Species assembly patterns and protected area effectiveness in times of change: a focus on African avifauna

by

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Declaration

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Abstract

The challenge of conserving biodiversity is daunting. Despite some local conservation gains, most indicators of the condition of global biodiversity show declines since the 1970's, while indicators of the threats to biodiversity all show increases. Humanity has in part responded to the global biodiversity extinction crisis by establishing protected areas (PA) and they are widely considered cornerstones of conservation.

However, their efficacy in maintaining biodiversity is much debated. Previous studies have been unable to provide a general answer because of their typically restricted geographic and/or taxonomic focus, or qualitative approach. Using a global meta-analysis with 861 pair-wise comparisons inside and outside PAs from 86 studies across five major taxon groups, I tested the hypothesis that PAs achieve significant conservation outcomes measured as higher biodiversity values compared with alternative land covers. I found that globally, PAs typically contain higher abundances of individual species, higher assemblage abundances and higher species richness. Variation in effect sizes among taxa nonetheless underscores that PA efficacy can be context specific.

To examine factors driving the context specific nature of PA efficacy, an exact distance, timed point count methodology was used to assess PAs ecological effectiveness in terms of bird assemblages of the Kruger National Park (KNP), South Africa, in the Phalaborwa section. Bird assemblages inside the KNP were compared to matched sites in rural and urban land cover, as well as the connecting habitat matrix outside the KNP. Species richness and abundance were significantly lower inside the KNP compared to other land covers. However, the species assemblages are markedly different. The artificial addition of resources in an otherwise resources poor area, mainly in terms of gardening, provide suitable habitat for a range of species, consistent with the more individuals hypothesis. Large-bodied and ground nesting species are virtually absent outside the KNP. Thus species richness and abundance differences between land cover regions mask insidious changes in species traits. Nonetheless, not formally protected land can contribute positively to the regional biodiversity portfolio.

Since an understanding of the mechanisms that structure species assemblages can aid in the consequences of anthropogenic drivers disentangling them, I describe and analyse the body size frequency distributions (BSFDs) of avian assemblages at several spatial scales in the

Afrotropical biogeographic realm. I found that the African avifaunal continental BSFD is unimodal and right-skewed. African avifaunal BSFDs are quantitatively dissimilar to the African mammal BSFDs, which are bimodal at all spatial scales. Much of the change in median body size with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD.

My results for the first time quantitatively demonstrate that PAs are a vital component of a global biodiversity conservation strategy. However, I also show that PA ecological effectiveness can be context specific, and understanding which species traits are at risk outside of PAs is critical to predicting their efficacy.

Opsomming

Dit is 'n uitnemende uitdaging om biodiversiteit te bewaar. Ten spyte van sommige sukses op 'n lokale skaal, dui die meeste indikators aan dat die toestand van globale biodiveristeit afgeneem het vanaf die 1970's, terwyl bedreigings daartoe toegeneem het. Die mensdom het gedeeltelik reageer op die biodiversiteits uitsterfings krisis deur die uiteensetting en instandhouding van bewaringsgebiede (BG). Hierdie metodiek word wêreldwyd geag as 'n hoeksteen van bewaring.

Die ekologiese doeltreffendheid van BG word egter baie debateer. Vorige studies was geografies beperk of het net op sekere takson groepe gefokus. Vorige studies is ook tipies statisties kwalitatief van aard. As gevolg daarvan het ek 'n globale meta-analiese gebruik, wat bestaan het uit 861 gepaarde meetings vanaf 86 studies, oor vyf verskillende taksonomiese groepe. Ek het die hipotese getoets dat BG statisties beduidende bewaring laat gekiet in terme van hoër biodiveristeits waardes binnekant hul grense, in kontras met areas buite BG. Ek het gevind dat BG juis hoër waardes van hoër indivuduele spesies hoeveelhede, gemeenskaps hoeveelhede en spesiesrykheid bevat. Tog dui die variasie in effek grootte onder takson groepe aan dat BG effektiwiteit konteks spesifiek is.

Aangesien BG effektiwiteit konteks spesifiek is, het ek verder 'n tydstip, eksakte-afstand punt-telling metodiek gevolg om die Kruger Nationale Park (KNP) in Suid Afrika, se ekologiese doeltreffendheid te bepaal. Ek het voëlgemeenskappe binne KNP vergelyk met

voëlgemeenskappe buite KNP. Metings is buite die KNP gedoen in tuislande, die stadsgebied van Phalaborwa, asook in die habitat matriks wat die areas verbind. Beide spesiesrykheid en hoeveelheid is hoër buite KNP, maar die voëlgemeenskap struktuur tussen gebiede verskil noemenswaardig. Die uitbreiding van bronne ten opstigte van nesmaak en voeding (meestal deur tuinmaak), bied vir voëls goeie habitat in die stadsgebied, soos verwag kan word uit die meer individue hipotese. Hierdie veranderinge in spesiesrykheid tussen die verskillende areas versteek veranderinge in die spesies einskappe. Voëls met groot liggaamsmassa, veral die wat op die grond nes maak, kom in baie minder getalle voor buite KNP. Tog bied onbewaarde areas 'n positiewe inpak tot die omgewing se biodiversiteit.

'n Holistiese begrip van die meganismes wat spesies gemeenskappe struktureer kan help om die menslike invloed daarop uit te lig. Daarvolgens beskryf ek die liggaamsmassa frekwensie verspreiding (LMFV) oor verkillende skale in die Afrotropies biografiese streek. Ek het bevind dat Afrika se voëlgemeenskappe op die kontinentale skaal unimodaal en regs-geskewe is. Afrika se voël LMFV is beduidend verskillend van Afrika soogdier LMFV, wat bimodaal is op verskeie skale. Baie van die verandering in mediaan liggaams massa oor verskillende skale kan verduidelik word met 'n verspreidings-aangepaste nul-model, wat voorstel dat die verskille in omset van voëls met of klein, of groot liggaamsmassa in die landskap die veranderings in LMFV verduidelik.

My studie is die eerste van sy soort wat kwantitatief bepaal dat die gebruik van BG krities is tot 'n globale bewaringsstrategie. Verder het ek bewys dat BG se ekologiese doeltreffendheid afhang van die kontkes op 'n lokale skaal, en dat spesies eienskappe geïnkorporeer moet word om BG se doeltreffendheid te bepaal.

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Dedication

For Johann and Steph.

Thank you both for your absolutely unwavering encouragement

and support to live my dreams.

"There are some who can live without wild things, and some who cannot. These essays are the delights and dilemmas of one who cannot."

Aldo Leopold - *A Sand County Almanac* - 1949

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Chapter 1 – General introduction

The outline of the National Forest Tapajós, in Brazil, can clearly be seen to the left of this satellite image. Deforestation along the rapidly expanding network of roads has created a unique fishbone pattern, as deforestation occurs orthogonally to the roads. The coordinates are 3°44'50.05"S; 55° 5'50.79"W. Photo courtesy of Google Earth (earth.google.com).

Protected areas and the conservation crisis

Biodiversity loss is now recognised as a driver of global change, the impacts of which rival those of other drivers such as climate change (Cardinale et al. 2012; Hooper et al. 2012). Consequently, the global extinction crisis not only represents the erosion of one of the most extraordinary features of Earth, but it is also intimately linked to human well-being and prosperity (MA 2005; Barnosky et al. 2012; Cardinale et al. 2012). The challenge of conserving biodiversity is daunting. Despite some local conservation gains, most indicators of the condition of global biodiversity show declines since the 1970's, while indicators of the threats to biodiversity all show increases (Butchart et al. 2010). Given concomitant increases in human population density and consumptive resources use, and the escalating pressure on biodiversity from climate change, expanding trade and expanding agriculture to improve human livelihoods (Butchart et al. 2010; Chown 2010; Tilman et al. 2011; Laurance et al. 2012; Lenzen et al. 2012), it seems likely that biodiversity loss will accelerate into the future (Pimm et al. 1995; Hoffman et al. 2010; Pereira et al. 2010). Despite this knowledge that the human enterprise is systematically eroding life on Earth (MA 2005; Chown 2010; Cardinale et al. 2012), there is still an incomplete understanding of how many species exist on Earth, let alone their life history characteristics, their patterns of spatial distribution and the processes responsible for those patterns (Hubbel 2001). The ruin of natural systems will perhaps never be fully comprehended without a broad understanding of how they are built (Ricklefs 1987).

One of the primary responses of humanity to address the global biodiversity crisis is the establishment and management of protected areas (PAs). Indeed, they are widely considered one of the bastions of conservation (Terborgh et al. 2002; DeFries et al. 2005; Naughton-Treves et al. 2005; Gaston et al. 2008a). Roughly 12% of the world's terrestrial surface is now classified as some form of PA following a global surge in their designation over the past century (Jenkins & Joppa 2009). PAs are vital to the global conservation portfolio and indeed are designated to serve a range of purposes. Protected areas do well at conserving habitat and stopping land clearing within their borders (Nagendra 2008; Gaveau et al. 2012). They can alleviate pressures on biodiversity (e.g. Craigie et al. 2010; Chown 2010), contribute to ecosystem goods and services provision (MA 2005), and deliver high economic return on investment to nations (Balmford et al. 2002; TEEB 2010). They have a major role in combating climate change in terms of avoided deforestation (Ricketts et al. 2010), and are essential scientific baselines to study natural species assemblages and

environments, and the effects of human impacts (Arcese & Sinclair 1997; Scholes & Biggs 2005).

However, the use of PAs as a conservation strategy does not come without controversy (see Lalasz et al. 2011). The designation of PAs has raised substantial criticism by infringing on the rights of indigenous people. Dowie (2009) estimated that almost half of terrestrial regions selected for conservation over the past century was either occupied or regularly used by indigenous peoples before PA proclamation, and often took place with forced removals of such peoples (du Toit et al. 2003; Dowie 2009; Lalasz et al. 2011). Furthermore, whether designated PAs even effectively protect biodiversity, meaning if they perform positively at the maintenance and representation of key biodiversity features (*sensu stricto* Gaston et al. 2008a), remains a complex question (Parish et al. 2003; Joppa et al. 2008). Two thirds of global PAs are insufficiently managed, lack funding and are consequently exploited, with a concomitant negative effect on biodiversity (Chape et al. 2005; UNEP-WCMC 2007). Many PAs are simply in the incorrect spatial position to capture the maximum number of species or species assemblages (Margules & Pressey 2000; Rodrigues et al. 2004), are inefficiently designated in terms of maximizing benefits to biodiversity (Fuller et al. 2010), or their political designations are ineffective for maintaining ecological processes within them (Liu et al. 2001; Curran et al. 2004). Designating a PA does not guarantee positive conservation outcomes. In Africa for example, a precipitous decline in large mammal assemblages has taken place inside PAs between 1970 and 2005, mainly due to anthropogenic threats (Craigie et al. 2010). Due to global change drivers, the continued performance of the global PAs network is uncertain, but it seems likely to be adversely affected, especially by climate change (DeFries et al. 2005; Hannah et al. 2007; Lee & Jetz 2007; Coetzee et al. 2009; Loarie et al. 2009 but see Hole et al. 2009).

In the face of the above criticisms a fundamental question is whether the designation of PAs is an effective conservation strategy in terms of conserving biodiversity. Therefore, comprehensive, evidence-based analyses of the performance of PAs are urgently required (Ferraro & Pattanayak 2006; Gaston et al. 2008a). Much attention has been given to testing their efficacy, meaning whether they actually conserve the species assemblages they are meant to (Gaston et al. 2008a; Caro et al. 2009; Greve et al. 2011; Laurance et al. 2012). One such approach is to compare biodiversity within PAs to areas outside of them, the argument being that higher biodiversity values indicate positive PA performance (Gaston et al. 2006).

However, the direction of the response can vary widely between PAs, with different studies finding both higher and/or lower biodiversity values across PAs (e.g. Caro et al. 2009; Laurance et al. 2012). Results from such studies suggest that PAs ecological performance is context-specific and can be influenced by several local factors (Gaston et al. 2006; Gaston et al. 2008a; Laurance et al. 2012). Greater richness or abundance of species assemblages found within and outside of PAs could arise for a variety of reasons. PAs could historically be located in areas of naturally higher (or lower) species richness/abundance, or the effects of altered management, land cover or reduced competition and predation, and their potentially synergistic effects, can confound inference (Gaston et al. 2008a). As a consequence, the generality of PAs efficacy in maintaining biodiversity across regions remains unclear.

The ecoinformatics revolution

Concern over rising pressures on the environment, uncertainty on the efficacy of conservation responses, and the consequences of biodiversity loss for human well-being has been met with increasingly sophisticated research methods. The field of 'ecoinformatics' has emerged to deal with the advances in information technology in terms of computing power and analytical techniques. One particular advance is that seemingly disparate databases can now be linked with names-based architecture, and it forms a central analytical technique of this thesis. As such, I here provide a succinct overview of advances in ecoinformatics as it pertains to the conservation scientist which describes the remit of the thesis in this rapidly advancing field.

Ecology and conservation science, like astro- or particle physics, is now truly moving into the realm of 'big data'. Large amounts of data are collected by remote-sensing platforms and sensor networks embedded in ecosystems worldwide. Dealing with the 'data deluge' is challenging, but ecoinformatics has emerged to deal with the synthesis of large volumes of data and represents the integration of ecology with the computer age. Its lies in the nexus between advances in computing and computer science, ecology, Geographic Information Science (GIS) and new quantitative methods in data gathering, relation and analysis. It is essentially a framework for scientists, and the public at large, to generate new knowledge through new and innovative tools for the discovery, management, integration and

preservation of biological and socioeconomic data, and to analyse and display the data in new and informative ways (Michener & Jones 2012). Recent special issues dedicated to ecoinformatics in both the *Journal of Vegetation Science* (Dengler et al. 2011) and *Trends in Ecology and Evolution* (Michener & Jones 2012), and a new dedicated journal, '*Ecological Informatics*', highlights the contemporary ecoinformatics revolution, and emphasizes its future role in ecology.

But what does the ecoinformatics revolution mean for conservation science? Many conservation scientists arguably already follow an ecoinformatics approach to their work, without necessarily realising the remit of the research or the opportunities for expansion. Here I briefly discuss six areas were an ecoinformatics approach is proving useful and its use being explored and expanded to advance the conservation agenda in: (1) using names-based architecture to link disparate databases (2) global change research (3) advances in taxonomy (4) conservation genetics (5) documenting functional and/or ecosystem services (6) monitoring conservation intervention effectiveness.

First, an ecoinformatics approach to conservation is actively employed to take advantage of names-based architecture. By using relational querying, disparate databases can now link via species names to advance our understanding of global change impacts on biodiversity (Patterson et al. 2010). The key here is the integration of various sets of information and techniques for analysis. Research that seeks to link broad conservation questions can now benefit from such names-based infrastructure (Patterson et al. 2010). 'Traditional' species level data, such as abundance, species richness and distributions can be interlinked with emerging information on species phylogenetics, physiology and other traits such as body size and ecosystem function. Together, these provide unprecedented level of resolution to spatial distribution of species and the mechanisms behind those patterns, the influence of human actions in terms of global change on those distributions, and projecting and anticipating future changes. For example, while latitudinal gradients in species richness are one of the oldest documented patterns in ecology and biogeography (Hawkins et al. 2001), its contemporary dynamics are poorly explored (Fisher et al. 2008; Fisher et al. 2010). Using seemingly disparate datasets on water temperature, species identity and fisheries independent trawling data, Fisher et al. (2008), showed temporal changes in a contemporary latitudinal gradient in fish and demonstrated how local environmental variations can alter such a relationship. The finding underscores the need to disentangle factors modifying such

patterns from those that create them, and the opportunities to do so using an ecoinformatics approach.

Second, the major use of ecoinformatics is arguably in global change research, and would here be most familiar to conservation biologists (i.e. Sala et al. 2000; Parmesan & Yohe 2003; Thomas et al. 2004). Advances and opportunities are apparent in climate change research in particular, indeed, in some regions climate change scenarios are now easier to obtain than species distribution data. Ecoinformatics provides the tools and frameworks to collect biodiversity and ecological data from many different sources and to detect, understand, forecast and ultimately counteract changes in biodiversity (see Dengler et al. 2011). New techniques combining a range of datasets have, for example, highlighted the velocity of climate change, or how quickly climate changes across landscapes at finer scales (Loarie et al. 2009). Increased concern has been raised on the variety of responses that species can take to climate change; given that factors like temperature variation and precipitation regimes can influence species responses above more typically used variables like average temperature (Sinervo et al. 2010; Clusella-Trullas et al. 2011). Also, current species distributions which are the major input into climate change projections (Thomas et al. 2004), could likely reflect environmental sorting due to phylogeny, rather than local adaptation (Kellerman et al. 2012). Taken together, these results mean that the next generation of climate change projection models will need to account for a range of climate velocities as well as species responses, traits and physiological differences (Huntley et al. 2010; Clusella-Trullas et al. 2011; Chown 2012). Consequently, synthesising trends in both time and space, and projecting complex changes requires permanent observations and the joint analysis of large time series data. By employing ecoinformatics approaches such as data exchange standards and networks, researchers can now move beyond individual case studies towards large scale synthesis of such trends (Dengler et al. 2011).

Third, taxonomy, the fundamental science for much conservation work, has particularly benefitted from an ecoinformatics framework since the launch of the Internet in the 1990's. Online repositories, such as Species 2000 and Catalogue of Life databases (Species 2000), store species descriptions and enable taxonomists to interact with the taxonomic data for all species and importantly 'forward link' those species to other relevant biological information (Bisby 2000). New taxonomic models even suggest online only electronic descriptions of species (Knapp 2010 and see Maddison et al. 2012). Citizen science projects too have and

continue to contribute to this framework, in that a range of digital technologies can produce user friendly tools for the identification of species that greatly enhance species identification in the field by non-specialists (Stevenson et al. 2003; Borrel 2007; Braschler 2009; Braschler et al. 2012; Hochachka et al. 2012).

However, to address the global Linnaean shortfall, Deans et al. (2012) suggest a transformation on the way species are currently described. Phenome annotations, or the verbal descriptions of species, are often unstandardised among taxonomists (e.g. using synonyms for body parts, or different descriptions for the same colours), which makes referencing database of such descriptions virtually impossible. By using semantic phenotypes, or standardised phenome annotations and descriptions following logical rules and referencing anatomy and trait ontologies, phenotype descriptions become computable and linkable to the wider world of digital data. The basic architecture to do so exists and is already in use, but requires a large commitment from taxonomists, to broaden the relevance and use of its outputs (Deans et al. 2012).

Fourth, genetic approaches are increasingly prominent in the conservation literature, including for systematic conservation planning (Forest et al. 2007), identifying species and populations facing extinction risk (Isaac et al. 2007) and identifying illegally traded species (see Ogden et al. 2009). With advances in rapid sequencing and non-invasive techniques, the potential utility of an ecoinformatics approach to incorporating genetic information lies in linking such data to other databases of interest via names-based infrastructure (see point one above). Lemmon et al. (2012) recently introduced a new method to vastly shorten rates of increasing genetic data by using specific probes in highly conserved loci of vertebrate genomes. The new method can accelerate the resolution of deep-scale portions of the Tree of Life and also resolve a large number of shallow clades (Lemmon et al. 2012). This creates a large potential utility to better understand the mechanisms responsible for structuring species assemblages, and the anthropogenic consequences of disaggregating such mechanisms (Cavender-Bares et al. 2009). It also aids in the identification of the spatial mismatches in conservation prioritisation between taxonomic, phylogenetic and functional diversity (Devictor et al. 2010).

Fifth, an ecoinformatics approach to conservation science is actively being used to describe ecosystem services and analyse the consequences of changes in biodiversity to those

services (Cardinale et al. 2012). A major need exists to understand the functional and ecosystem services consequences of biodiversity loss (Cardinale et al. 2012), especially since it seems to provide a conduit for mainstreaming conservation thinking into the socio-political arena (but see McCauley 2006 and Reid 2006). The landmark Millennium Ecosystem Assessment (MA 2005) collated and synthesized the implications of biodiversity declines for ecosystem services across the globe. Its successor, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES 2012), aims 'to bring information together and synthesize and analyse it for decision making'. To this end, the Assessment and Research Infrastructure for Ecosystem Services (ARIES 2012) project will build infrastructure to assist decision-makers and researchers through all phases of ecosystem service assessment and valuation. Their Ecosystem Services Database contains spatially-explicit, peer-reviewed valuation data as well as methods of analysis, visualisation, publications and projection models (ESD 2012). Together with names-based infrastructure mentioned above, conservationists are potentially in a position to document the consequences of biodiversity loss for ecosystem services, and consequently, the impacts thereof for human well-being.

