuals.

3.3. Individual functional groups association

Results of the correlation across all functional groups (Fig. 6) indicated strong positive associations between Visual Traits and Seed Dispersers ($r = 0.53$, $t = 27.76$, $df = 1936$, $p < 0.05$), Granivores ($r = 0.55$, $t = 29.30$, $df = 1936$, $p < 0.05$) and Ecosystem Engineers ($r = 0.50$, $t = 25.92$, $df = 1936$, $p < 0.05$). Movement and Ecological Traits had a similarly strong relationship with Seed Dispersers ($r = 0.34$, $t = 15.91$, $df = 1936$, $p < 0.05$) and Granivores ($r = 0.42$, $t = 20.46$, $df = 1956$, $p < 0.05$), while Place Association and Abundance Indicators had a positive relationship with Seed Dispersers ($r = 0.34$, $t = 15.70$, $df = 1936$, $p < 0.05$). There was evidence of a positive relationship between Behavioural Traits and Raptors ($r = 0.46$, $t = 22.71$, $df = 1936$, $p < 0.05$). Negative Visual and Behavioural Traits had a positive association with Insectivores ($r = 0.42$, $t = 20.60$, $df = 1936$, $p < 0.05$). 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 ($r = -0.37$, $t = 17.57$, $df = 1936$, $p < 0.05$), Movement and Ecological Traits ($r = -0.32$, $t = 14.77$, $df = 1936$, $p < 0.05$), and Negative Visual and Behavioural Traits ($r = -0.44$, $t = 21.45$, $df = 1936$, $p < 0.05$), suggesting areas of high richness with Nutrient Depositors would have lower representation of these cultural functional groups.

4. Discussion

Our results demonstrate a clear but nuanced relationship between avian cultural and ecological functional groups, suggesting that the