Lastly, ecoinformatics is being actively used and can be harnessed in assessing and testing conservation effectiveness, and promoting evidence based conservation (Sutherland et al. 2004). As an example, Gibson et al. (2011) recently used meta-analysis, a technique originally designed for psychology and popular in medicine, to provide a global assessment of the impact of disturbance and land conversion on biodiversity in tropical forests. By synthesising data presented in 138 studies since 1975, they could for the first time analytically demonstrate the irreplaceability of primary forests for biodiversity conservation. Furthermore, scientific workflow software systems allows researchers to link together processes drawn from multiple and different ecosystems, and enable reproducible and iterative adaptive management as more data become available, to ensure evidence based interventions (Michener & Jones 2012). Ecological restoration projects too can also be continually evaluated to determine its effectiveness, at least in terms of the particular goals of the project. Region specific satellite data can also be used to assess conservation effectiveness in near real time similar to how the Satellite Sentinel project monitors evolving conflict in Southern Sudan (SPP 2012), for example, by assessing changes in tree cover due to logging.

Thesis outline

Overarching aim

In this thesis I study species assembly patterns and protected area efficacy in the face of the biodiversity extinction crisis using names-based architecture, a technique rooted in ecoinformatics. All chapters essentially use the same framework: To address the Chapters' aims, a variety of attributes for individual species, such as species traits, threat status or community parameters, are coalesced from a variety of opensource databases using names-based architecture in a relational database framework. As an indication of its potential utility across research disciplines relevant to conservation science, these case studies cover disparate fields such as establishing conservation evidence, community ecology, and biogeography.

Chapter structure and contents: Protected area efficacy

Given that the global efficacy of PAs is still much debated (Rodrigues et al. 2004; Gaston et al. 2008a; Caro et al. 2009; Lalasz et al. 2011; Laurance et al. 2012), and that the findings from comparisons of biodiversity inside and outside PAs do not generalise widely across regions and PAs (Gaston et al. 2008a; Caro et al. 2009; Laurance et al. 2012), **Chapter 2** follows a quantitative, global meta-analytical approach to synthesise such studies. My aim is to test the hypothesis that globally, PAs achieve significant conservation outcomes measured as higher biodiversity values compared with alternative land uses. Essentially, I tested the overall significance of terrestrial PAs for maintaining species assemblage values. I use three key biodiversity attributes: the abundances of individual species, assemblage abundances, and assemblage species richness. Meta-analysis is widely used to document quantitative trends in medicine and psychology, and its use has steadily permeated ecology (i.e. Osenberg et al. 1999; Gates et al. 2002; Borenstein et al. 2009). It combines results from many published studies to statistically calculate the 'effect size' value, which is a measure of the strength of the relationship between two sets of variables in a statistical population. It is considered a cost-effective and rapid method for generating robust estimates of current states of biodiversity (Côté et al. 2005). Meta-analysis has been used to estimate the status of Caribbean coral reefs (Gardner et al. 2003) and the effects of land cover change on

biodiversity in South East Asia (Sodhi et al. 2009) and in the tropics globally (Gibson et al. 2011).

To better investigate the mechanisms driving context specificity in PA efficacy (e.g. Caro et al. 2009), **Chapter 3** examines the efficacy of the Kruger National Park (KNP) protected area, by comparing birds inside and outside the KNP. Here, I use birds as a study exemplar since they are arguably among the world's best studied taxa (Şekercioğlu 2006). This means that much information is available on their life history, feeding ecology and morphometric characteristics, which can be 'forward-linked' with relational querying to data on species assemblage composition (Bisby 2000). The study area also has a particularly high avifaunal richness, and so observational data can be acquired relatively easily to increase statistical power. The aims are to: (1) compare avian species assemblage change inside and outside the KNP, and (2) investigate species life history, breeding, functional, and morphometric traits that are associated with the change in assemblage structure.

The study site surrounds the town of Phalaborwa, adjacent to the Kruger National Park (Figure 1; [-23°56'44''S; 31°9'56''E]), where I surveyed birds both inside and outside the KNP over a two-year period. It is a low summer rainfall region with precipitation varying around 460 mm to 480 mm per annum. Average winter temperatures range from 10.9 to 25.2 °C and average summer temperatures vary from 20 to 35 °C. The entire region has a history of low extractive land use by indigenous people (du Toit et al. 2003).

KNP was established in 1931 and although it is intensively managed, it represents a historically pristine and largely intact ecosystem (du Toit et al. 2003). The surrounding region, outside of KNP, is characterised by a rural land cover type where people mainly practice subsistence farming. The town of Phalaborwa was established in the 1950's to a serve the nearby copper mining operations, has a population of approximately 140 000, and is characterised by semi-urban households. These regions outside the PA are connected by an unfarmed habitat matrix under low utilization in terms of extractive use and grazing pressure.

The sampling area is within one vegetation type (Phalaborwa Sandy Mopaneveld; *sensu* Mucina & Rutherford 2006) and covers a relatively small spatial scale (~100 km^2), so other confounding variables which can affect bird species assemblages are minimized, such as latitude, altitude or environmental energy gradients. The Phalaborwa study site thus

provides a unique site to investigate comparisons of alterations in species assemblages inside and outside of a PA, as a consequence of intensifying land use change. The different land cover areas represent the extremes when moving from historically pristine to greatly transformed land cover types.

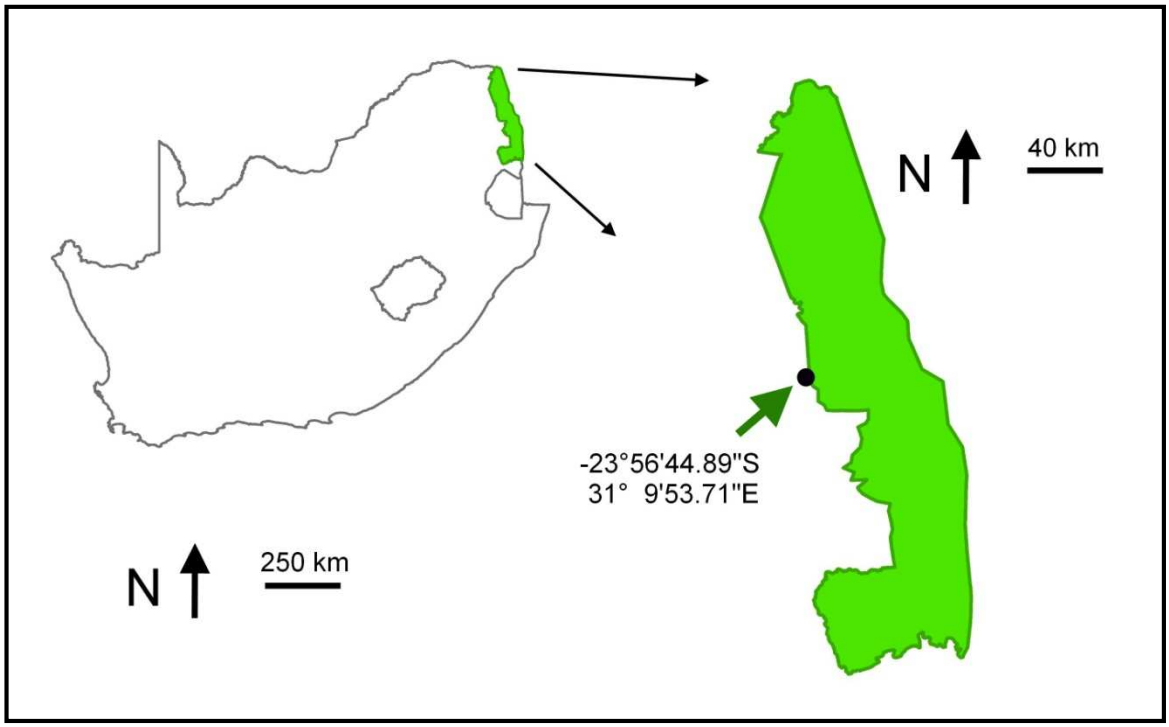

Figure 1. Location of the town of Phalaborwa in South Africa (green arrow) in relation to the Kruger National Park (green).

Habitat structure is known to drive bird species assemblages (Rompré et al. 2007), but since the study site is historically of a uniform and single habitat type of similar structure, any alteration to the habitat reflects anthropogenic alteration, and so is indicative of expected changes in birds assemblages with altered land use regimes outside the PA, at least in the region.

Chapter structure and contents: Body size and assembly patterns

Understanding the mechanisms that structure species assemblages is key to addressing a broad range of topics in ecology, such as species extinctions (Koh et al. 2004; Fritz et al.

2009), ecosystem food web structure (Petchey et al. 2008), invasion biology (Stachowicz et al. 2002), ecosystem functioning (Chapin et al. 2000) and ecosystem services (Kremen 2005; Egoh et al. 2009).

Figure 2. Aerial photographs of the four main habitat types surveyed for birds around the town of Phalaborwa (Chapter 2). (A) Kruger National Park, characterized by low human disturbance and grazing by large herbivores; (B) The suburban Phalaborwa town; (C) Rural land cover under a heavy grazing regime and high extractive use, where people mainly practice subsistence farming; (D) the surrounding habitat matrix, under low extractive use and under low grazing pressure. The flight was funded by the Bateleurs (2011).

Understanding how species assemblages are constructed can aid in anticipating the consequences of community disassembly by human activities (Ricklefs 1987). Community disassembly is particularly pronounced under anthropogenic alterations of the biosphere. In

the Sunda Shelf in Indonesia, terrestrial mammal communities have historically been reduced by extinction, with virtually no additions via colonization. The pattern indicates the influence of body size and other characteristics, such as habitat affinity and a species trophic status, can differentially affect a species susceptibility to extinction even under natural conditions (Okie & Brown 2009). However, this is of considerable concern since anthropogenic habitat fragmentation is globally prevalent and is a major cause of community disassembly (Lomolino & Perault 2000; Larsen et al. 2008). Similarly, invasive species can also rapidly disassemble communities, and also maintain such artificially structured community organizations over time (Sanders et al. 2003).

As a consequence, there is particular interest in how species traits relate to species assembly patterns (Larsen et al. 2008; Chown 2012; Luck et al. 2012). Body size is a fundamental trait of organisms, and influences many physiological and ecological traits (Gaston & Blackburn 2000). Since species extinction probabilities are also linked to body size (Gaston & Blackburn 1995; Gaston & Blackburn 1996; Fritz et al. 2009), investigations of spatial variation in body size have provided important insights into the ecological and evolutionary processes structuring biological assemblages, with considerable implications for conservation (Brown & Nicoletto 1991; Bakker & Kelt 2000; Gaston et al. 2008b). Species body size frequency distributions (BSFDs) form a significant means of understanding spatial variation in body size (Gaston & Blackburn 2000). Thus, determining the generality of BSFDs across taxa, regions, and spatial scales, and the mechanisms underlying deviations from general patterns are fundamental questions in macroecology (Gaston & Blackburn 2000). Although much is now known about general patterns in BSFDs at the broadest spatial scales (Blackburn & Gaston 1994; Roy et al. 2000; Smith et al. 2004), at smaller spatial scales the nature of variation in BSFDs and the mechanisms underlying this variation are not as comprehensively understood.

Since the work in Chapters 2 and 3 showed that species with certain traits, in this case large-bodied bird species, are at particular risk outside reserves under land transformation, in **Chapter 4** I describe and analyse the BSFDs (Brown & Nicoletto 1991; Bakker & Kelt 2000) of avian assemblages at several spatial scales in the Afrotropics, as far possible under natural conditions. In doing so, historical and contemporary mechanisms structuring this assemblage can be investigated and provide a platform for anticipating future changes and the consequences of species disassembly. In an increasingly transformed world, separating

“natural” historical and contemporary patterns and mechanisms structuring species assemblages, from those caused by anthropogenic processes, is of critical importance.

The analysis combines data on the body mass of 1960 species (Dunning 2008; Hockey et al. 2005), with species distribution data at the ecoregion level (Olson et al. 2001; WildFinder 2009), and is updated with modern taxonomy (Sinclair & Ryan 2003). I also test if the variation in median body size across assemblages at different spatial scales was related to environmental variables and whether purely stochastic processes could explain BSFDs.

A general synthesis of the main results of the pervious chapters and the implications thereof is provided in the concluding **Chapter 5**, and it discusses future research directions as a consequence of those results.

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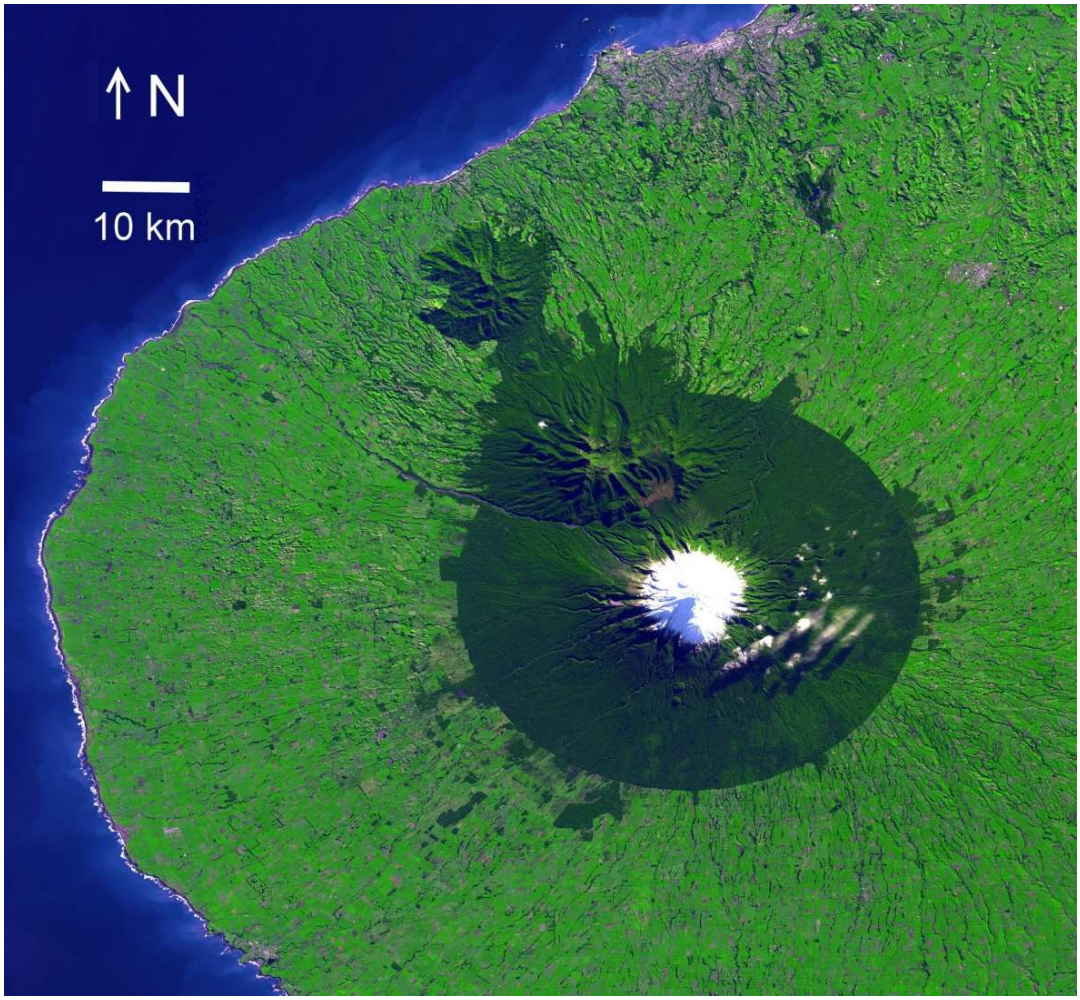
Chapter 2 – Protected areas achieve significant conservation outcomes[1]



A satellite image of Egmont National Park in New Zealand. The dark green natural vegetation of the Park contrasts starkly with the light green pastureland surrounding the protected area. Central coordinates: 39°18'1.38"S; 174°3'47.45"E. Image courtesy of NASA (www.nasa.gov).

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Main Text

Nearly 12% of the world's terrestrial surface is now classified as some form of protected area (PA; Jenkins & Joppa 2009). Indeed, the designation and maintenance of PAs are considered important to address the growing extinction crisis (Jenkins & Joppa 2009). Nonetheless, biodiversity loss continues unabated (Butchart et al. 2010), raising doubts about the efficacy of the global PA network for biodiversity conservation (Lalasz et al. 2011). These concerns have been amplified by evidence that: (i) in many cases PA systems are inefficiently planned in terms of maximising benefits to biodiversity (Margules & Pressey 2000; Rodrigues et al. 2004; Fuller et al. 2010), (ii) a high proportion of PAs are insufficiently funded and managed (Hockings 2003; Boitani et al. 2008); and (iii) even after designation PAs in some areas are threatened by habitat loss, over-exploitation and invasive species (Laurance et al. 2012) with concomitant declines in species populations (Craigie et al. 2010). Given the mounting pressure on biodiversity from alternative land uses to improve human livelihoods into a future of climate change (Butchart et al. 2010; Tilman et al. 2011; Laurance et al. 2012), comprehensive, evidence-based analyses of the performance of conservation interventions, like PAs, are urgently required (Ferraro & Pattanayak 2006; Gaston et al. 2008; Fuller et al. 2010).

Although assessments of PAs efficacy in maintaining biodiversity values have been undertaken previously, they have typically been restricted to small spatial scales and particular taxa (Caro et al. 2009; Greve et al. 2011), with no clear indication of the generality of their often contrasting outcomes (Gaston et al. 2008; Caro et al. 2009). Even those studies that are more extensive have retained a focus on specific areas, such as the tropics (Laurance et al. 2012) or particular taxa, such as mammals (Craigie et al. 2010). Nonetheless, negative pressures on biodiversity and evidence for population declines are global in extent (Butchart et al. 2010; Chown et al. 2012). In consequence, the overall significance of terrestrial PAs for maintaining biodiversity values remains unclear.

I address this question using a global, meta-analytical approach. Specifically, I assess the performance of terrestrial PAs, compared with areas in close proximity that are not protected (hereafter "NPAs"), using three key biodiversity attributes: the abundances of individual species (hereafter 'species abundances'), assemblage abundances (summed across species) and assemblage species richness. My assessment is based on 861 pairwise observations from 86 studies distributed amongst 32 countries and 57 PAs (Supplementary

Figure S1; Supplementary Appendix 1). I compare PA performance across (i) five major taxonomic groups (mammals, birds, herptiles [reptiles and amphibians combined due to low sample size], arthropods, plants), (ii) IUCN Protected Area Management Categories (a global PA categorisation system based primarily on their management objectives, in which categories 1-4 reflect stricter goals for biodiversity conservation [1 being the strictest], and 5-6 generally allow extractive use; IUCN UNEP 2012) and (iii) the status of species on the IUCN Red List (a global inventory of the threat status of species according to predetermined criteria; using IUCN 2012).

To compare the effect size between PAs and NPAs I calculated the unbiased Hedges g (Hedges g*), the difference between protected and non-protected comparisons means, standardised by the pooled standard deviation (Borenstein et al. 2009; Gibson et al. 2011). I used a random effects model (Borenstein et al. 2009), and set effect size as positive if biodiversity values for PAs were greater than for NPAs (Gaston et al. 2006). Using the usual metrics, my analysis is generally robust to publication bias (Supplementary Table S1; Supplementary Figure S2 and Supplementary Figure S3; see Materials and Methods).

The mean effect size using the random effects model, across all 861 comparisons, was 0.444 (95 % confidence intervals 0.324 – 0.564; Supplementary Table S2). Substantial variation was present in the direction and size of effects in response variables for different pairwise comparisons. However, when fitting the random effects model, PAs had higher species abundances (Figure 1A; n = 330), assemblage abundances (Figure 1B; n = 297) and assemblage species richness (Figure 1C; n = 234) than NPAs.

In general, PAs contain higher numbers of species and more individuals across all taxa. The effects were marked for birds, herptiles and arthropods, but less so for mammals and plants (Figure 1D-F). Small mammals show a smaller effect size for species abundance (< 1 kg; n = 25; 0.042; CI: -0.236 – 0.320), than do large mammals (> 1 kg; n = 114; 0.372; CI: 0.131 – 0.613), in keeping with other evidence that smaller mammals are typically better able to tolerate conditions outside PAs than are larger mammals (Woodroffe & Ginsberg 1998; Peres 2000; Gaston et al. 2008; Laurance et al. 2012).

While IUCN Category 2 PAs have a high positive effect size across response variables, Protected Area IUCN management status generally had no consistent influence on effect sizes (Figure 1G-I). Consequently, the relationship between the designated management

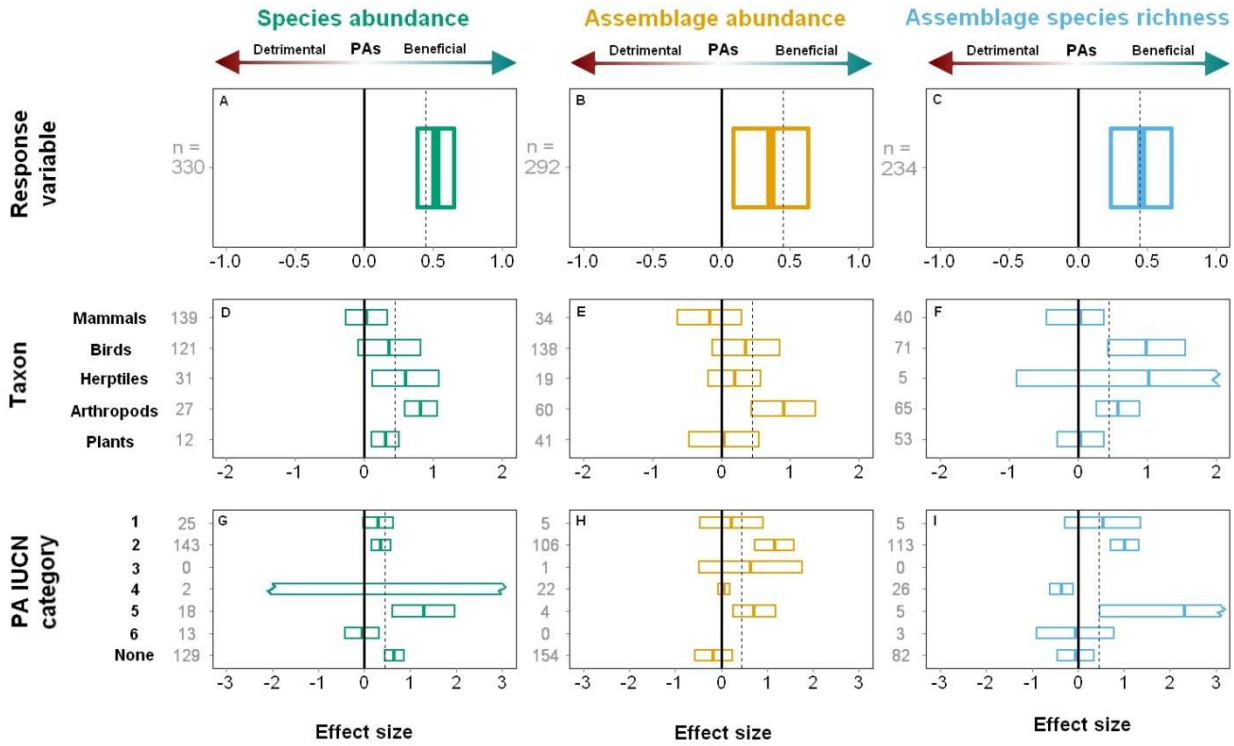

Figure 1. Effect sizes and 95% confidence intervals for response variables of overall species abundance, assemblage abundance and assemblage species richness, and by taxon and Protected Areas IUCN category. Positive boxplot values indicate a net positive impact of protected areas (PAs) on biodiversity. Samples sizes are in grey, the vertical black lines show a zero effect size, while the dashed lines in the upper panels show the overall effect size of 0.444 and in the lower panels effect sizes for corresponding response variables. Values for truncated bars with large variance due to low sample sizes are in Supplementary Table S2.

status of a PA and effective conservation of its biodiversity features is unclear, and affirms calls that IUCN PA management categories should be reassessed to reflect biodiversity outcomes rather than management objectives (Boitani et al. 2008).

Species generally had greater abundances inside than outside a PA relative to their Red List status in categories of Least Concern, Near Threatened, Vulnerable and Endangered. Six observations from one species (*Gorilla gorilla*) that is Critically Endangered were negative

(Figure 2). However, at least for species abundance, few data on those species of greatest conservation concern, as measured by their Red List status, are available (Figure 2). Indeed, published studies comparing the abundances of highly threatened species both inside and outside PAs are rare, and many such species do not occur in PAs (Gaston et al. 2008; Ricketts et al. 2005).

Although the positive effect of PAs generalises widely across taxa and the Red List status of species, further consistent patterns in effect size variation would provide further insight into the reasons for varying conservation efficacy. I used an information theoretic approach (Burnham & Anderson 2002) to investigate possible reasons for the variation in effect size, fitting three candidate models. Variables of the first model were those examined in our meta-analytical approach: taxon, PA management category and species Red List status. The second model examined geographical and historical descriptors of the PAs themselves (latitude, longitude, continent, PA age since establishment and PA size; hereafter the PA-model), while the third model examined the socio-economic conditions of the countries in which PAs are embedded (World Governance Index, Gross Domestic Product, Country Population size, Gini coefficient of family income per country, using the World Factbook 2012 and Worldbank 2012). The variation explained by these models was low, with the meta-analytical and socio-economic models each accounting for about 5% and 7%, respectively, of the variation in effect size. By contrast the PA-model accounted for 25% of the variation (Tables S3 and S4). This outcome suggests that while socio-economic factors clearly affect conservation outcomes in some regions (Balmford et al. 2001), they fare relatively poorly at explaining variation in the efficacy of PAs at retaining the biodiversity values measured here. Rather, the presence of PAs is significant, but that significance is influenced by geographical, ecological and historical contingency.

Conditions within and outside of PAs may differ starkly, and can also do so between different areas within PAs, as a consequence of variation in history, management and the incursion of external pressures (Gaston et al. 2006; Gaston et al. 2008; Laurance et al. 2012). During the literature search, I identified an additional 623 pairwise comparisons from 41 papers between sites within PAs only.

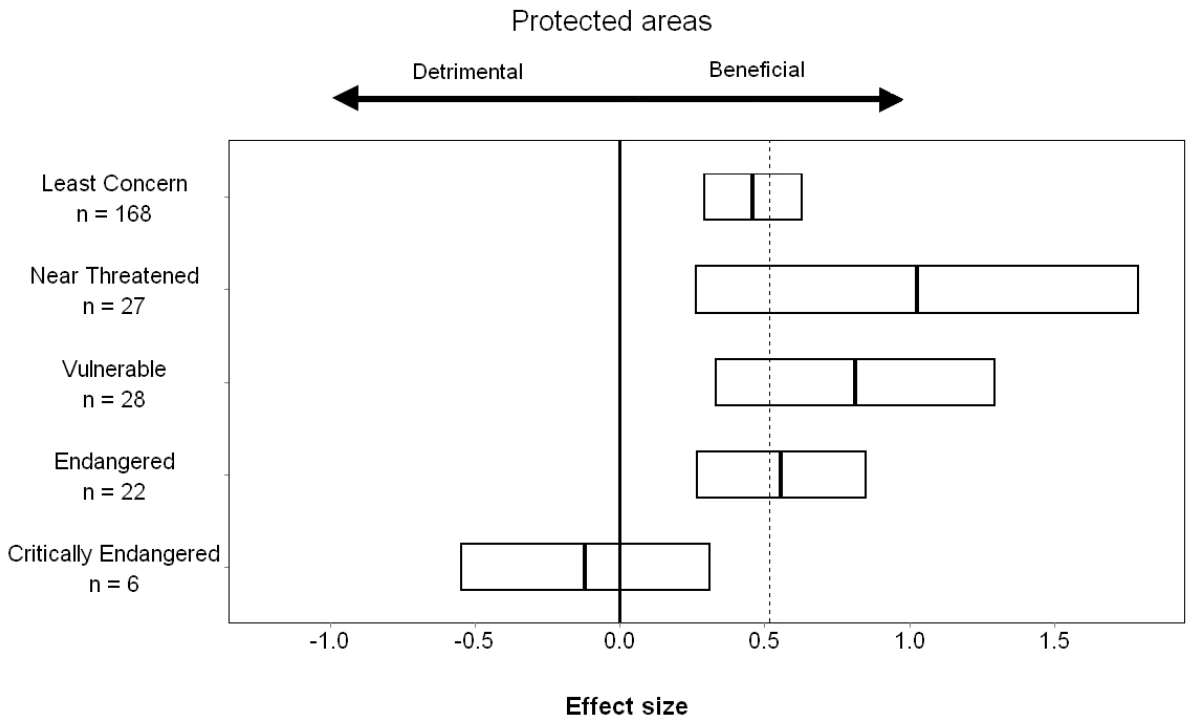

Figure 2. Effect sizes and 95% confidence intervals for species abundance responses by their IUCN Red List status. Positive boxplot values indicate a net positive impact of protected areas on species abundance. Note that multiple responses may be reported for one species (unique species = 168, total cases = 251) and taxonomic uncertainties, Not Evaluated and Data Deficient species are excluded (n = 79). The vertical black line shows a zero effect size while the dashed line indicates the overall effect size for species abundance responses (0.517). Taxa included mammals, birds, herptiles and plants.

These were typically in a pristine baseline site (as judged by the authors) and an anthropogenically disturbed area also inside the PA (disturbances such as logging, clearing or hunting pressure). The overall effect size from pairwise comparisons inside PAs only (0.172; 95% confidence intervals: 0.083 – 0.261) is lower than that of the inside and outside comparisons only (their 95% confidence intervals do not overlap), suggesting that PAs offset negative anthropogenic influences within their borders to a greater degree than no PA designation.

To address the potential spatial pseudoreplication in the dataset arising from multiple responses reported within studies (Gibson et al. 2011), PAs, countries or species, I recalculated effect sizes after sampling one pairwise comparison only per study, PA, country or species, respectively. This resampling was repeated 10 000 times for each of these four parameters and the estimated mean and 95 % confidence interval thereof compared with the overall effect size. These effect sizes remained positive and overlapped with the overall effect size for both PA-NPA and inside PA only comparisons, but were less positive for species responses (Supplementary Table S5). The variance of these resampled effect sizes also increased, but I note that effect size precision increases with the addition of more data (Supplementary Figure S3). A similar resampling procedure selecting one pairwise comparison per study also confirmed the findings from the explanatory models (Supplementary Table S4). Thus, the present results overall can be considered robust to any pseudoreplication. At least some of the variation in effect sizes may also be accounted for by the scale over which studies are conducted. However, distance among comparison sites explains only *c*. 1% of the variation in effect size for studies included in my meta-analysis where appropriate data were reported (Supplementary Table S6). Indeed, despite being significant the relationship between effect size and the greatest distance between comparison sites is weak (Pearson's $r = 0.146$; $p < 0.001$) as is the relationship with distance to PA boundary ($r = 0.081$; $p < 0.05$). In consequence, the extent of site matching, which may play a role in increasing estimates of PA efficacy outcomes in some cases (Andam et al. 2008), is unlikely to be influencing substantially the outcomes of our analyses. The small amount of deviance explained (25%; Supplementary Table S3) when the geographic context of the PAs is used to explore effect size variation is likewise supportive of this conclusion.

Several factors might account for higher species abundances, assemblage abundances, and species richness inside compared with outside PAs. These include: (i) the persistence of existing differences in abundance and richness between the areas at the time of PA designations, as a result of the choice of location; (ii) lower levels of threatening processes, like habitat alteration or exploitation, inside PAs than have prevailed elsewhere; and/or (iii) active management of PAs to maintain or increase abundance and richness relative to NPAs (Gaston et al. 2008). The relative importance of each mechanism is challenging to determine, but varies widely amongst PAs (Gaston et al. 2006; Andam et al. 2008; Gaston et al. 2008; Laurance et al. 2012). Clearly, the extent to which PAs stem the erosion of

biodiversity of any given area may vary considerably, as has been demonstrated here and in region-specific studies (Laurance et al. 2012). However, it would seem that irrespective of how these factors relate to PA proclamation, my quantitative data show that globally, PA establishment itself confers a net benefit to biodiversity. That is, the abundance of individual species, including several of those on the IUCN Red Lists, assemblage abundance, and assemblage species richness are all typically higher inside than outside PAs across a suite of representative terrestrial biodiversity. This outcome is encouraging given the global scale of threat to biodiversity (Butchart et al. 2010), and indications that Marine Protected Areas may be similarly effective (Halpern & Warner 2002). Thus, better protection and management of those PAs that are already in place and careful planning of new PAs (Margules & Pressey 2000; Fuller et al. 2010; Laurance et al. 2012; Gaston et al. 2008), will help safeguard biodiversity into the future.

Methods

I searched Web of Science, Scopus, and Google Scholar for relevant papers published from 1975-2011, and their references, and included those reporting pairwise comparisons of biodiversity measurements either inside and outside protected areas (PAs) or between areas within PAs. Three response variables were captured: (i) species abundances (where taxonomy was resolved to the species level), or comparisons of (ii) abundances per assemblage or (iii) species richness per assemblage, following Gibson et al. (2011). WebPlotDigitizer v2.4 (Rohatgi 2012) was used to capture data from figures. Data on demographics or community structure were omitted, as the direction of the expected response was not straightforward to interpret. I then calculated Hedges g* across pairwise comparisons and calculated the average effect size using the random-effects model (Gibson et al. 2011), with a maximum likelihood variance estimator in the “metaphor” package (Viechtbauer 2010) in R (R Development Core Team 2012). Effect sizes were fit for all data, response variables, taxon, PA IUCN management status (IUCN UNEP 2012) and species Red List Status (IUCN 2012). Effect sizes for PAs with no IUCN category designation were lower than those with a designation, but remained positive and overlapped with the overall effect size and so I included them here (Supplementary Table S2). Studies that reported across clusters of PAs rather than individual PAs remained positive and were thus included (Supplementary Table S2). I also performed three tests for publication bias (Supplementary

Table S1; Supplementary Figure S2 and Supplementary Figure S3), and assessed possible influence of pseudoreplication across studies, species, countries, and PAs with a resampling procedure for both PA-NPA and PA only comparisons, following Gibson et al. (2011). I used an information theoretic approach to assess the influence of a candidate set of models and variables to explain the variation in effect size, where data were available for all variables (Burnham & Anderson 2002). Models tested the influence of (i) pre-planned subgroups in the meta-analysis (variables: response variable, taxonomic group, PA IUCN Category using IUCN UNEP 2012), (ii) design, location and structural attributes of the PAs (variables: continent, latitude, longitude, PA area in km^2, and PA establishment date; using IUCN UNEP 2012) and (iii) influence of socio-economic conditions of the countries in which PAs are located (variables: World Governance Index, Gross Domestic Product, Country Population size and Gini coefficient of income inequality using the World Factbook 2012 and Worldbank 2012). An exhaustive search approach, with a GLM fit assuming a Gaussian distribution with a log link function, using the "glmulti" package (Calcagno & Mazancourt 2010), showed that models had generally poor explanatory power (Supplementary Table S3), and there were multiple competing explanatory models (Supplementary Table S4). Furthermore, to address possible pseudoreplication, one pairwise comparison per study was selected at random and the respective GLM model fit as above. I selected the highest ranked model based on the Akaike Information Criterion, and repeated this procedure 1000 times, to calculate the proportionally highest ranked model for each candidate dataset (Supplementary Table S4). All 127 studies included in the meta-analysis are referenced in Supplementary Appendix S1.

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Supplementary Material

Supplementary Table 1. Orwin's *Fail safe N* is 1238 to reach an overall effect size of 0.222, meaning that 1238 pair-wise comparisons with null results on average would have to be added to reduce the observed effect size by half (Borenstein et al. 2009; Viechtbauer 2010), which even in that hypothetical event would nonetheless remain a positive value.

Overall effect size	Overall sample size	Target effect size	Orwin's *Fail safe N*
0.444	861	0.222	1238

Supplementary Table 2. Effect sizes (ES), lower bound (lb CI) and upper bound (ub CI) confidence intervals and sample sizes (N), for pairwise comparisons at different subgroup designations. PA = Protected area.

Description	Subgroup	ES	lb CI	ub CI	N
Overall	Inside Outside PAs	0.444	0.324	0.564	861
Overall	Comparisons inside PAs only	0.172	0.083	0.261	623
Overall	PAs with IUCN designation	0.621	0.488	0.755	496
Overall	PAs with no IUCN designation	0.161	-0.050	0.372	365
Overall	Clusters of PAs	0.560	0.400	0.719	189
Overall	Unique PAs identified	0.413	0.264	0.562	672
Response variable	Species abundance	0.517	0.382	0.652	330
Response variable	Assemblage abundance	0.349	0.083	0.615	297
Response variable	Assemblage species richness	0.457	0.238	0.676	234
Response variable	Species abundance (inside only)	-0.086	-0.235	0.063	295
Response variable	Assemblage abundance (inside only)	0.165	0.044	0.286	152
Response variable	Assemblage species richness (inside only)	0.529	0.364	0.694	176
Taxon	Species abundance - Mammals	0.305	0.106	0.504	139
Taxon	Species abundance - Birds	0.822	0.588	1.056	121
Taxon	Species abundance - Herptiles	0.606	0.123	1.088	31
Taxon	Species abundance - Arthropods	0.364	-0.085	0.812	27
Taxon	Species abundance - Plants	0.035	-0.263	0.334	12
Taxon	Assemblage abundance - Mammals	-0.109	-0.523	0.305	37
Taxon	Assemblage abundance - Birds	0.343	-0.141	0.826	140
Taxon	Assemblage abundance - Herptiles	0.196	-0.187	0.579	19
Taxon	Assemblage abundance - Arthropods	0.906	0.440	1.371	60
Taxon	Assemblage abundance - Plants	0.044	-0.466	0.554	41
Taxon	Assemblage species richness - Mammals	-0.036	-0.453	0.380	40
Taxon	Assemblage species richness - Birds	0.994	0.434	1.554	71
Taxon	Assemblage species richness - Herptiles	1.027	-0.885	2.940	5
Taxon	Assemblage species richness - Arthropods	0.576	0.261	0.891	65
Taxon	Assemblage species richness - Plants	0.041	-0.299	0.382	53
PA IUCN Category	Species abundance - 1	0.304	-0.025	0.632	25
PA IUCN Category	Species abundance - 2	0.364	0.157	0.572	143
PA IUCN Category	Species abundance - 3	No data	No data	No data	0
PA IUCN Category	Species abundance - 4	6.148	-5.557	17.853	2
PA IUCN Category	Species abundance - 5	1.291	0.617	1.965	18
PA IUCN Category	Species abundance - 6	-0.041	-0.411	0.328	13
PA IUCN Category	Species abundance - None	0.653	0.440	0.866	129
PA IUCN Category	Assemblage abundance - 1	0.220	-0.466	0.905	5
PA IUCN Category	Assemblage abundance - 2	1.096	0.694	1.499	111

PA IUCN Category	Assemblage abundance - 3	0.646	-0.473	1.764	1
PA IUCN Category	Assemblage abundance - 4	0.063	-0.059	0.185	22
PA IUCN Category	Assemblage abundance - 5	0.720	0.264	1.176	4
PA IUCN Category	Assemblage abundance - 6	No data	No data	No data	0
PA IUCN Category	Assemblage abundance - None	-0.164	-0.573	0.244	154
PA IUCN Category	Assemblage species richness - 1	0.536	-0.287	1.359	5
PA IUCN Category	Assemblage species richness - 2	1.012	0.704	1.321	113
PA IUCN Category	Assemblage species richness - 3	No data	No data	No data	0
PA IUCN Category	Assemblage species richness - 4	-0.361	-0.611	-0.111	26
PA IUCN Category	Assemblage species richness - 5	2.321	0.480	4.163	5
PA IUCN Category	Assemblage species richness - 6	-0.056	-0.899	0.786	3
PA IUCN Category	Assemblage species richness - None	-0.059	-0.455	0.338	82
IUCN Red List	Not Evaluated	0.596	0.234	0.957	62
IUCN Red List	Data deficient	-0.479	-1.170	0.212	6
IUCN Red List	Least Concern	0.460	0.291	0.628	168
IUCN Red List	Near Threatened	1.027	0.262	1.791	27
IUCN Red List	Vulnerable	0.814	0.333	1.294	28
IUCN Red List	Endangered	0.557	0.266	0.848	22
IUCN Red List	Critically Endangered	-0.119	-0.548	0.311	6
	Small mammals	0.042	-0.236	0.320	25
	Large mammals	0.372	0.131	0.613	114

Supplementary Table 3. Best GLM models by exhaustive fit for the Meta Analysis model, Protected Areas (PA) model and Socio-Economic model, respectively. The models were constructed across pairwise comparisons where data were available, and excluded data where results were reported across clusters of PAs as explanatory data could not be obtained for them. Variables: *pa_iucn_cat* = protected area IUCN category; *area* = area of the PA in km^2; *PA age* = establishment year of the PA; c*ontinen*t = continent in which the PA is embedded. *wgi* = World Governance Index; *gini* = Gini coefficient; *popsize* = country human population size; *gdp* = Gross Domestic Product. Interactions between terms are shown by " : ".