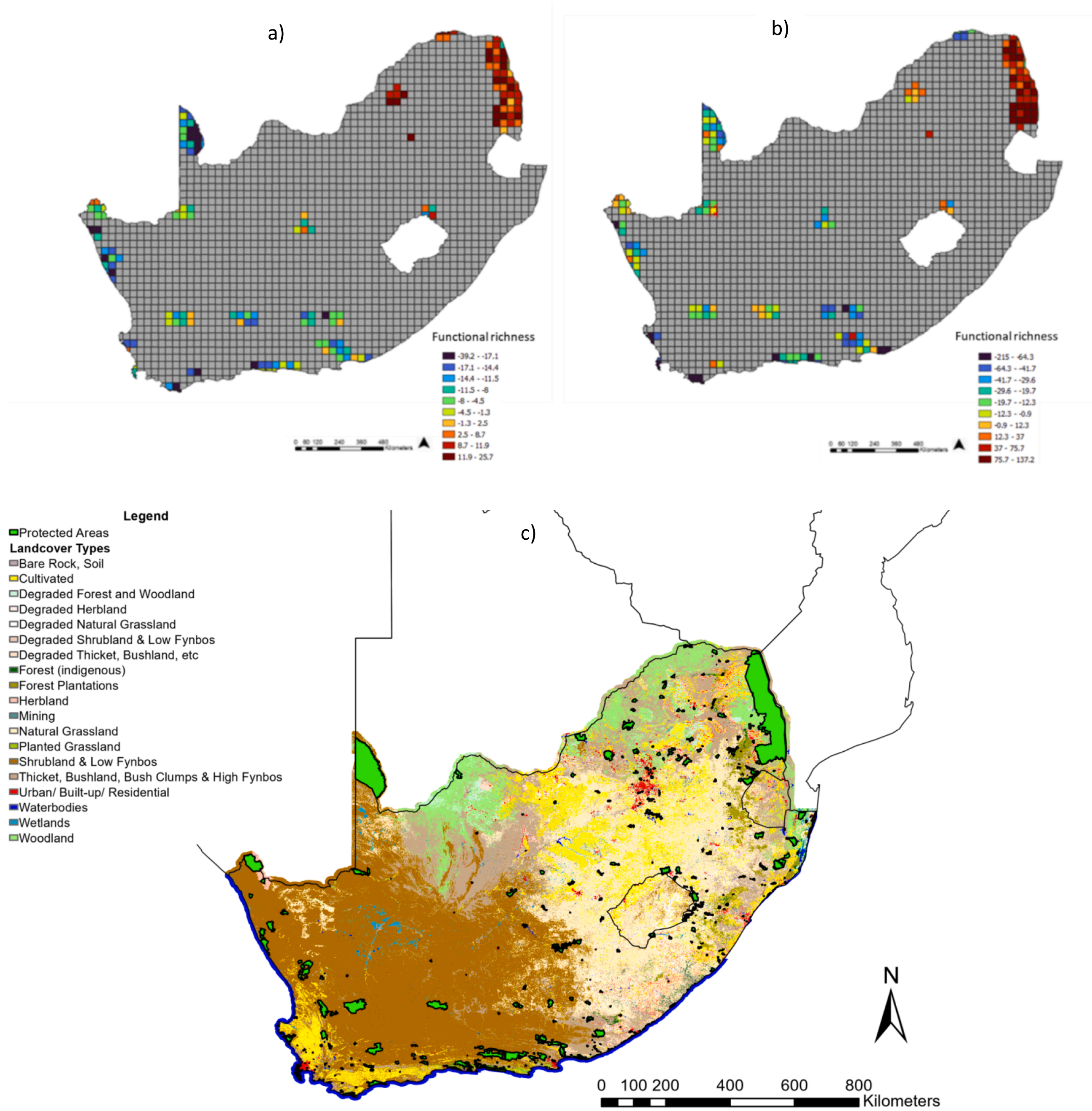

Fig. 4. Functional group richness of bird species in South African National Parks for ecological functional groups (a) and cultural functional groups (b), and land cover types in South Africa and the context in which protected areas (bright green) are located (c). Fig. 5a and 5b represent residuals of the relationship between functional group richness and taxonomic richness (i.e., corrected for species richness). Higher values indicate greater functional richness. Outliers have been removed.

provision of cultural ecosystem services is also correlated with ecologically relevant traits. This relationship was apparent when correcting both for the number of species present per functional group and spatial autocorrelation. The relationship between cultural and ecological functional groups was particularly strong in National Parks. Since national parks represent areas with limited capacity for human selection of functional traits, these results provide insight into the balance of cultural functional traits and ecological functional traits associated with avifauna when human preference is not the primary selective pressure.

Understanding the overlap between cultural and functional groups may offer insight into 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 cultural functional groups and ecological 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

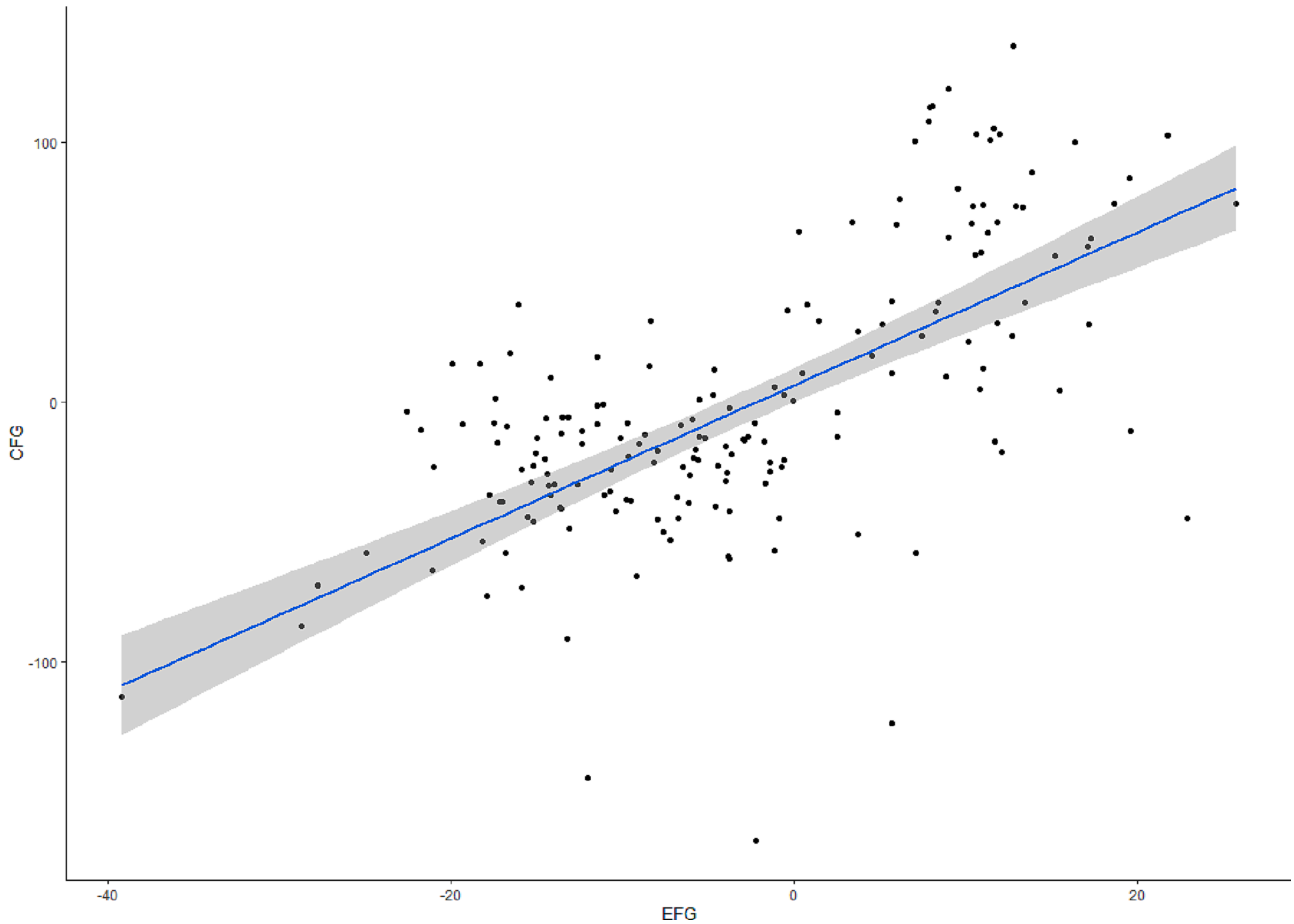

Fig. 5. Regression of the residuals of cultural functional group (CFG) on the residuals of ecological functional group (EFG) in South African National Parks ($n = 184$, Pearson's $r = 0.64$, $t = 11.37$, $df = 182$, $p < 0.05$). This figure shows the relationship between CFG and EFG after correction for the shared influence of species richness and with outliers removed. Note that it is not corrected for spatial autocorrelation.

limiting the effect of herbivore damage on plants (Sekercioglu, 2006). Understanding the relationship between ecological and cultural functions has the potential to inform conservation management by providing critical insight into how ecological functions may be perceived through their association with particular cultural functional traits. As a result, conservation initiatives may tailor their approach to species protection initiatives by targeting perception-based preferences for particular functional traits.

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; Hamann et al., 2016), understanding whether the strength of the relationship between cultural and ecological functional groups changes along an urban–rural gradient could offer insight into the potential of environmental parameters to influence the balance of ecological and cultural functions. Indeed, some research has shown that differences in land use between protected areas and agricultural landscapes impact species richness and consequently, ecological functional group composition (Child et al., 2009). Child et al. (2009) reported a decrease in raptors and scavengers outside protected areas, whereas nutrient dispersers and grazers increased. Given the correlation of these ecological functional groups with specific cultural functional groups, it is likely that the loss of specific ecological functions will be reflected in the composition of cultural functions. However, it has also been demonstrated that ecological functional group composition does not necessarily change in urban areas relative to the national composition, even if species richness decreases (Suri et al., 2017). Depending on the circumstances, cultural functional groups may also be similar between urban and rural environments, albeit with fewer groups and less variety in group composition (Suri et al., 2017).