Meta Analysis - model

	n = 861		
	Deviance explained		5.17%
Variables:	Slope	SE	P
Intercept	**3.68**	**0.002**	***
pa_iucn_cat	0.008	0.002	***
pa_iucn_cat:birds	0.0007	0.0027	
pa_iucn_cat:herptiles	0.0007	0.00379	
pa_iucn_cat:mammals	-0.0087	0.002667	**
pa_iucn_cat:plants	-0.0108	0.00291	***

Protected Areas - model

	n = 527		
	Deviance explained		25.03%
Variables:	Slope	SE	P
Intercept	**4.204**	**0.307**	***
continent.Australia	-0.136	1.561	
continent.Europe	8.028	3.312	*
continent.North America	0.068	0.016	***
continent.South America	1.690	1.050	
latitude	-0.003	0.002	
area	0.001	0.001	*

PA age	-0.001	0.001	
area:longitude	-0.001	0.001	*
continent.Asia:area	0.001	0.001	**
continent.Europe:area	-0.001	0.001	
continent.North America:area	-0.001	0.001	
continent.South America:area	-0.001	0.001	*
continent.Asia:PA age	0.001	0.001	
continent.Europe:PA age	-0.003	0.001	*
continent.South America:PA age	-0.001	0.001	

Socio Economic - model

	n = 769		
	Deviance explained		7.41%
Variables:	Slope	SE	P
Intercept	**3.665**	**0.012**	***
gdp	0.001	0.001	*
gini	0.001	0.001	*
gdp:wgi	-0.001	0.001	**
gini:popsize	-0.001	0.001	***
wgi:popsize	0.001	0.001	***

Significance codes: *** = p < 0.0001; ** = p < 0.001 ; * = p < 0.05

Supplementary Table 4. Proportion of five highest ranked models for Meta Analysis model, PA model and the socio-economic model. One pairwise comparison per study was selected, and the respective GLM model fit as in Supplementary Table S3. I selected the highest ranked model based on the Akaike Information Criterion, and repeated this procedure 1000 times, to calculate the proportionally highest ranked model for each candidate dataset. Number and proportion of remaining models that were selected as the highest ranked model at least once is shown in italics. *wgi* = World Governance Index; *gini* = Gini coefficient; *popsize* = country human population size; *gdp* = Gross Domestic Product; *null* = Intercept only model, and see legend in Supplementary Table S3.

Model type	**Model formulae**	**Proportion as top ranked model**
Meta analysis	Null	0.529
Meta analysis	pa_iucn_cat	0.362
Meta analysis	Metric	0.071
Meta analysis	1 + pa_iucn_cat + metric:pa_iucn_cat	0.024
Meta analysis	1 + metric + pa_iucn_cat + metric:pa_iucn_cat	0.005
Meta analysis	*Remaining models (5)*	*0.009*
Protected areas	area_km2 + pa_age + continent:area_km2	0.066
Protected areas	continent + pa_age + continent:pa_age	0.064
Protected areas	continent + lat + pa_age + continent:pa_age	0.058

Protected areas	continent + lat + area_km2 + pa_age + pa_age:area_km2 + continent:pa_age	0.049
Protected areas	continent + pa_age	0.047
Protected areas	*Remaining models (141)*	*0.716*

Socio-Economic	Wgi	0.209
Socio-Economic	Null	0.151
Socio-Economic	popsize:gini + wgi:popsize	0.135
Socio-Economic	gdp + wgi + popsize:gini + wgi:gdp + wgi:popsize	0.069
Socio-Economic	Gini	0.054
Socio-Economic	*Remaining models (61)*	*0.382*

Supplementary Table 5. Effect sizes determined by resampling one pairwise comparison per unit of study, per species, per country and per protected area (PA), to assess the potential spatial pseudoreplication in our dataset arising from multiple responses. These randomisations were repeated 10 000 times for each of these four parameters and the estimated mean and 95% confidence interval thereof compared to the overall effect size for all data for both pairwise comparisons inside and outside PAs and also for those within PAs only.

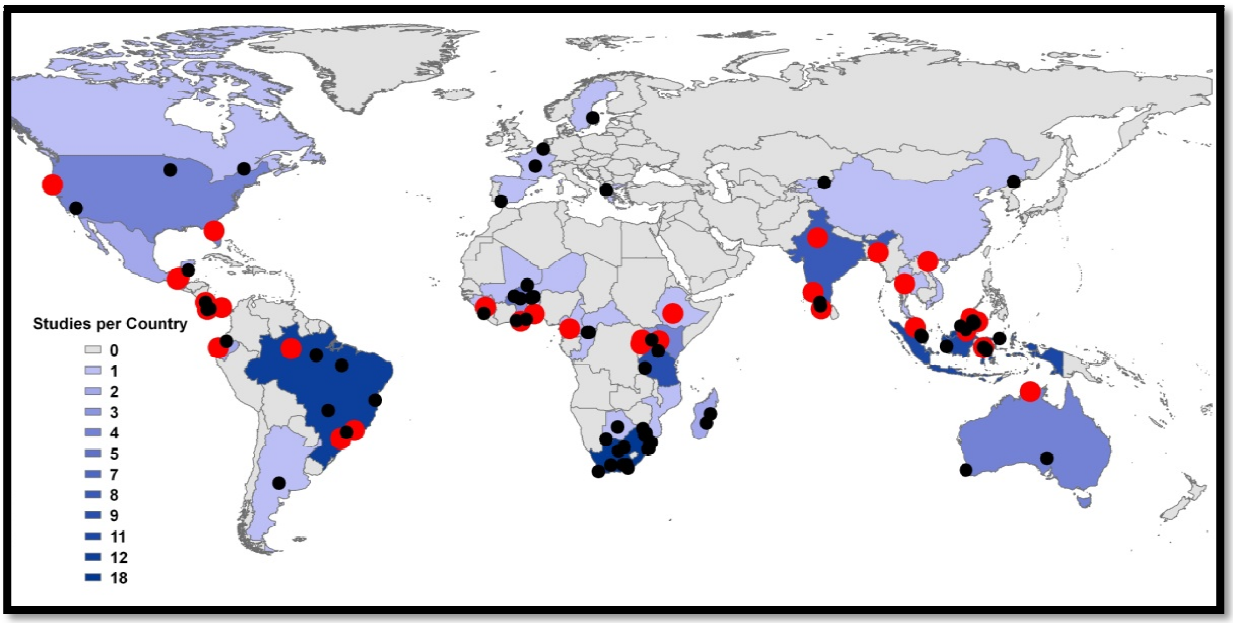
*The resampling by country for inside PA comparisons only used a Hunter-Schmidt estimator since the maximum likelihood estimator could not converge at such a low sample size (see Viechtbauer 2010).

Comparison	Resample unit	Effect size	Lower CI	Upper CI	N
Inside Outside PA	*All data*	*0.444*	*0.324*	*0.564*	*861*
Inside Outside PA	Study	0.591	0.240	0.941	86
Inside Outside PA	Species	0.502	-0.011	0.654	241
Inside Outside PA	Country	0.674	-0.021	1.359	32
Inside Outside PA	Protected Area	0.827	0.317	1.337	57
Within PA only	*All data*	*0.172*	*0.083*	*0.261*	*623*
Within PA only	Study	0.194	0.004	0.385	43
Within PA only	Species	-0.212	-0.364	-0.061	186
Within PA only	Country*	0.104	-0.200	0.408	20
Within PA only	Protected Area	0.237	0.024	0.451	35

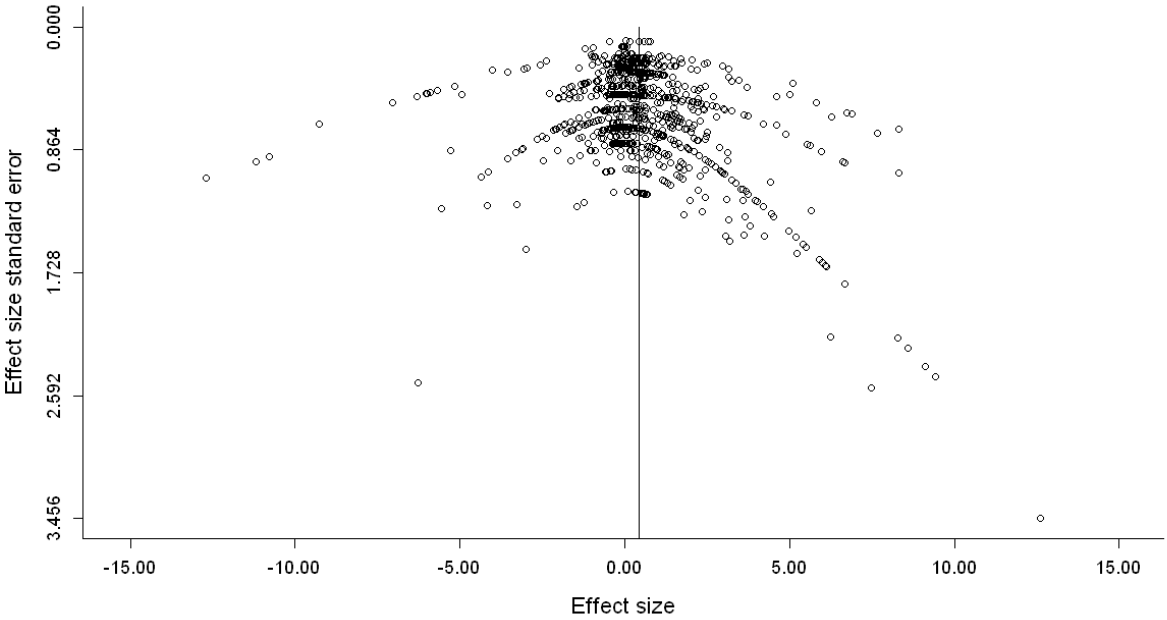
Supplementary Table 6. Best GLM model by exhaustive fit for two variables, the maximum distance to protected area boundary within studies, and the maximum distance between pair wise comparisons within studies, meaning, within each study, the maximum distance between sampling points assigned to all points in that study. The models were constructed across pairwise comparisons where data were available. Only the distance between comparisons enters the model as an explanatory variable.

	Distance between pair wise comparisons		
	n = 569		
	Deviance explained		1.00%
Variables:	Slope	SE	P
Intercept	**3.67**	**0.001**	***
Distance between comparisons	0.001	0.001	*

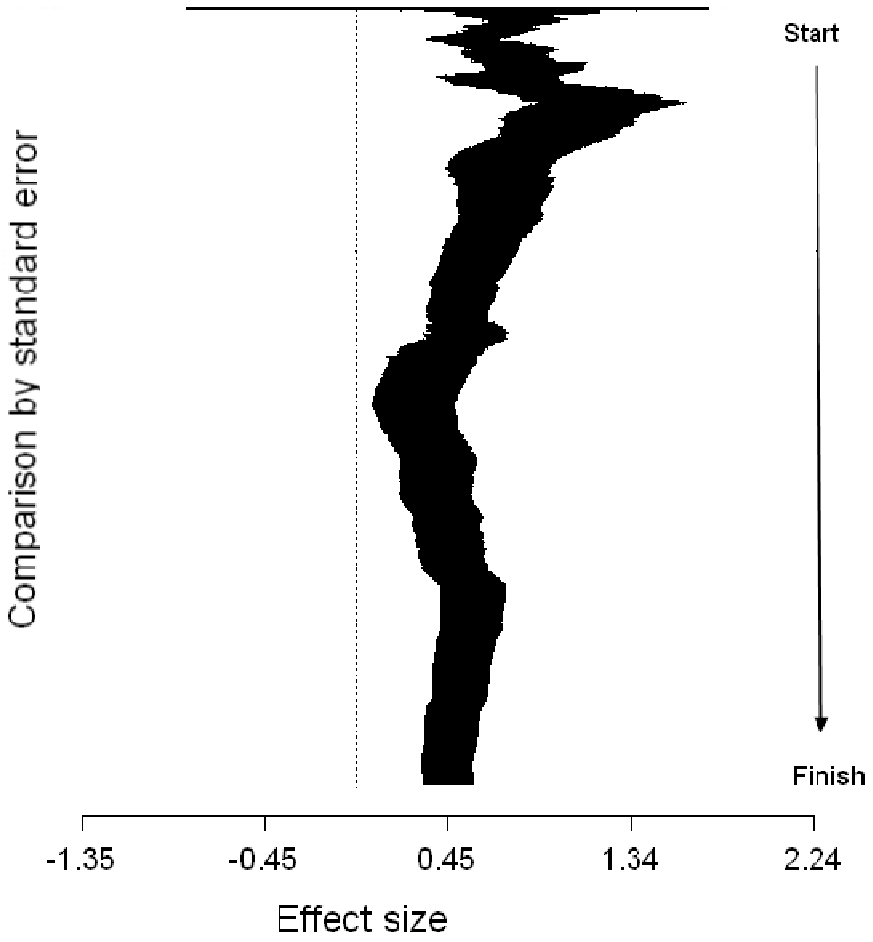
Significance codes: *** = p < 0.0001; ** = p < 0.001 ; * = p < 0.05



Supplementary Figure 1. Map of the study sites by the centroid coordinates of protected areas for inside-outside pairwise comparisons (black dots; n = 71) and inside only comparisons (red dots; n =32). Both categories include data where studies reported across clusters of Protected Areas.



Supplementary Figure 2. Funnel plot of effect size standard error plotted against effect size for all inside-outside pairwise comparisons. The relatively symmetrical plot suggests that those studies with small (or negative) effect sizes are not necessarily published at a lower frequency, so publication bias in our study can be considered slight (Borenstein et al. 2009). The solid reference line indicates the overall effect size of 0.444 (n = 861). A funnel plot assumes that studies with the largest sample sizes will have lower standard error, and so will be near the average effect size, while studies with smaller sample sizes will be spread on both sides of the average effect size. Variation from this assumption can indicate bias. For example, positive asymmetry can indicate bias, in that those studies which found that PAs are effective where submitted and/or accepted for publication.



Supplementary Figure 3. Cumulative meta-analysis of the dataset sorted by precision, with effect sizes and 95% confidence intervals (n = 861). The analysis starts with the comparison with the largest standard error, after which the comparison with the next largest standard error is added and the effect size is recalculated, and so continues iteratively until the analysis finishes with the comparison with the lowest standard error (Borenstein et al. 2009; Viechtbauer 2010). Essentially, the graph allows inspection of the development of the observed effect size with the addition of more precise data. The dotted line equals zero, or no effect. While the addition of the most imprecise studies does initially cause the cumulative effect size to decrease, it remains positive and does not overlap with zero at any point after the addition of the more precise studies, which reaffirms that the impact of publication bias in my study is negligible (Viechtbauer 2010).

Supplementary Appendix 1. Reference list of all 127 papers included in the meta-analysis for both inside-outside and inside only comparisons.

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Chapter 3 – Which species traits are at risk outside of protected areas? A test with South African avifauna[2]

A selection of species from the study region shows a diversity of species traits, here in terms of body mass and beak morphology. Clockwise from top left are: European Roller, Southern Yellow-billed Hornbill*, African Hoopoe* and Little Bee-eater*.

[2] For submission as "**Coetzee, B.W.T.**, Chown, S.L. 2012. Which species traits are at risk outside of protected areas? A test with South African avifauna." *Conservation Biology.*

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Introduction

The designation of protected areas (PAs) is a major global strategy to avert the biodiversity extinction crisis. However, global biodiversity loss continues unabated (Butchart et al. 2010), questioning the effectiveness of the global protected areas network at biodiversity conservation (Lalasz et al. 2011). Consequently, much attention has been given to testing the efficacy of protected areas. That is, whether they actually conserve the biodiversity features they are meant to (Gaston et al. 2008a; Laurance et al. 2012). One method to assess the efficacy of protected areas at the local scale is to compare biodiversity features within PAs with those outside them (Gaston et al. 2006; Gaston et al. 2008a). However, the direction of the response can vary substantially between PAs (e.g. Caro et al. 2009; Laurance et al. 2012). Species richness and abundance can be greater inside than outside PAs (e.g. Greve et al. 2011). Conversely, species richness, abundance and/or biomass can be greater outside than inside PAs (Caro 2002; Smart et al. 2005; Rannestad et al. 2006), or there may be no significant difference (Caro 2002; Smart et al. 2005). These results suggest that PA efficacy is context-specific, and can be influenced by a variety of local factors (Gaston et al. 2006; Gaston et al. 2008a; Caro et al. 2009; Laurance et al. 2012).

Comparisons of biodiversity inside and outside of PAs may also detect changes in other measures of biodiversity composition, since habitat alteration can non-randomly affect species with specific traits as they respond to changing environmental conditions (Schweiger et al. 2007). Trait-based analyses relate species traits to environmental conditions, and so enable the identification of those traits which most strongly mediate responses (Luck et al. 2012). Analyses of species traits in response to land use change can inform a predictive understanding in terms of conservation for identifying at-risk species in an increasingly transformed world (Newbold et al. 2013). Birds in particular respond strongly in terms of species traits to changes in land use (Newbold et al. 2013). Since the loss of species with particular traits may influence the delivery of ecosystem services, understanding the responses of species to land use change has important consequence for understanding ecosystem functioning (Şekercioğlu et al. 2004; Şekercioğlu 2006; Luck et al. 2012; Newbold et al. 2013).

Previous work has shown that large frugivorous or insectivorous are both less likely to occur and less abundant in more intensively used habitats in the worlds tropics (Newbold et al.

2013). Species resource use and dispersal limitation explained declines in local hoverfly communities in response to changes in land cover across Europe (Schweiger et al. 2007). Medium-sized bird species with both short incubation and fledging periods fair relatively poorly in farmland areas across North America and Europe (Pocock et al. 2010). As for the impacts of species traits measured inside and outside of PAs, the abundance of large-bodied mammal species are reduced outside of PAs primarily through human-wildlife conflicts (Woodroffe & Ginsberg 1998) as is the abundance of large-bodied bird species (Herremans & Herremans-Tonnoeyr 2000). Dietary specialization, habitat affinity, and body mass determined the distribution of bird species in forest fragments within and outside a South African protected area (Neuschulz et al. 2012). Greve et al. (2011) assessed bird assemblages inside and outside of three PAs in South Africa and found that species composition and functional diversity, but not body size, are reduced or altered outside of PAs in transformed landscapes. Certain functional groups such as granivores, frugivores and mixed feeders may benefit in response to favourable anthropogenic alterations of their habitat through agricultural or urban conversion (e.g. Clergeau et al. 1998). Understanding which groups, or which traits, are particularly at risk outside of PAs has implications for ecosystem functioning (Şekercioğlu et al. 2004; Şekercioğlu 2006; Luck et al. 2012) and effective conservation management, both in terms of current processes and predicting future extinction risk (Lee & Jetz 2011).