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 cultural functional groups and ecological functional groups can further enhance our 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. Specifically, extrapolating our approach to different species and systems would benefit our understanding of cultural ecosystem services more broadly. There is a more general need to develop model taxa and data sets that can help us

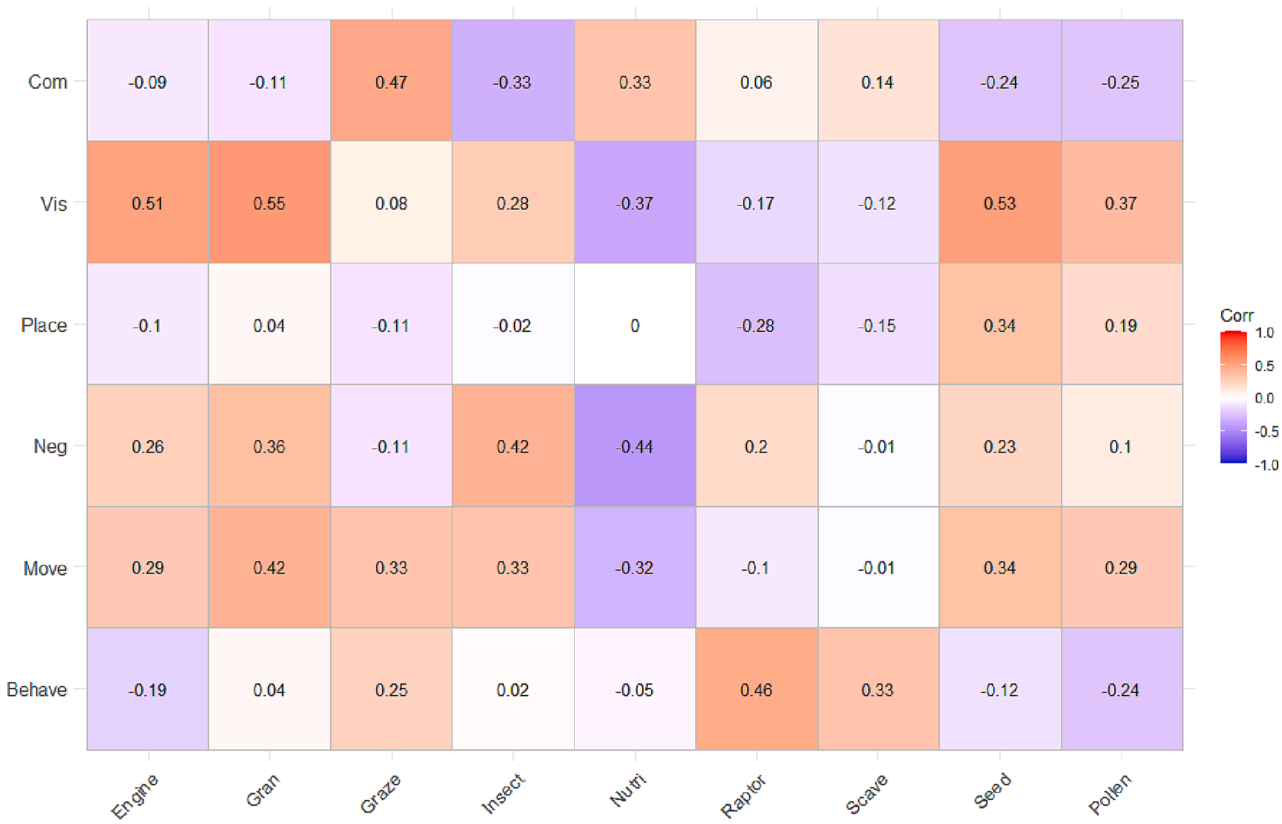

Fig. 6. Correlation coefficients indicating the association between functional group richness for individual ecological functional groups (Seed Dispersers, Pollinators, Nutrient Depositors, Insectivores, Granivores, Grazers, Raptors, Scavengers and Ecosystem Engineers), and individual cultural functional 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 are for residuals of functional group richness on species richness; they are corrected for species richness, but not for spatial autocorrelation.

interrogate and test ecosystem service concepts more deeply. Further, determining whether human preferences create bundles of ecological and cultural functions 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 considered to account for the effect of socio-demographic characteristics on perceptions of ecosystem services (Zoeller et al., 2021). In so doing, our approach to grouping cultural functional groups can be assessed more rigorously, and the potential for a western scientific epistemology to limit our understanding of cultural ecosystem services can be explored. 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 produced in a landscape (Bennett et al., 2009). Consequently, a key objective for ecosystem service research should be to understand the association between cultural and ecological functional groups to identify trade-offs between cultural and ecological services (Kremen, 2005). Our 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 cultural and ecological functions, 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). For conservation initiatives that aim to maximise the delivery of ecosystem services in a given landscape, consideration needs to be given to the potentially critical role cultural functions play in ecosystem service production (Marshall et al., 2018).