To further explore these complexities, here, I assess avian assemblage change across the boundary of the Kruger National Park (KNP), one of the world's premier PAs, using an explicit, traits-based approach. My aim is to: (1) compare avian assemblage change among land use types including the protected area; (2) investigate species morphometric, feeding functional and nesting traits that might be strongly associated with and perhaps mediate the response to changes in assemblage structure among land use types. I focus on three different land cover types outside the PA, in comparison to inside the KNP (hereafter 'protected'). First, an urbanized area mainly characterised suburban houses, tar roads and a few commercial buildings (hereafter "urban"). The impact of urbanization on biodiversity is an important concern globally. It is the world's fastest growing land use (UN 2007), and can significantly affect biodiversity, particularly in replacing native species with those that are well adapted to human-dominated landscapes (Clergeau et al. 1998; McKinney 2006; Kark et al. 2007; van Rensburg et al. 2009; Evans et al. 2011). Second, a subsistence farming region

where humans typically produce crops or raise livestock primarily for their own consumption, and under heavy grazing from cattle and goats (hereafter “rural”). Subsistence farming forms a significant land use especially in sub-Saharan Africa as almost 65% of its population (640 million people) is dependent on rural land for as the primary supporter of livelihood (IFPRI 2004). It is the dominant land use outside the borders of many African PAs, particularly KNP (du Toit et al. 2003). The third land cover type is the connecting habitat matrix between rural and urban land cover types, which here is characterised by currently unfarmed, unprotected land under low extractive use and with minimal grazing impact (hereafter “matrix”). In southern Africa in particular, such areas under low extraction contain almost the same level of biodiversity as PAs, and preventing their degradation may prevent biodiversity loss (Scholes & Biggs 2005).

All sampling was located within one historically intact vegetation type (Phalaborwa Sandy Mopaneveld; *sensu* Mucina & Rutherford 2006), distributed both inside and outside the PA. As a consequence, a major strength of the study is that it specifically controls for a range of potentially confounding variables that may influence avian assemblage structure. As a consequence, changes in assemblages should largely reflect anthropogenic alteration to the landscape outside the KNP by comparison with the situation inside the PA, rather than varying original vegetation types, energy availability and other variables that influence avian assemblages (e.g. Van Rensburg et al. 2002; Pautasso et al. 2011). Importantly, the analysis then combines examinations of both the influence of PA effectiveness in terms of land use change, and goes a step further in relating species traits to the influence of land use change, so that a better trait based understanding can be made to predict species vulnerability outside PAs.

While the direction of the expected response is not necessarily straightforward to predict (Laurance et al. 2012), I hypothesize, in keeping with general global trends, that both higher species richness and abundance will be found inside the PA (Caro 2002; Sinclair et al. 2002; Thiollay 2006; Thiollay 2007; Devictor et al. 2007; Greve et al. 2011 and see Chapter 2). Furthermore, I hypothesize that feeding guilds may be much affected, in particular that insectivores will be reduced outside the KNP, but that mixed feeders could increase, consistent with results found in other studies (i.e. Sinclair et al. 2002). I also hypothesize that at least some species traits will show significant changes outside the KNP, and in particular

that larger bodied species will decline outside the KNP, as found in other regions (Herremans & Herremans-Tonnoeyr 2000; Thiollay 2006; Thiollay 2007; Devictor et al. 2007).

Methods

Study region

The study region was located close to the town of Phalaborwa, South Africa, adjacent to the Kruger National Park (KNP; -23°56'44.89"S; 31° 9'53.71"E). It is a low summer rainfall region with a warm, tropical savanna climate. Mean annual rainfall varies around 460 mm to 480 mm per annum, with mean annual temperatures ranging from 10.9 to 25.2 °C, with very hot temperatures over 40°C regularly recorded in summer. KNP was established in 1931. Although it is intensively managed, it represents a historically pristine and largely intact ecosystem (du Toit et al. 2003). Sampling was conducted in four distinct land cover types in the region: protected, matrix, rural, urban; which represent a gradient of intensifying land use from least (protected) to greatest (urban) transformed (see Figure 2 in Chapter 1).

Study design

I followed an exact distance point count approach (Bibby et al. 2000; Buckland et al. 2001). I have prior experience birding in the region and received additional region specific training (Lawson 2012). I counted birds at point count stations for 10 minutes, which commenced after a 2 minute period to acclimatize bird species upon arrival. All birds seen and heard were noted, and the distance from observer recorded with a laser rangefinder, up to 100 m. Flying birds were omitted. Surveys were conducted between 06:00 and 10:00 during peak bird activity and only in good weather (no heavy wind or rain).

Point counts were located at random in each of the land cover types: protected (n = 20), rural (n = 20), matrix (n = 20) and urban (n = 10; due to its small spatial area). Extensive obstructions (roads, fences, private lands, settlements and safety concerns) prevented true random placement of points outside the PA, but in those cases they were relocated to the nearest point which met the sampling criteria. Points in the rural land cover type were located in grazing lands away from dense human settlements. Two points in rural areas

where relocated after the first year to similar areas due to destruction via building and safety concerns, respectively. Points were at least 400 m from conspicuous boundaries (major roads, boundaries between land cover types, any water body etc.), and at least 300 m apart, but typically much further (average distance between all points: 11.95 km; Standard deviation = 7.7 km). A distance between points of 400 m is typical in bird surveys to avoid pseudoreplication (Bibby et al. 2000; van Rensburg et al. 2009; Greve et al. 2011). Sampling was conducted during two periods yearly, in February-March and October-November, which coincides with peak migrant species activity in the area, and repeated in 2010 and 2011, respectively (thus four sampling events in total). Points were visited twice per sampling event and so a total of 560 point counts where conducted. Data of repeat counts per sampling event were pooled.

Species and land cover traits

The selection of predictive species traits in an analysis can be critical to its interpretation (Petchey & Gaston 2006). As far as possible, the choice of traits has to avoid redundancy and trivial correlations between them, while describing the functional attributes that are sought (Villéger et al. 2010). I captured traits in three classes; morphometric, feeding functional, and nesting traits, using data for all recorded species (Hockey et al. 2005). Morphometric traits were: mean body mass, mean tarsus-, wing-, culmen- and tail-length. Where multiple data were reported (males, females and juveniles etc.), I did the following: where mean male and mean female trait values of a species were available, their arithmetic mean was used. Otherwise the mean of unsexed individuals was used. Data on juveniles was excluded. Functional traits followed the classification of Greve et al. (2011), and designated species into groups of: frugivores, granivores, insectivores, mixed feeders, nectarivores and predators. Data on nesting behaviour was also captured from Hockey et al. (2005), and variables were clutch size, egg length and nest type (either hole-, cup-, oval-, platform-, or ground nester and also brood parasites). While some traits may be correlated with body size, they fundamentally express different aspects of species ecology. For example, while culmen length and body size are correlated, culmen length is a surrogate for functional feeding behaviour not necessarily captured by body size (e.g. Wolf et al. 1976; Kulemeyer et al. 2009). Similarly, morphometric traits such as wing length and tail length may have

different functional expressions, in terms of species adaptation to vegetation structure or foraging strategies (Norberg et al. 2001).

Traits for different land cover regions were PA status (binary for PA or not), land cover (protected, matrix, rural or urban), and binary variables for the four land cover types (presence absence of protected, matrix, rural, urban) to test the individual contributions among land cover types to overall effects. I also investigated nine vegetation structural variables, using a variation of the point-height-intercept method (Park 1973) to characterize frequency of grass, trees and forbs and the maximum and median grass, tree and forb height. Four 50 m transects of 25 points (thus 2 m apart) where located in a grid design centred around each point count, and vegetation recorded at each point in 25 cm intervals up to height of 5 m. Canopy cover was estimated by calculating the percentage vegetation cover on a level and fixed width photograph upwards at 1.5 m at each stick-point. Data were only collected in protected, rural, and matrix land cover types due to the logistic difficulties using these methods in this particular urban area. Vegetation sampling was conducted in February 2011, during the peak of the plant growing season.

Data analysis

A General Linear Model (assuming a Gaussian distribution with a log link function, fitted using an exhaustive search algorithm in R [R Development Core Team 2012]) revealed that only land cover type had a significant influence over both species richness and species abundance, and not seasonality or year (Supplementary Table S1). As a consequence, I only report on and conduct all analysis further with point count data combined across years and seasons.

Since there could be interspecific differences in species detectability during point counts (Thomas et al. 2010), a detection function, calculated in R (R Development Core Team 2012), was used to assess species detectability (Buckland et al. 2001). Due to low sample sizes of rare species, typical in community ecology, detection functions could not be fitted to all species, and so were fitted across land cover types for all species, following the approach of Mulwa et al. (2012). The best fit detection function (using a half-normal key with cosine adjustments at a 40 m truncation [so only including observations within 40 m from the

observer]), was identified using the Akaike Information Criterion (Johnson & Omland 2004). The best fit model across all species led to a monotonically decreasing detection function, (Supplementary Figure S1). When fitting the above model, there was no significant difference in species density when correcting for detection, or not, between land cover types (t-test; $t = 2.164$; $df = 3$; $p = 0.116$). However, a surrogate species approach may better address interspecific detection differences, where species are grouped based on similar characteristics and the relationship between detectability and distance evaluated (Buckland et al. 2001; Greve et al. 2011). When correcting for detection across the seven emergent species clusters (details follow, see Figure 7; Table 2), a high correlation remains between observed density, and density corrected for detection (Supplementary Figure S2; Pearson's $r = 0.994$; $p < 0.001$). For each group, the best fit detection function was also a monotonically decreasing detection function (Supplementary Figure S3). Taken together, these results confirm that at least in my study region, the influence of species detectability is negligible and so densities were not adjusted for detectability (Buckland et al. 2001), but all analysis are reported at a 40 m truncation, unless otherwise stated.

Sampling adequacy was assessed with EstimateS v. 8.20 (Gotelli & Colwell 2001; Colwell et al. 2004; Colwell 2005). If observed sample-based rarefaction curves and estimators approach an asymptote at the highest observed richness, then observed species richness may be considered to be representative (Magurran 2004). If they do not, richness estimators provide a more unbiased estimate of overall species richness.

Rank abundance curves provide a graphical representation of species abundance distributions, and were fit for each land cover type (McGill 2012). Such a plot may be easier to interpret than the single, non-dimensional outputs typically provided by diversity indices (Steenkamp & Chown 1996). The characteristic and common species from all land cover types were identified using the Indicator Value Method (IndVals; Dufrêne & Legendre 1997). It describes the extent to which each species fulfils the criteria of specificity (uniqueness to a land cover type), or fidelity (the frequency of occurrence within a land cover type). It is expressed as a percentage, and higher values indicate that a species is more representative of a particular land cover type (McGeoch & Chown 1998). For illustrative purposes I selected species with IndVals higher than 60 % as indicator species for the land cover type, although 70 % is more typically used (McGeoch et al. 2002).

Overall, bird assemblage between land cover types where compared using an Analysis of Similarity (ANOSIM) and non-metric multidimensional scaling plots (nMDS), using the PRIMER v.5 software package (Clarke & Warwick 2001). Rare and common species were weighted equally by square-root transformation of the data before analysis and a Bray-Curtis similarity measure was used to calculate the similarity matrix (Clarke & Warwick 2001). An ANOSIM broadly analyzes the difference in overall assemblages structure, where the closer a significant Global *R* statistic is to one, the more distinct the differences.

I calculated beta diversity across land cover types to further characterize the turnover of species in my study region. Since beta diversity patterns originate from two distinct processes (either the replacement or loss [or gain] of species), I used recently introduced measures to differentiate between these processes (Carvalho et al. 2012). By partitioning beta diversity $ß_{cc}$ (the dissimilarity in terms of the Jaccard index) into its two additive fractions $ß_{-3}$ (dissimilarity due to species replacement) and $ß_{rich}$ (dissimilarity due to richness differences), species replacement can readily be distinguished from species richness change among land cover types (Carvalho et al. 2012). The approach uses presence-absence data for all species in the regional species pool across each of the four land cover types, and was implemented in R (R Development Core Team 2012), with scripts detailed in Carvalho et al. (2012). The method compares the variance between land cover areas with the variance within land cover areas for a dissimilarity matrix by means of the sum of squared distances. For ease of representation I performed a hierarchical cluster analysis in R (R Development Core Team 2012) on these dissimilarities to produce a dendrogram for each of the three beta diversity metrics illustrating their respective turnover components between land cover types. The mean number of species in each feeding guild (frugivore, granivore, insectivore, mixed feeder, nectarivore, predator) was compared among land cover type's allocations and analysed with Wilcoxon-Mann-Whitney U-tests (Quinn & Keough 2002).

To characterise the relationship between species traits and land cover traits, I use the fourthcorner statistic to combine spatially explicit environmental data with species traits (Legendre et al. 1997; Dray & Legendre 2008; Gaston et al. 2008b; Chown et al. 2009; Neuschulz et al. 2012) in R (R Development Core Team 2012). The approach can identify positive or negative correlations between the biological or other traits of organisms and the environmental characteristics of the locations at which they are found (Legendre et al. 1997; Dray & Legendre 2008). Consequently, the results of the fourthcorner analysis can be

interpreted as correlation coefficients, where significant positive relationships indicate a positive correlation between the species trait under investigation, and that particular land cover trait (Dray & Legendre 2008). The method links three data matrix tables: a table "L" with abundance values for species across points, a table "R" with variables describing the traits of land cover areas (environmental conditions) and a table "Q" containing traits (e.g., morphological or functional attributes) of the species (Dray & Legendre 2008). The fourthcorner statistic is being increasingly used to document species traits- environment relationships (Azeria et al. 2011; Neuschulz et al. 2012). I used the first permutation method (modeltype = 1), as all permutation methods showed very similar results (data not shown) and 10 000 permutations on species abundance data. Data for vegetation characteristics in land cover areas was only fitted to bird abundance data across protected, matrix and rural areas. The fourthcorner analysis with land cover vegetation characteristics was conducted with abundance data across all years and seasons, since similar results were obtained when repeating the analysis for bird data collected during February 2011 only (when the vegetation data was collected). This result is unsurprising since apart from seasonal leaf flushing, vegetation structure would change little over the duration of the study.

All trait data for species was used to create a trait dendrogram with a hierarchical cluster analysis on a dissimilarity matrix in R (R Development Core Team 2012), to examine if certain clusters of traits are absent from any land cover types. Emergent species clusters were matched with the abundance of species in that particular trait cluster across land cover types.

Lastly, I used species body size frequency distribution histograms (e.g. Bakker & Kelt 2000), with body mass in grams for all species, to visually examine the change in body size of the assemblage in each land cover type. Although log-transformed data is typically used for body size histograms, here, due to the small spatial scale of the study region such histograms are flat (indistinguishable from log-uniform; see Chapter 4) and so did not aid inference.

Unless otherwise stated, all analysis was conducted in R (R Development Core Team 2012), using the following packages: "ade4" (Thioulouse et al. 1996); "Distance" (Miller 2012); "glmulti" (Calcagno & Mazancourt 2010); and "vegan" (Oksanen 2011).

Results

Following the 40 m right truncation I recorded a total of 106 species and 2382 individuals. Since sample-based rarefaction curves approached an asymptote at the highest observed species richness for the study region, observed species richness can be considered a robust and comparable approximation across the study region (Supplementary Figure S4). However, species additions may be expected with increased survey effort within individual land cover types, which would mainly consist of singleton additions (Colwell et al. 2004). Although not shown here, overall patterns in terms of assemblage structure and abundances between land cover regions remain when truncating the data at 100 m (using a rank abundance curve, fourthcorner traits analysis and non-metric multi dimensional scaling plot).

Table 1. Total species richness and abundance, and mean species and abundance, respectively, together with two richness estimators: Jacknife2 (obtained without re-sampling) and Chao1, across all land cover types at a 40 m truncation. Abund = species abundance. SD = Standard deviation. CI = Confidence Intervals.

40 m Truncation	Protected (n = 20)	Matrix (n = 20)	Rural (n = 20)	Urban (n = 10)
Total species rich.	48	65	58	59
Total species abund.	387	621	517	857
Mean species rich. (SD)	7.7 (2.72)	13.65 (3.5)	10.3 (3.18)	21.9 (5.65)
Mean abund. (SD)	19.35 (27.48)	31.05 (13.26)	25.75 (7.86)	85.7 (22.84)
Mean Jackknife2	79.18	94.47	104.98	82.77
Chao1 (95% CI)	61.13 (51.88;92.38)	80.11 (69.76;112.96)	72.15 (63.38;98.48)	70.14 (62.06;99.63)

Species richness and abundance was typically higher outside the PA (Table 1), and there are significant difference between land cover types ($F_{(2,69)} = 31668$, $p = 0.001$). Abundances were particularly high in urban regions, although the matrix habit type harbours the greatest species richness (Table 1). These assemblage differences are also illustrated by the rank abundance curves, which show that on average, the urban region contains a higher abundance across its suite of species, similar to that of the matrix land cover type (Figure 1).

The protected area contains less individuals, but does contain great abundances of, for example, Red-billed Quelea (species names are detailed in Supplementary Appendix S1), which are found at much lower abundance in the other land cover types and absent from urban (Supplementary Appendix S1). All land cover types contain Laughing Dove, a ubiquitous and very abundant granivore country-wide (Hockey et al. 2005), but urban on average contains six times as many individuals than the other land cover types (Supplementary Appendix S1).

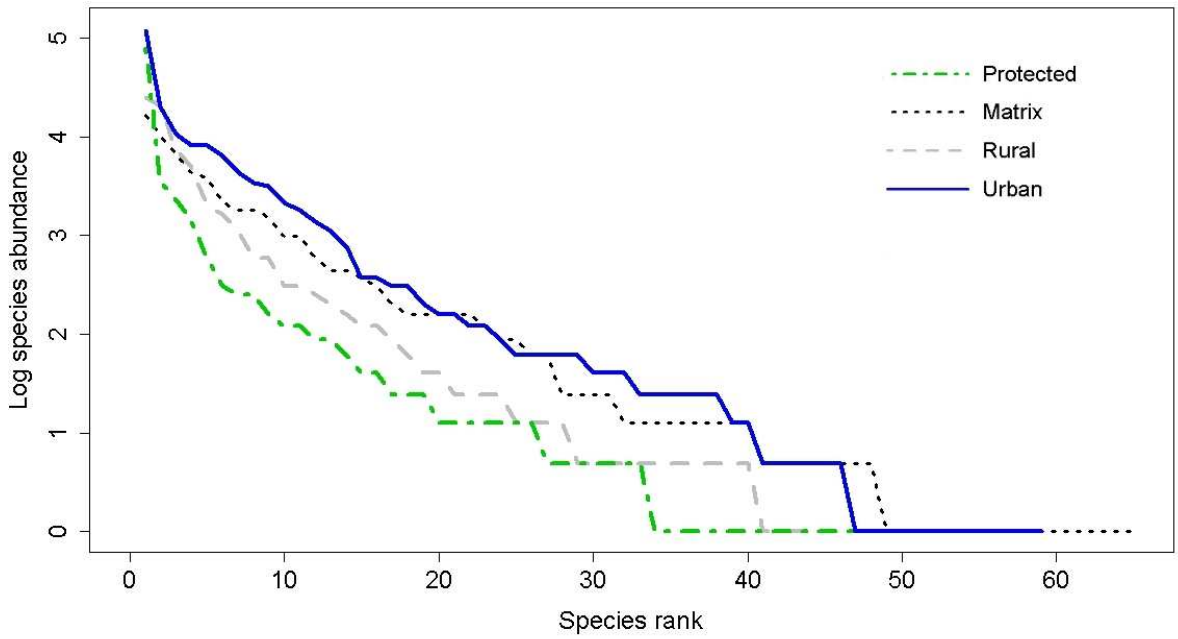

Figure 1. Rank abundance graph for species in protected (inside Kruger National Park) and outside in rural and urban land covers and the connecting matrix.

The urban land cover type in particular consists of a unique assemblage, indicated by the clustering in a multi dimensional scaling plot, but assemblage differences are not as pronounced across the other land cover types (Figure 2; ANOSIM = Global R = 0.44, p = 0.01). The nMDS indicates that in general there is less variation within the assemblage in the urban region than the other land cover types (Figure 2). When considering only species presence-absence this result broadly holds (ANOSIM = Global R = 0.41, p = 0.01; nMDS not shown).

The Jaccard index of beta diversity emphasises the turnover in species between land cover types. The urban area shows great dissimilarity to the other land cover types, while protected, matrix and rural land cover types show less of a pronounced turnover between species (Figure 3A). In all cases, species replacement differences between the protected area and the other land cover types contributed more to the total dissimilarity between land cover areas than species richness differences (in all comparisons: $ß_{-3} > ß_{rich}$; see Supplementary Table S3). While protected area and matrix support similar species, there are much turnover in species identities to rural, and a very large turnover in species between all land cover types and that of urban (Figure 3C).

When considering only raw species abundances, high insectivore abundance within the urban land cover type was mainly driven by two typical sub-tropical garden birds, the African Paradise Flycatcher and Kurrichane Thrush. However, the urban land cover type is missing an otherwise highly abundant insectivore, the Rattling Cisticola, also a significant contributor to the differences among land cover areas and specific to many land cover areas (Supplementary Table S2). Mixed feeders highly abundant in urban areas but nearly absent in other land cover types include the Bronze Manniken, and Red-faced- and Speckled Mousebirds. Another highly abundant mixed feeder, Sabota Lark is absent from urban areas (Supplementary Appendix S1).

All feeding guilds had the highest abundance in urban (Figure 5), and indeed differed significantly in all cases to that of the protected area. There were less pronounced differences in feeding guilds between the other land cover types (Figure 5). Apart from granivores, insectivores and predators, the protected area had significantly lower abundances of all functional groups compared against all the other land cover types. Nectarivores and frugivores were not detected from the protected land cover region that I sampled.

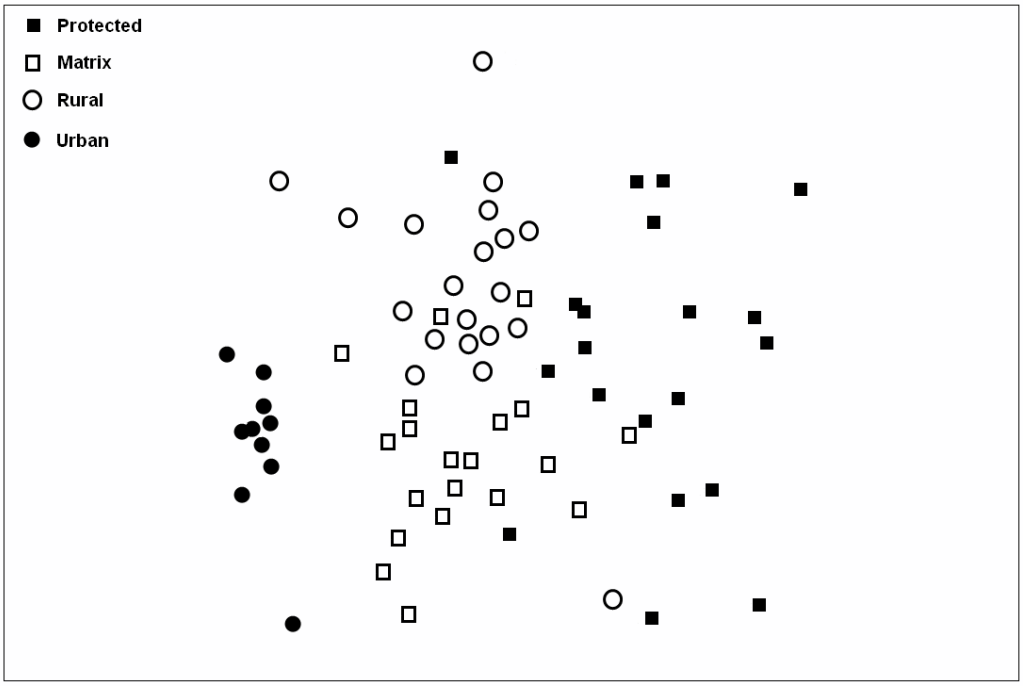

Figure 2. Non-metric multi dimensional scaling plot of bird assemblages inside Kruger National Park (filled squares), and outside the protected area in rural (open circles) and urban (filled circles) land covers and the connecting matrix (open squares). The greater the distance between sampling points, the greater the differences in their assemblages are. In terms of their overall assemblage structure, apart from urban, land cover areas are overlapping and only somewhat different (ANOSIM ; Global R = 0.44, P = 0.01; Stress = 0.26).

The fourthcorner analysis revealed a complex relationship between species traits and land cover types. However, the land cover designation had a positive correlation on all species traits (apart from clutch size), indicating the significant role of land cover changes on species traits (Figure 6). A significant positive correlation was found between body mass and land cover change (Figure 6; Supplementary Table S2). Body size frequency distribution plots indicate that this pattern occurs concomitantly with the loss of larger-bodied species outside the PA, particularly in rural areas (Figure 4).

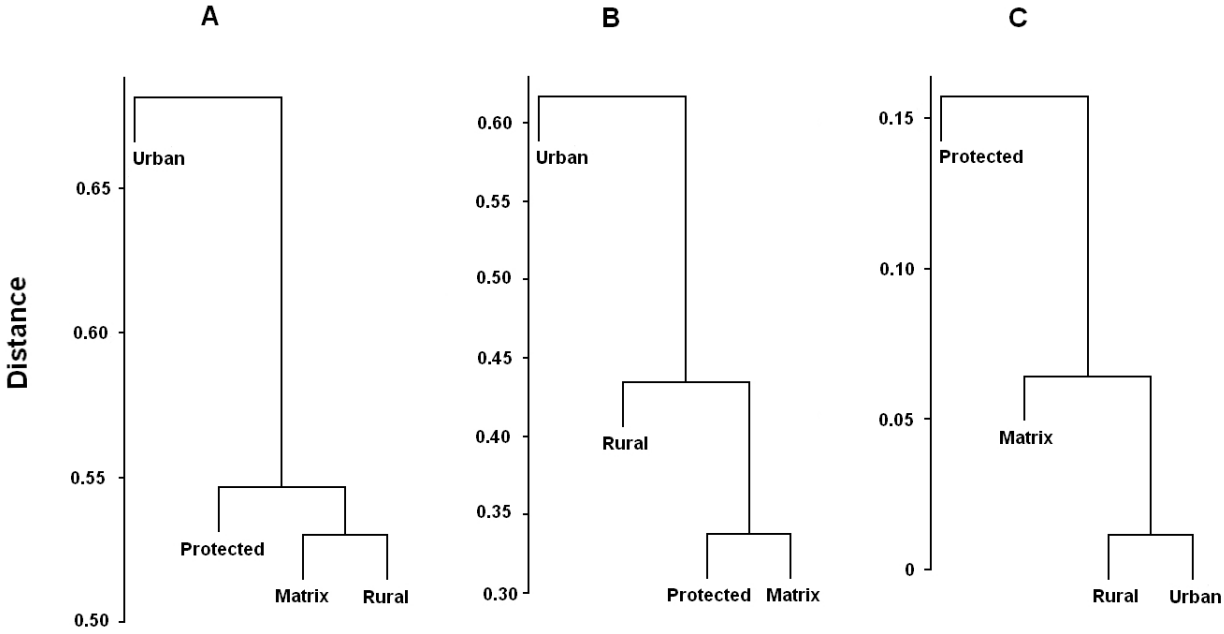

Figure 3. Dendrograms for beta diversity (A; $ß_{cc}$) decomposed into components of both the dissimilarity due to species replacement (B; $ß_{-3}$) and dissimilarity due to richness differences (C; $ß_{rich}$). For change values, see Supplementary Table S3.

A negative correlation between body mass with abundance in all land cover areas also suggests that land cover types with higher abundance, e.g. outside the protected areas, on average contain species of smaller body size (Figure 6; Supplementary Table S2). Clutch size had no association with any land cover variables, but both nest type and egg length are correlated with land cover variables. The rural land cover in particular showed significant positive correlations across a suite of species traits (Figure 6; Supplementary Table S2). Species traits also had a complex relationship with vegetation structure variables. In general, only body morphology and nesting variables showed a positive correlation to canopy cover, tree maximum and median heights, and tree frequency (Supplementary Figure S5).

Most species groups in the trait dendrogram were represented in all land cover types, with most groups reaching their greatest abundances in the urban region. Two groups however, did not (groups 6 and 7; Figure 7; Table 2). These consist either of relatively large-bodied ground living nesters (Helmeted Guineafowl and Francolin species, group 7; Figure 7; Table 2), and hornbill species (group 6; Figure 7; Table 2). Species from both groups are completely

absent from rural, and reach their highest abundance in protected, and matrix land cover types, respectively.

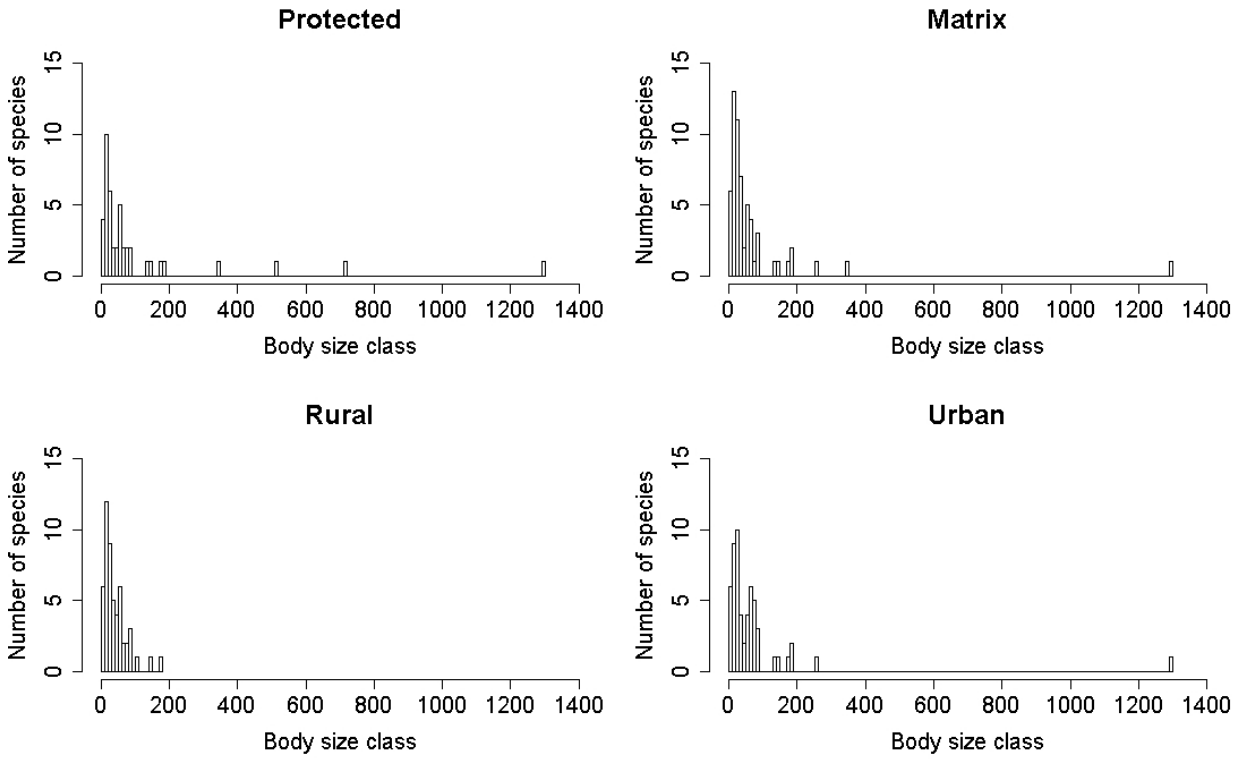

Figure 4. Body size frequency distribution histograms for all species across land cover types. Body weight is in grams.

Discussion

Contrary to expectation, both bird species richness and abundance are generally higher outside the Kruger National Park (KNP) protected area (PA). While the bird communities within rural and matrix land cover type do share many affinities with the KNP (Figure 2; Figure 3), the vastly dissimilar assemblage in urban is strongly driven by species replacement, rather than just species richness differences (in all comparisons: $ß_{-3} > ß_{rich}$; see Supplementary Table S3). The urban species pool is mainly composed of regionally common species at greatly increased abundances.

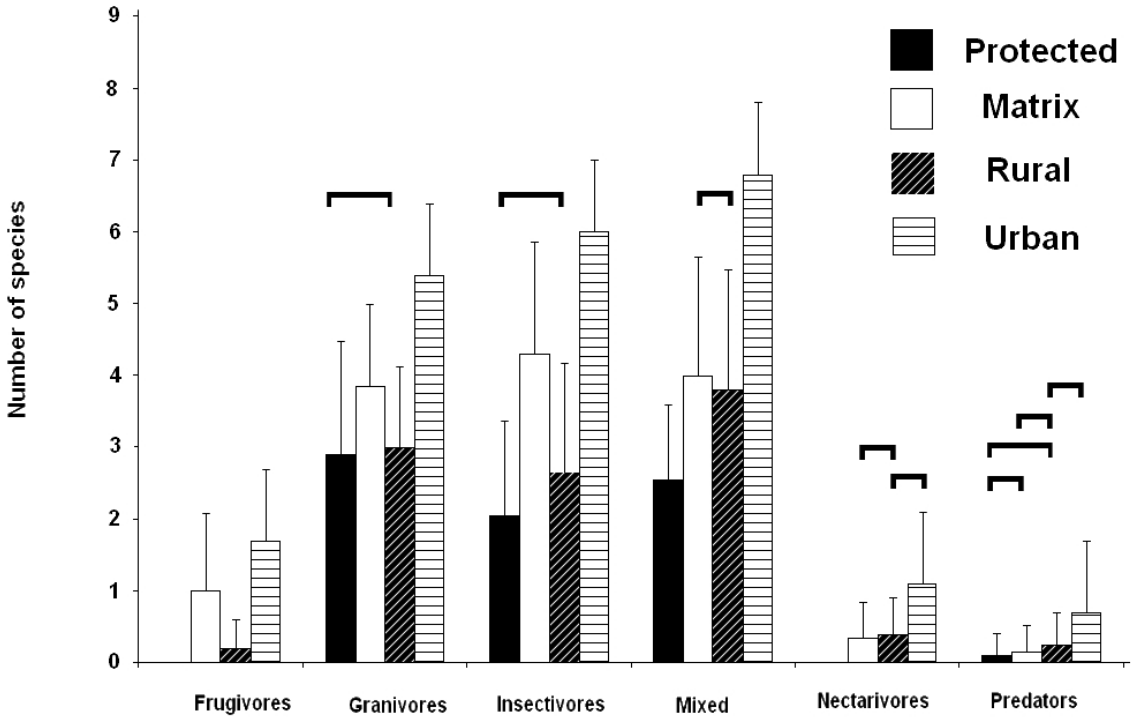

Figure 5. Mean number of species per point count as a function of six feeding guilds, across protected, rural, urban and matrix land cover types. Bars indicate standard deviation. Since most comparisons of respective functional groups differ significantly between land cover types (Wilcoxon-Mann-Whitney; $p < 0.05$), brackets show only those that are non significant (Wilcoxon-Mann-Whitney; $p > 0.05$). For all comparisons: $62.5 < U < 312$.

For example, one regionally very common granivore, the Laughing Dove, which is an indicator species in most habitat types (Supplementary Table S2), accounts for much of the large increases in abundance in the urban land cover type (see Figure 1; Supplementary Appendix S1). Elsewhere, urban bird species assemblages are characterized by invasive species as found here for House Sparrows (Shochat et al. 2006; van Rensburg et al. 2009; Supplementary Appendix S1). Greater abundances of a few common species adapted to human disturbance can be expected (typically granivores and mixed feeders; Shochat et al. 2006).

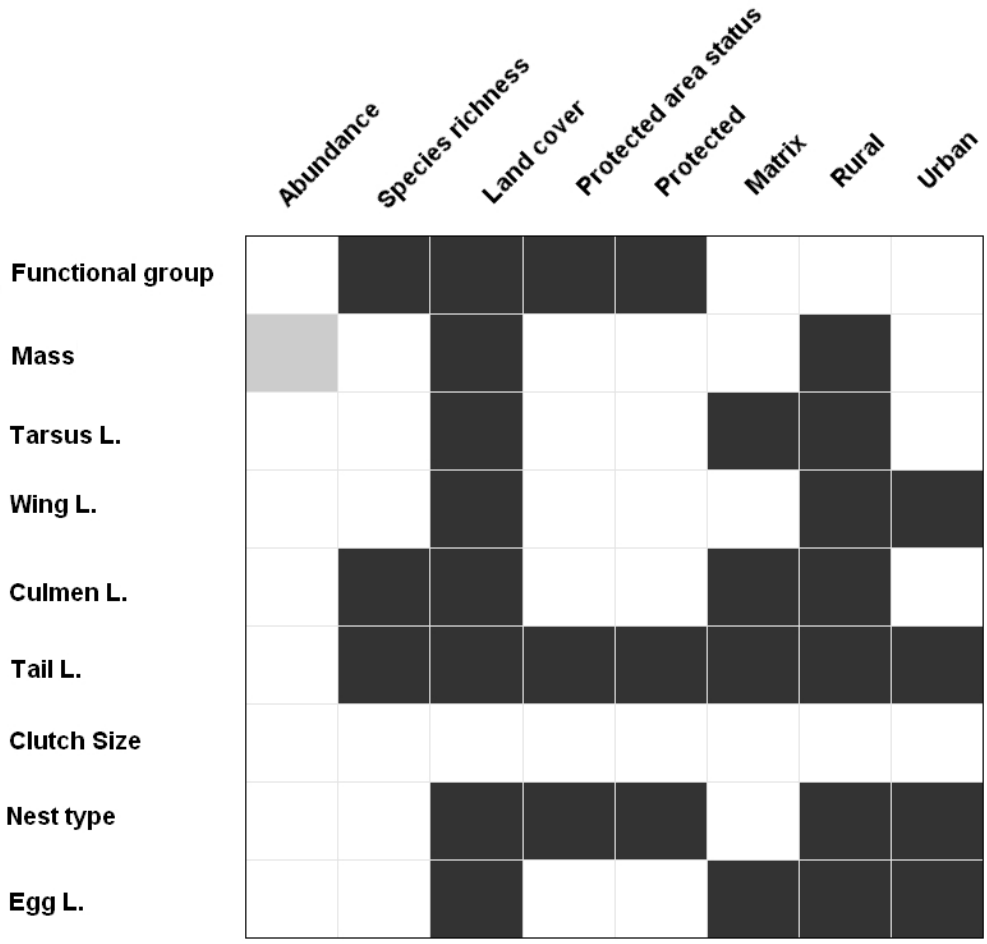

Figure 6. Fourthcorner statistics results for species abundances across species traits and land cover categories. White indicates non-significant correlations, black indicates significant positive correlations, and light grey indicates significant negative correlations. Land cover traits run in columns while species traits are in rows. L. = Length. Full results are reported in Supplementary Appendix S2. See Results for details on interpretation.

It is clear that alteration to land cover in the urban area has had pronounced influences on the local bird community. The Phalaborwa Mopane Sandveld, in which all land cover types historically occurred, is located on coarse fersialitic soils which leach nutrients (Mucina & Rutherford 2006).