Funding

This work was supported by the National Research Foundation (NRF) through a Blue Skies grant, the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, and James Cook University.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank the numerous respondents who participated in interviews and enthusiastically volunteered their time and personal insight. We would also like to extend our gratitude to Dominic Henry and Kristine

Maciejewski, who provided early support and feedback on the sampling protocol. This research was funded by the National Research Foundation of South Africa through a Blue Skies grant to GSC, by the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, South Africa, and by the Australian Research Council Centre of Excellence for Coral Reef Studies at James Cook University. Ethics approval was provided by the University of Cape Town (SFREC 48_2012).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2023.101519.

References

Ament, J.M., Moore, C.A., Herbst, M., Cumming, G.S., 2017. Cultural ecosystem services in protected areas: understanding bundles, trade-offs, and synergies. Conserv. Lett. 10, 440–450.

Bartelet, H.A., Barnes, M.L., Zoeller, K.C., Cumming, G.S., 2022. Social adaptation can reduce the strength of social–ecological feedbacks from ecosystem degradation. People and Nature 4, 856–865.

Belaire, J.A., Westphal, L.M., Whelan, C.J., Minor, E.S., 2015. Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. Condor 117, 192–202.

Bellwood, D.R., Streit, R.P., Brandl, S.J., Tebbett, S.B., Graham, N., 2019. The meaning of the term 'function' in ecology: a coral reef perspective. Funct. Ecol. 33, 948–961.

Bennett, E.M., Peterson, G.D., Gordon, L.J., 2009. Understanding relationships among multiple ecosystem services. Ecol. Lett. 12, 1394–1404.

Berkes, F., 2008. Sacred Ecology, 2nd ed. Routledge, New York.

Blondel, J., 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231.

Cheng, X., Van Damme, S., Li, L., Uyttenhove, P., 2019. Evaluation of cultural ecosystem services: a review of methods. Ecosyst. Serv. 37.

Child, M.F., Cumming, G.S., Amano, T., 2009. Assessing the broad-scale impact of agriculturally transformed and protected area landscapes on avian taxonomic and functional richness. Biol. Conserv. 142, 2593–2601.

Clements, H.S., Cumming, G.S. 2017b. Positives and pathologies of natural resource management on private land conservation areas. Conserv. Biol. 31: 707-717.

Clements, H.S., Cumming, G.S., 2017a. Manager strategies and user demands: determinants of cultural ecosystem service bundles on private protected areas. Ecosyst. Serv. 28, 228–237.

Cumming, G., Peterson, G., 2005. Ecology in global scenarios. Ecosystems and human well-being: scenarios 2, 45-70.

Cumming, G.S., Child, M.F., 2009. Contrasting spatial patterns of taxonomic and functional richness offer insights into potential loss of ecosystem services. Philos. Trans. R. Soc., B 364, 1683–1692.

De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins Da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodivers. Conserv. 19, 2873–2893.

De Graaf, R.M., Tilghman, N.G., Anderson, S.H., 1985. Foraging guilds of North American birds. Environ. Manage. N. Y. 9, 493–536.

de Groot, R.S., Wilson, M.A., Boumans, R.M.J., 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecol. Econ. 41, 393–408.

Diaz, S., Quetier, F., Caceres, D.M., Trainor, S.F., Perez-Harguindeguy, N., Bret-Harte, M. S., Finegan, B., Pena-Claros, M., Poorter, L., 2011. Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. Proc Natl Acad Sci U S A 108, 895–902.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography (Copenhagen) 30, 609–628.

Echeverri, A., Karp, D.S., Naidoo, R., Tobias, J.A., Zhao, J., Chan, K.M.A., 2019. Can avian functional traits predict cultural ecosystem services? People and Nature 2, 138–151.

Hamann, M., Biggs, R., Reyers, B., Stockholms, u., Naturvetenskapliga, f., Stockholm Resilience, C., 2016. An exploration of human well-being bundles as identifiers of ecosystem service use patterns. PloS one 11, e0163476.