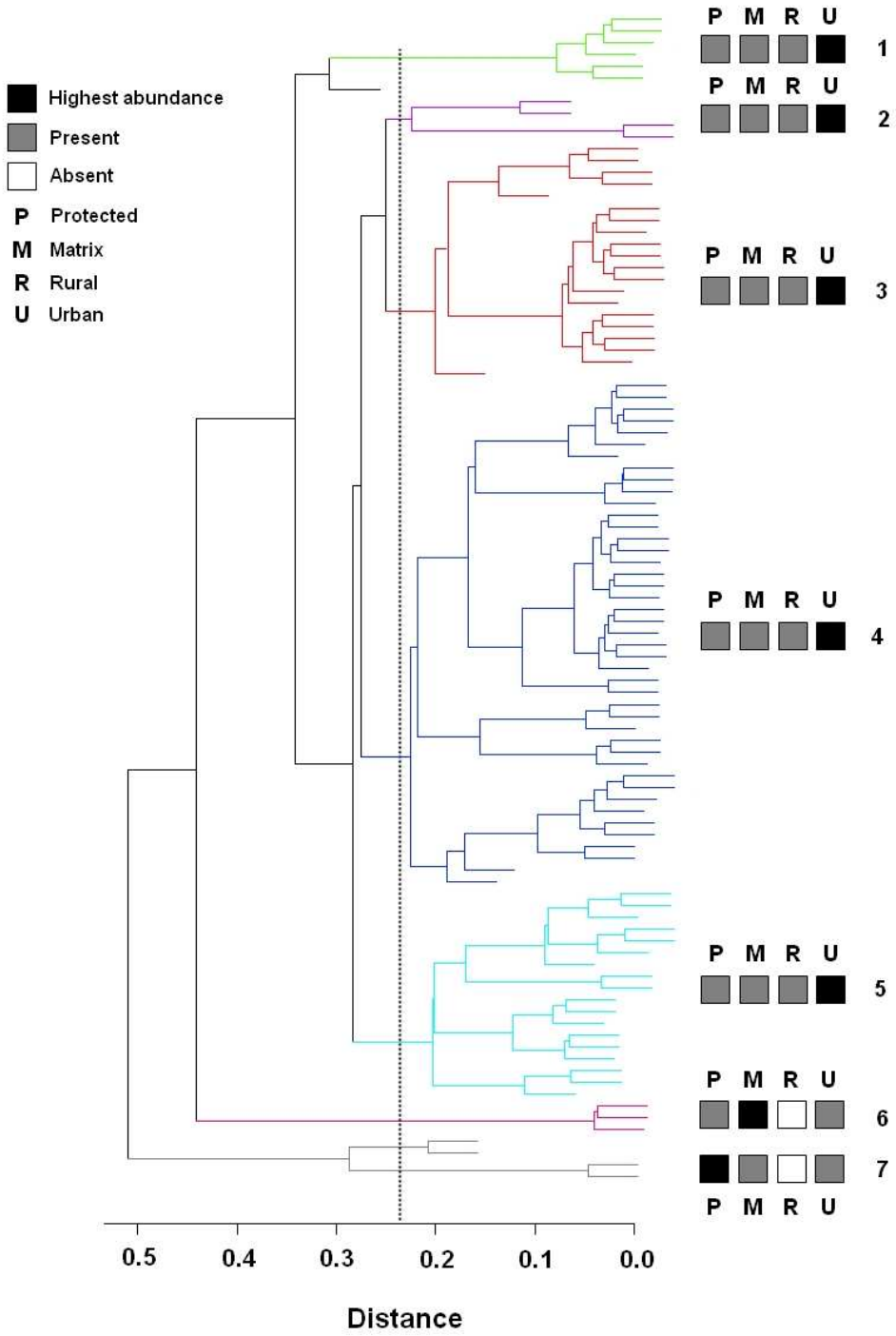

Figure 7. Trait dendrogram for all species analysed at 40 m truncation. Major emergent groups at an arbitrarily selected cut-off (dashed line) are coloured for groups 1-7. Descriptions of these groups in terms of their typical functional, morphometric and nesting behaviours are in Table 2.

Table 2. Description of the typical functional, morphometric and nesting behaviours of the emergent species clusters descriptions from the trait dendrogram in Figure 7 (Groups 1-7).

Group	Typical characteristics	Exemplar species groups
1	Medium bodied, Granivores, Platform nesters	Doves
2	Frugivores, Predators	Mousebirds, Shrikes
3	Medium bodied, Parasitic breeders, insectivores	Honeyguide's, Thrushes, Babblers, Cuckoos, Batis
4	Small bodied, mainly Granivores/ Mixed feeders	Drongos, Finches, Waxbills, Weavers, Sunbirds
5	Insectivores/Frugivores, hole nesters,	Barbets, Woodpeckers, Kingfishers
6	Large-bodied, insectivores, hole nesters, long culmen length	Hornbills
7	Large-bodied, Ground nesters	Francolins, Korhaans, Guineafowl

Consequently, the protected land cover type is mainly dominated by Silver cluster-leaf trees (*Terminalia sericea*), and also hardy and drought resident Mopani trees (*Colophospermum mopane*), a gregariously growing species which may exclude other plants (van Wyk & van Wyk 2000). Mopani is predominately a low shrub-like tree, and offers few nesting and feeding opportunities for many resident birds and so typically has a reduced bird diversity compared to, for example, *Acacia* dominated woodlands (Hockey et al. 2005). The urban land cover type mostly consist of suburban regions with large gardens, and there is little commercial infrastructure within the small town of Phalaborwa. As a consequence, the provisioning of water (either for irrigation or by bird feeders), and the promotion of gardening adds a diversity of plant species, particularly large trees. Importantly, water provisioning occurs throughout the year in an otherwise seasonally very dry environment. As a consequence, there is an increase in habitat structure, productivity and resource availability in the urban landscape, factors which typically cause higher abundance and

richness changes (Shochat et al. 2006; Woodward & Kelly 2008; Pautasso et al. 2011). Species nesting traits respond strongly to tree height in the other land cover types (Supplementary Figure S5), and likely so in the urban area. It also promotes higher abundance across feeding guilds through nesting and feeding opportunities, and is responsible for the large turnover between land cover types, particularly via species replacement (Figure 3B; Supplementary Table S3). Such a vast change in the local environment is perhaps best typified by two indicator bird species. African Paradise Flycatcher is characteristic of indigenous forest regions and also well wooded urban gardens (Hockey et al. 2005) and it finds the addition of resources in terms of increased tree cover particularly suitable. Conversely, Rattling Cisticola is a dry savanna specialist and an indicator species in both matrix and rural land cover types, and also very prevalent in the protected area, but absent from the urban region. The dominant tree species in the protected region, are either wind pollinated (Mopani) or wind dispersed (Silver cluster-leaf; van Wyk & van Wyk 2000), and this likely explains the absence of frugivores and nectarivores there at the local scale.

The pattern of high abundance in the urban region is consistent with the more individuals hypothesis (Srivastava & Lawton 1998; Gaston 2000; Storch et al. 2005). The hypothesis states that greater resource and energy availability should support greater biomass. Under such conditions, more individuals can coexist, and consequently more species at higher abundance can maintain their populations (Gaston 2000). Since species-rich communities have larger populations, the hypothesis predicts that the net result is a reduction in the chance of local extinctions (Srivastava & Lawton 1998). While much evidence exists for the hypothesis under natural conditions (Gaston 2000), the generality of such a pattern in highly modified habitats is less clear (Chiari et al. 2010). Increases in net primary productivity as a consequence of human activities have the capacity to increase local scale diversity for plants (Woodward & Kelly 2008), and a similar mechanism seems to operate here for birds, as it does in urban regions elsewhere (Chiari et al. 2010), and my work provides further evidence for it. Indeed, at the local scale, areas with favourable resource levels are known to elevate bird diversity, and typically these areas contain large proportions of transformed lands (Fairbanks et al. 2002). Furthermore, Fairbanks (2004) found that, at a more regional scale in South Africa, bird richness increases due to the retention of vegetation specific bird species in untransformed fragments, combined with species that can exploit heavily transformed

areas. Of great concern with this interpretation is that the future diversity capacity through such alterations to the landscape are likely to be filled by common species from the regional species pool (Woodward & Kelly 2008), as is this case here.

Furthermore, the overall high species richness in the habitat matrix and also rural may be due to complex source-sink effects in combination to patterns generated by the more individuals hypothesis (Table 1; Runge et al. 2006). The matrix in particular is transitional between all the land cover areas and under moderate extractive use, and so a range of bird species from the surrounding local species pool may find it suitable. That species are at a higher abundance in matrix than both protected and rural areas support this interpretation, as does the intermediate assemblage composition of matrix between all other land cover types (Figure 2).

However, these documented changes in species richness and abundance mask insidious changes in the species trait characteristics of assemblages across land cover types. It is clear that in this region, and elsewhere (Schweiger et al. 2007; Posa & Sodhi 2006; Pocock et al. 2010; Neuschulz et al. 2012), species traits have a strong correlation with the land cover in which they occur (Figure 6; Figure 7). I found that in particular, large-bodied species, ground nesters, and those with specific feeding requirements (e.g. insectivorous hornbills) are virtually absent outside of the protected area. Such a result is likely an underestimate, as large-bodied ground nesters are cryptic, and hard to detect using a point count methodology, since they do not flush as they would during line transects (Bibby 2000), and conduct much evasive movement. Their absence in rural is likely due to their direct exploitation as a food resource, and that, due to heavy grazing and resource extraction, there is reduced nesting opportunities (i.e. Du Plessis 1995; Herremans & Herremans-Tonnoeyr 2000; Fairbanks 2004; Thiollay 2006; Thiollay 2007; Chown 2010). A pattern of direct exploitation of wildlife in subsistence farming areas seems ubiquitous in much of Africa and in developing nation's worldwide (Peres 2000; Milner-Gulland & Bennett 2003; Chown 2010).

There are clearly apparent paradoxes in the contrasting directions of the responses of biodiversity to PA establishment (Caro 2002; Sinclair et al. 2002; Thiollay 2006; Thiollay 2007; Devictor et al. 2007; Greve et al. 2011; Laurance et al. 2012 and see Chapter 2). As a consequence, my finding emphasizes that disentangling the effects of PA proclamation from

other factors that may enhance or reduce biodiversity is critical to understanding the nature of PA efficacy given its context specific nature (Andam et al. 2008; Gaston et al. 2008; Caro et al. 2009; Laurance et al. 2012 and see Chapter 2). Here, I could quantify some of the local scale factors responsible for the contrasting direction in biodiversity responses. I have shown that consistent with the more individuals hypothesis, the addition of resources artificially increases bird abundance substantially outside PAs, albeit at a very local scale and consisting of a much altered assemblage. Regarding species traits, the PA is critical for maintaining a certain suite of species (typically large-bodied species). However, human alteration to an otherwise resource poor landscape outside the KNP has proven beneficial for a different suite of species traits (typically small bodied granivores and mixed feeders), but detrimental to those of larger body size due to direct exploitation.

There is no doubt that the Kruger National Park is, and remains, a PA of global importance for the conservation and maintenance of the world's birds (Barnes et al. 1998; Hockey et al. 2005). Globally as well, across a range of taxa, PAs achieve significant conservation outcomes compared to alternative land covers outside their borders (see Chapter 2). Nonetheless, in many regions of the world, the bulk of biodiversity lies outside of PAs (Rodrigues et al. 2004; Chown 2010). Ultimately, PAs establishment and maintenance is only a component of an effective conservation strategy, and my results highlight that areas under extraction and transformation can positively contribute to a region's biodiversity portfolio. Preventing areas under moderate extractive use from becoming completely degraded and restoring habitats where possible can and should continue to play a fundamental role at landscape level conservation (Dobson et al. 1997; Scholes & Biggs 2005). Ultimately, a holistic approach to conservation is needed, with a greater understanding of which species, and which traits, are at particularly risk in an increasingly transformed world.

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Supplementary Material

Supplementary Table S1. Results from general linear models comparing both species richness and abundances between land use type as a function of sampling year, sampling month (a measure of seasonality) and land cover type, across sampling trips.

Response variable: Species richness

n = 280

Deviance explained 37.60%

AIC 1779.80

Variables:	Slope	SE	P
Intercept	1.54	0.72	*
Land cover type	-0.55	0.14	***
Year	-0.007	0.068	
Month	0.134	0.06	.

Response variable: Abundance

n = 280

Deviance explained 7.41%

AIC 1853.90

Variables:	Slope	SE	P
Intercept	**2.45**	**1.12**	*
Land cover type : Urban	0.89	0.141	***
Land cover type : Rural	-0.25	0.19	
Land cover type : Protected	-0.43	0.23	.
Year	-0.0279	0.1	
Month	0.02	0.1	

Significance codes:
0.001 = ***; 0.01 = **
0.05 *; 0.1 = .

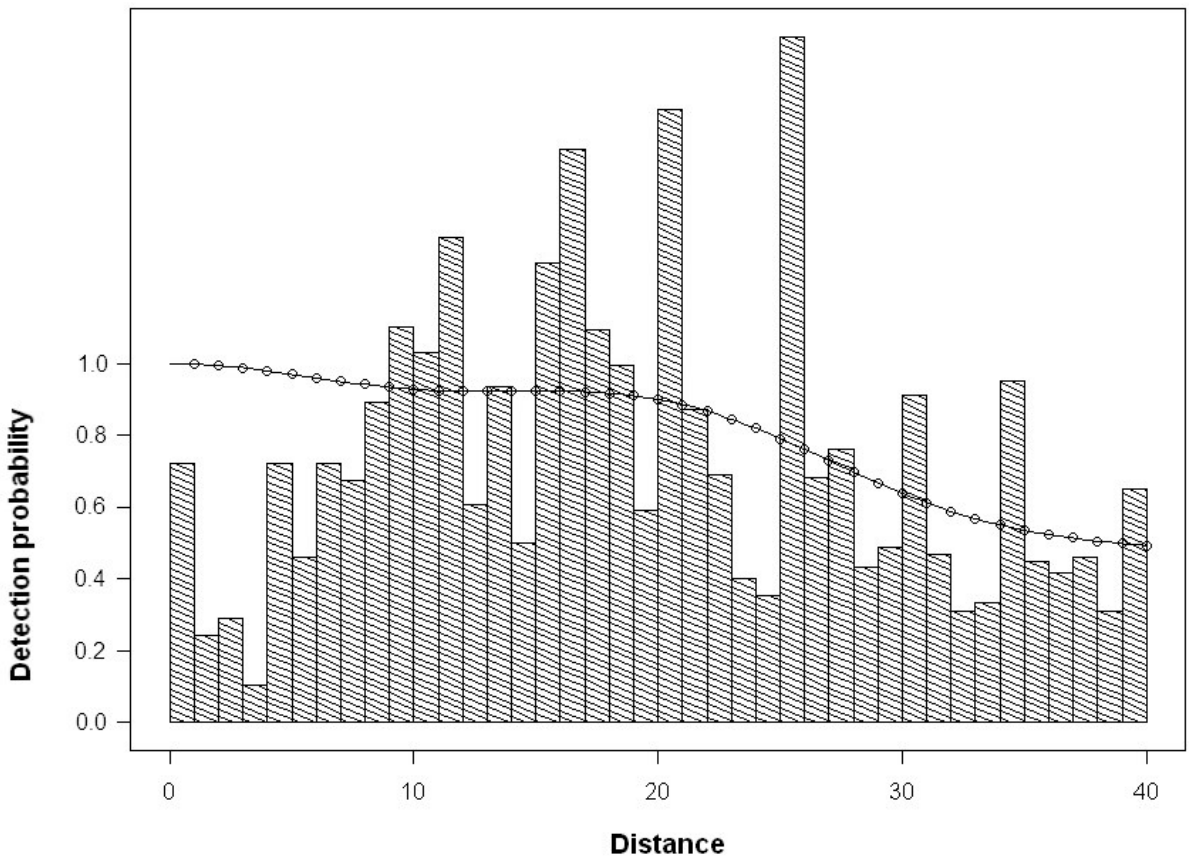
Supplementary Table S2. Indicator values (IndVals) for species from four land cover types. IndVal describes the extent to which each species fulfils the criteria of specificity (uniqueness to a land cover type), or fidelity (the frequency of occurrence within a land cover type). It is expressed as a percentage, and higher values indicate that species is more representative of a particular land cover type. For illustrative purposes I selected species with IndVals higher than 60 % as indicator species for the land cover type.

Protected	Indval	Matrix	Indval	Rural	Indval
Sabota Lark	80	Blue Waxbill	100	Yellow fronted Canary	90
Laughing Dove	60	Laughing Dove	85	Blue Waxbill	85
Blue Waxbill	60	Red backed Shrike	75	Sabota Lark	80
		Rattling Cisticola	70	Rattling Cisticola	70
		Cape Turtle Dove	65	Tawny flanked Prinia	60
		Yellow fronted Canary	60		

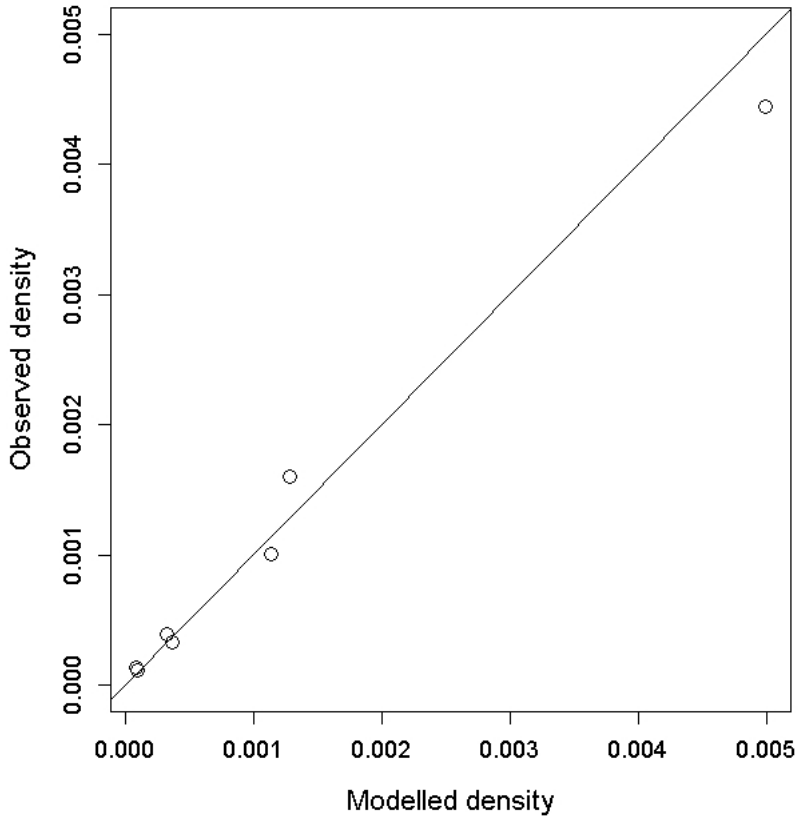
Urban	Indval
African Paradise Flycatcher	100
Kurrichane Thrush	100
Laughing Dove	100
Blue Waxbill	90
Dark Capped Bulbul	90
Forktailed Drongo	90
Red eyed Dove	90
African Hoopoe	80
Bronze Mannikin	80
Southern Masked Weaver	80
Yellow fronted Canary	80
Red Faced Mousebird	70
Southern Grey Headed Sparrow	60
Speckled Mousebird	60
White Bellied Sunbird	60

Supplementary Table S3. Algebraic decomposition of beta diversity ($ß_{cc}$) into two additive components, species replacement ($ß_{-3}$) plus richness difference ($ß_{rich}$). Species replacement differences, resulting from the loss of between sites, contributed more to the total dissimilarity than replacement, since in all comparisons: $ß_{-3} > ß_{rich}$.