Hockey, P., Crawford, R., Dean, W., Ryan, P., 2005. Roberts' Birds of Southern Africa. John Voelcker Bird Book Fund, Cape Town, South Africa.

Kremen, C., 2005. Managing ecosystem services: what do we need to know about their ecology? Ecol. Lett. 8, 468–479.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G., Douzet, R., 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. J. Ecol. 99, 135–147.

Legras, G., Loiseau, N., Gaertner, J.C., 2018. Functional richness: Overview of indices and underlying concepts. Acta Oecologica (Montrouge) 87, 34–44.

Maciejewski, K., De Vos, A., Cumming, G.S., Moore, C., Biggs, D., 2015. Cross-scale feedbacks and scale mismatches as influences on cultural services and the resilience of protected areas. Ecol. Appl. 25, 11–23.

Marshall, N., Barnes, M.L., Birtles, A., Brown, K., Cinner, J., Curnock, M., Eakin, H., Goldberg, J., Gooch, M., Kittinger, J., Marshall, P., Manuel-Navarrete, D., Pelling, M., Pert, P.L., Smit, B., Tobin, R., 2018. Measuring what matters in the Great Barrier Reef. Front. Ecol. Environ. 16, 271–277.

Martínez-Harms, M.J., Balvanera, P., 2012. Methods for mapping ecosystem service supply: a review. Int. J. Biodiversity Sci. Ecosystems Services Manage. 8, 17–25.

Martín-López, B., Iniesta-Arandia, I., García-Llorente, M., Palomo, I., Casado-Arzuaga, I., Del Amo, D.G., Gómez-Baggethun, E., Oteros-Rozas, E., Palacios-Agundez, I., Willaarts, B., González, J.A., Santos-Martín, F., Onaindia, M., López-Santiago, C., Montes, C., 2012. Uncovering ecosystem service bundles through social preferences. PLoS One 7, e38970.

Moran, P.A.P., 1948. The interpretation of statistical maps. J. R. Statistical Society. Series B, Methodological 10, 243–251.

Potschin-Young, M., Haines-Young, R., Gorg, C., Heink, U., Jax, K., Schleyer, C., 2018. Understanding the role of conceptual frameworks: Reading the ecosystem service cascade. Ecosyst. Serv. 29, 428–440.

Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J., Hardtle, W., He, J.S., Klein, A.M., Kuhn, P., Liu, X., Ma, K., Niklaus, P.A., Pietsch, K. A., Purahong, W., Scherer-Lorenzen, M., Schmid, B., Scholten, T., Staab, M., Tang, Z., Trogisch, S., von Oheimb, G., Wirth, C., Wubet, T., Zhu, C.D., Bruelheide, H., 2018. Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nat. Commun. 9, 2989.

Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.

Shipley, B., De Bello, F., Cornelissen, J.H.C., Laliberté, E., Laughlin, D.C., Reich, P.B., 2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180, 923–931.

Suri, J., Anderson, P.M., Charles-Dominique, T., Hellard, E., Cumming, G.S., 2017. More than just a corridor: a suburban river catchment enhances bird functional diversity. Landsc. Urban Plan. 157, 331–342.

Tengö, M., von Heland, J., 2013. Trees and Tree-Planting in Southern Madagascar: Sacredness and Remembrance. Springer, Netherlands, Dordrecht, pp. 333–337.

Underhill, L.G., Brooks, M., Loftie-Eaton, M., 2017. The Second Southern African Bird Atlas Project: protocol, process, product. Vogelwelt 137, 64–70.

Verner, J., 1984. The guild concept applied to management of bird populations [Environmental assessment and resource monitoring, California]. Environ. Manage. N. Y. 8, 1–13.

Yang, Y., Zheng, H., Kong, L., Huang, B., Xu, W., Ouyang, Z., 2019. Mapping ecosystem services bundles to detect high- and low-value ecosystem services areas for land use management. J. Clean. Prod. 225, 11–17.

Zoeller, K.C., Gurney, G.G., Heydinger, J., Cumming, G.S., 2020. Defining cultural functional groups based on perceived traits assigned to birds. Ecosyst. Serv. 44.

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. Ecol. Soc. 26.