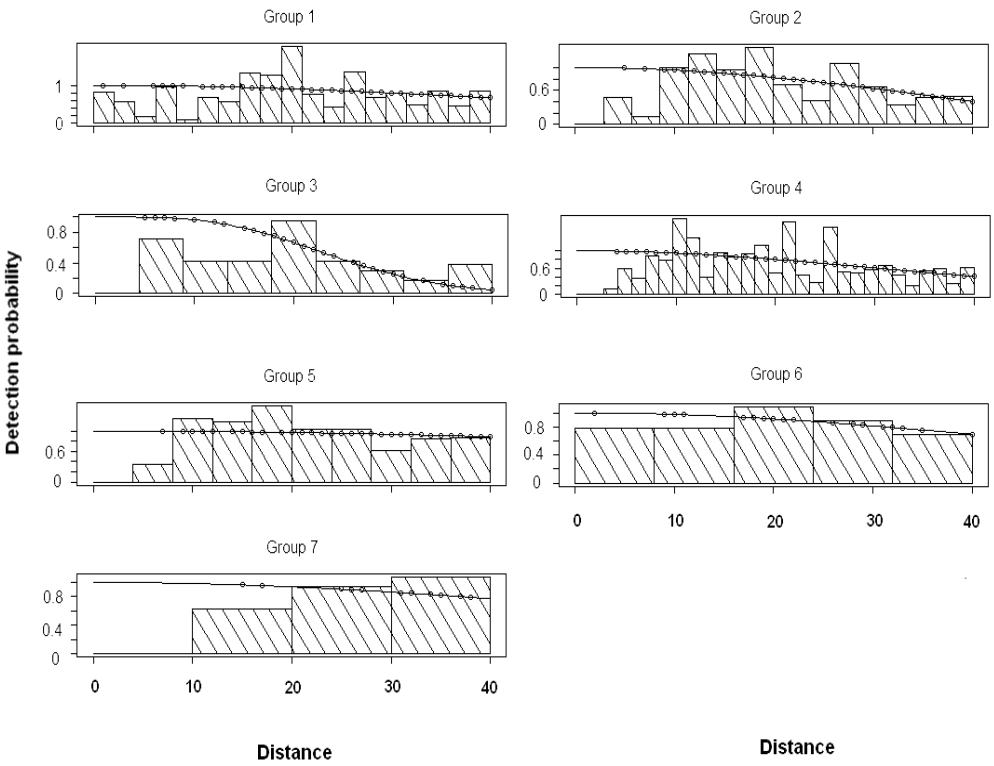
	Beta diversity ($ß_{cc}$)		
	Protected	**Matrix**	**Rural**
Matrix	0.55	-	-
Rural	0.55	0.53	-
Urban	0.77	0.62	0.66
	Species replacement differences ($ß_{-3}$)		
	Protected	**Matrix**	**Rural**
Matrix	0.34	-	-
Rural	0.41	0.46	-
Urban	0.64	0.56	0.64
	Species richness differences ($ß_{rich}$)		
	Protected	**Matrix**	**Rural**
Matrix	0.21	-	-
Rural	0.14	0.07	-
Urban	0.13	0.06	0.01



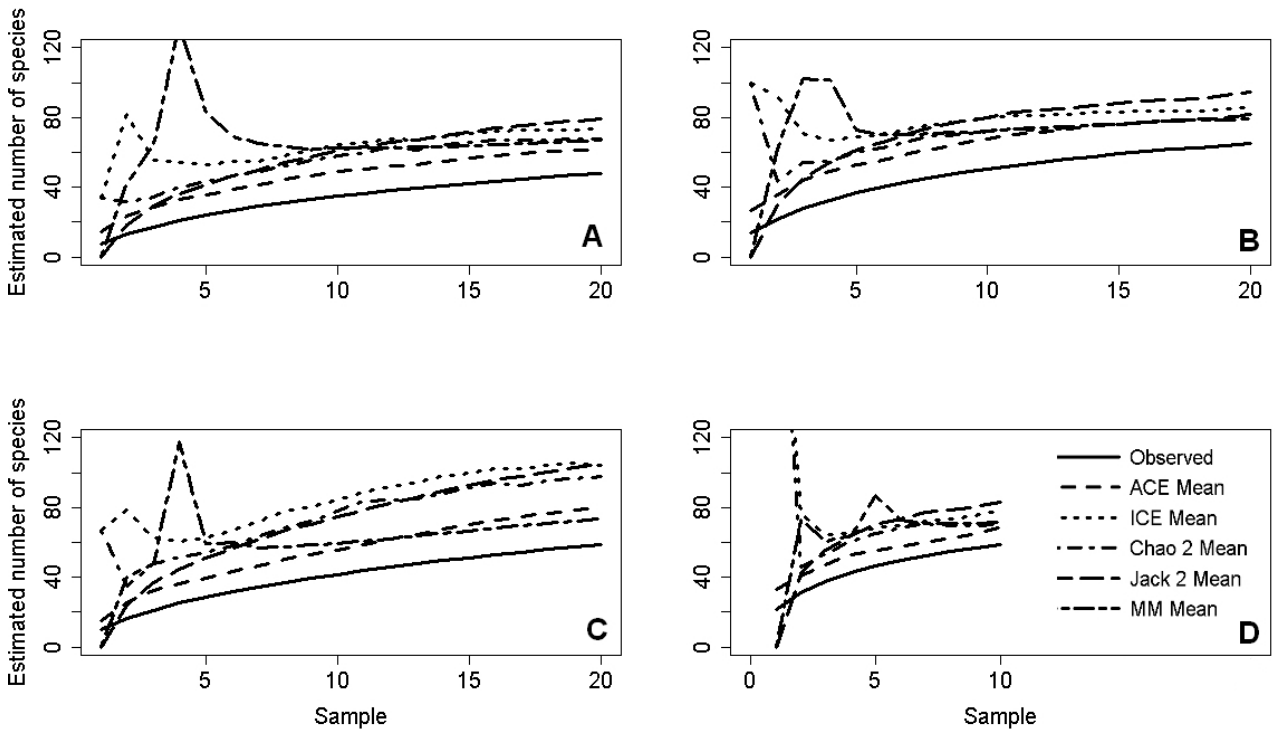
Supplementary Figure S1. Detection function plot for all data showing the best fit model, for a half-normal key with cosine adjustments at a 40 m right truncation, for all point counts across all land cover types, showing a monotonically decreasing detection function.



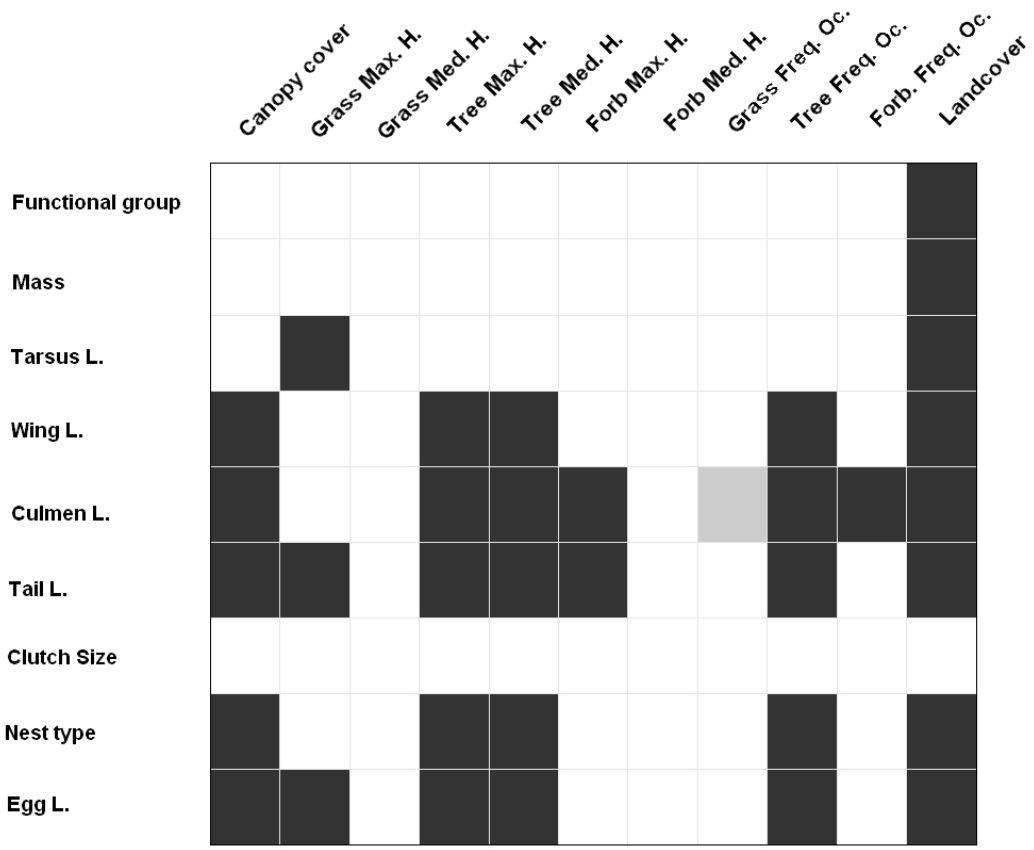
Supplementary Figure S2. Goodness of fit between observed density and modelled density is highly correlated (Pearson's r = 0.994; p < 0.001), indicating that the influence of species detection is low, at least in this study region. The diagonal with a slope of one shows the hypothetical line of best fit if observed density = modelled density.



Supplementary Figure S3. Best fit detection models for the seven surrogate species groups examined, all showing monotonically decreasing detection functions. Best fit detection models for Groups 1-5 where uniform key with polynomial adjustments, while for Groups 6-7 where half-normal key with cosine adjustments, with the best fit models for all groups found at a 40 m truncation. Details of species groups are contained in Table 2.



Supplementary Figure S4. Species rarefaction curves by land cover type, for five major richness estimators and observed mean species richness (Observed). (A) protected (B) matrix (C) rural (D) urban.



Supplementary Figure S5. Fourthcorner statistics results for species abundances across species traits and land cover vegetation characteristics. White indicates non-significant correlations, black indicates significant positive correlations, and light grey indicates significant negative correlations. Land cover traits run in columns while species traits are in rows. L. = Length. Full results and abbreviation definitions are reported in Supplementary Appendix S3.

Supplementary Appendix S1. Mean abundance for all bird species in all land cover types, at a 40 m truncation. Values in brackets indicate standard deviations. Func. = Functional feeding group (where F = Frugivore; M = Mixed feeder; I = Insectivore; G = Granivore; P = Predator; N = Nectarivore). M = Mean body mass in grams.

ID	Common name	Scientific name	Protected	Matrix	Rural	Urban	Func.	M
1	Acacia Pied Barbet	*Tricholaema leucomelas*	0	0.15(0.37)	0.05(0.22)	0	F	32.2
2	African Black-headed Oriole	*Oriolus larvatus*	0	0	0	0.1(0.32)	M	66.1
3	African Firefinch	*Lagonosticta rubricata*	0	0.15(0.67)	0	0	M	10.18
4	African Grey Hornbill	*Tockus nasutus*	0	0.2(0.52)	0	0.2(0.42)	I	182.3
5	African Hoopoe	*Upupa africana*	0	0.05(0.22)	0.1(0.45)	1.8(1.69)	I	53.05
6	African Mourning Dove	*Streptopelia decipiens*	0	0	0	0.9(1.45)	G	134
7	African Paradise-Flycatcher	*Terpsiphone viridis*	0	0.3(0.8)	0.05(0.22)	3.4(2.88)	I	13.25
8	Arrow-marked Babbler	*Turdoides jardineii*	0.2(0.89)	0	0	0.5(1.08)	I	78.2
9	Black Cuckoo-shrike	*Campephaga flava*	0	0.05(0.22)	0	0	I	32.3
10	Black-backed Puffback	*Dryoscopus cubla*	0	0.1(0.31)	0	0.4(0.52)	I	26.25
11	Black-collared Barbet	*Lybius torquatus*	0	0.15(0.49)	0	0.1(0.32)	F	51.7
12	Black-crowned Tchagra	*Tchagra senegalus*	0.05(0.22)	0.05(0.22)	0.1(0.45)	0	I	53.5
13	Blue Waxbill	*Uraeginthus angolensis*	1.75(2)	3.4(1.88)	4.05(2.86)	5(3.65)	G	9.9
14	Bronze Mannikin	*Spermestes cucullatus*	0	0	0.15(0.67)	7.4(7.69)	G	9.9
15	Brown-crowned Tchagra	*Tchagra australis*	0.05(0.22)	0.2(0.52)	0.1(0.31)	0	I	32.3
16	Brown-hooded Kingfisher	*Halcyon albiventris*	0	0	0.05(0.22)	0.1(0.32)	P	65.1
17	Brubru	*Nilaus afer*	0.2(0.62)	0	0	0	I	19.4
18	Cape Glossy-Starling	*Lamprotornis nitens*	0	0	0.05(0.22)	0.9(2.23)	M	85.6
19	Cape Turtle Dove	*Streptopelia capicola*	0.55(0.94)	1.8(1.99)	0.25(0.55)	0.6(0.7)	G	142
20	Cardinal Woodpecker	*Dendropicos fuscescens*	0	0	0	0.1(0.32)	I	26
21	Chinspot Batis	*Batis molitor*	0.3(0.57)	0.15(0.37)	0.15(0.49)	0.6(1.26)	I	11.65
22	Cinnamon-breasted Bunting	*Emberiza tahapisi*	0.15(0.37)	0	0	0	G	13
23	Common Scimitar-bill	*Rhinopomastus cyanomelas*	0	0	0.05(0.22)	0.1(0.32)	M	28
24	Common Waxbill	*Estrilda astrild*	0	0.05(0.22)	0	0	M	8.3
25	Crested Barbet	*Trachyphonus vaillantii*	0	0	0	0.3(0.67)	M	69.45
26	Crested Francolin	*Dendroperdix sephaena*	0.15(0.49)	0.6(1.14)	0	0	M	341.5
27	Cut-throat Finch	*Amadina fasciata*	0	0	0.1(0.45)	1.3(2.26)	M	18
28	Dark-Capped Bulbul	*Pycnonotus tricolor*	0	0.3(0.92)	0	4.5(3.47)	M	37.3
29	Diderick Cuckoo	*Chrysococcyx caprius*	0	0.15(0.49)	0.2(0.52)	1(1.41)	I	33
30	Emerald-spotted Wood-Dove	*Turtur chalcospilos*	0.1(0.45)	0.15(0.37)	0	0	G	60.6
31	European Bee-eater	*Merops apiaster*	0.15(0.37)	0	0.05(0.22)	0	I	56.6
32	European Roller	*Coracias garrulus*	0.1(0.31)	0	0.05(0.22)	0	P	146
33	Fiery-necked Nightjar	*Caprimulgus pectoralis*	0.05(0.22)	0	0.1(0.31)	0	I	52.5
34	Fork-tailed Drongo	*Dicrurus adsimilis*	0.35(0.67)	1(1.38)	0.55(0.76)	2.3(1.77)	M	40.3
35	Golden-breasted Bunting	*Emberiza flaviventris*	0.6(0.88)	0.1(0.31)	0.4(0.82)	0.1(0.32)	G	18.25
36	Golden-tailed Woodpecker	*Campethera abingoni*	0.05(0.22)	0.15(0.37)	0.05(0.22)	0.1(0.32)	I	68.5
37	Greater Blue-eared Glossy-Starling	*Lamprotornis chalybaeus*	0	0	0	0.6(1.9)	M	86.5
38	Greater Double-collared Sunbird	*Cinnyris afer*	0	0	0.05(0.22)	0	N	11.15
39	Greater Honeyguide	*Indicator indicator*	0.05(0.22)	0	0	0	I	50.4
40	Green Woodhoopoe	*Phoeniculus purpureus*	0	0	0	0.7(1.64)	I	74.25
41	Green-backed Camaroptera	*Camaroptera brachyura*	0	0.05(0.22)	0	0	I	9.825
42	Green-winged Pytilia	*Pytilia melba*	0.1(0.45)	0.05(0.22)	0	0	M	15.4
43	Grey Go-away-bird	*Corythaixoides concolor*	0	0.35(0.75)	0	0.8(1.62)	F	258
44	Grey-headed Bushshrike	*Malaconotus blanchoti*	0	0	0	0.1(0.32)	P	78.7
45	Groundscraper Thrush	*Psophocichla litsipsirupa*	0	0	0.2(0.89)	0.2(0.42)	I	74
46	Helmeted Guineafowl	*Numida meleagris*	0.4(1.79)	0.1(0.31)	0	0.2(0.63)	M	1299

47	House Sparrow	*Passer domesticus*	0	0	0	2.6(4.43)	M	25.8
48	Icterine Warbler	*Hippolais icterina*	0	0.05(0.22)	0	0	I	13.2
49	Jacobin Cuckoo	*Clamator jacobinus*	0	0.05(0.22)	0.05(0.22)	0	I	81.5
50	Klaas' Cuckoo	*Chrysococcyx klaas*	0.05(0.22)	0.1(0.31)	0.1(0.31)	0	I	27.4
51	Kurrichane Thrush	*Turdus libonyanus*	0	0.05(0.22)	0	3.8(2.04)	I	60.6
52	Laughing Dove	*Streptopelia senegalensis*	1.15(1.46)	2.75(2.27)	1.35(1.6)	16(5.27)	G	83.89
53	Lesser Grey Shrike	*Lanius minor*	0	0	0.05(0.22)	0	I	46.5
54	Lesser Honeyguide	*Indicator minor*	0.05(0.22)	0.05(0.22)	0	0	I	28.2
55	Lesser Masked-Weaver	*Ploceus intermedius*	0	1.4(2.96)	0	0.6(0.97)	M	20.6
56	Lesser Striped-Swallow	*Hirundo abyssinica*	0	0	0	0.1(0.32)	I	13.5
57	Lilac-breasted Roller	*Coracias caudatus*	0	0	0.25(0.64)	0	P	110
58	Little Bee-eater	*Merops pusillus*	0.05(0.22)	0.2(0.7)	0.1(0.45)	0	I	15.1
59	Longbilled Crombec	*Sylvietta rufescens*	0.05(0.22)	0.45(0.76)	0.05(0.22)	0	M	11.6
60	Long-tailed Paradise-Whydah	*Vidua paradisaea*	0	0.1(0.31)	0.1(0.45)	0	M	20.4
61	Magpie Shrike	*Corvinella melanoleuca*	0.15(0.49)	0.1(0.31)	0	0	P	82.2
62	Marico Sunbird	*Cinnyris mariquensis*	0	0	0	0.4(0.7)	N	11.5
63	Monotonous Lark	*Mirafra passerina*	0.05(0.22)	0	0.05(0.22)	0	M	24.7
64	Namaqua Dove	*Oena capensis*	0	0	0.05(0.22)	0	G	40.59
65	Natal Francolin	*Pternistis natalensis*	0.15(0.67)	0	0	0	M	516
66	Neddicky	*Cisticola fulvicapilla*	0.1(0.31)	0.05(0.22)	0.2(0.52)	0.1(0.32)	I	8.25
67	Pale Flycatcher	*Bradornis pallidus*	0	0	0.05(0.22)	0	I	23.6
68	Rattling Cisticola	*Cisticola chiniana*	0.8(1.44)	2.3(2.62)	2.4(2.66)	0	I	16.25
69	Red Faced Mousebird	*Urocolius indicus*	0	1.3(3.03)	0.05(0.22)	2.8(4.34)	F	56.4
70	Red-backed Shrike	*Lanius collurio*	0.35(0.67)	1(0.79)	0.65(1.84)	0	I	28.45
71	Red-billed Buffalo-Weaver	*Bubalornis niger*	0.05(0.22)	0.65(2.25)	0.1(0.45)	0	M	76.4
72	Red-billed Firefinch	*Lagonosticta senegala*	0	0	0	0.1(0.32)	M	9.27
73	Red-billed Quelea	*Quelea quelea*	6.65(24.51)	0.5(2.24)	1.05(3.55)	0	G	18.6
74	Red-crested Korhaan	*Lophotis ruficrista*	0.1(0.31)	0	0	0	M	714
75	Red-eyed Dove	*Streptopelia semitorquata*	0.55(0.76)	1.9(5.28)	0.15(0.49)	5.6(6.19)	G	176
76	Red-faced Cisticola	*Cisticola erythrops*	0	0	0.05(0.22)	0	I	14.8
77	Red-headed Weaver	*Anaplectes melanotis*	0	0.2(0.52)	0.1(0.45)	0.4(0.7)	I	22.6
78	Rufous-naped Lark	*Mirafra africana*	0	0	0.05(0.22)	0	M	45.22
79	Sabota Lark	*Calendulauda sabota*	1.45(1.1)	0.45(0.69)	2(1.41)	0	M	24.7
80	Scarlet-chested Sunbird	*Chalcomitra senegalensis*	0	0	0	0.4(0.97)	N	12.43
81	Small Buttonquail	*Turnix sylvaticus*	0.1(0.31)	0	0	0	M	54.25
82	Southern Black-Flycatcher	*Melaenornis pammelaina*	0	0	0	0.3(0.67)	I	30.2
83	Southern Black-Tit	*Parus niger*	0.4(0.88)	0.8(1.15)	0.45(0.83)	0.2(0.63)	M	21.5
84	Southern Grey-Headed Sparrow	*Passer diffusus*	0.2(0.52)	0.2(0.52)	0.3(0.73)	1.2(1.55)	M	24.2
85	Southern Masked-Weaver	*Ploceus velatus*	0.25(1.12)	0.7(1.56)	0.8(1.77)	3.3(2.41)	M	31.05
86	Southern Redbilled Hornbill	*Tockus erythrorhynchus*	0.05(0.22)	0.7(0.98)	0	0	I	139
87	Southern Yellow-billed Hornbill	*Tockus leucomelas*	0.05(0.22)	0.35(0.93)	0	0.2(0.63)	I	189.5
88	Speckled Mousebird	*Colius striatus*	0	0.45(1.23)	0.1(0.31)	2.1(2.85)	F	51.45
89	Spectacled Weaver	*Ploceus ocularis*	0	0.05(0.22)	0	0.4(0.84)	M	25.2
90	Spotted Flycatcher	*Muscicapa striata*	0.1(0.31)	0.05(0.22)	0.4(0.75)	0.4(0.97)	I	15.9
91	Stierlings Wren-Warbler	*Calamonastes stierlingi*	0	0.1(0.31)	0	0	I	13.15
92	Streaky-headed Seedeater	*Crithagra gularis*	0	0.05(0.22)	0	0.1(0.32)	M	16
93	Striped Kingfisher	*Halcyon chelicuti*	0	0.05(0.22)	0	0	P	44.5
94	Tawny-flanked Prinia	*Prinia subflava*	0.05(0.22)	0.45(0.6)	1.25(1.68)	1.2(1.81)	M	8.649
95	Violet-backed Starling	*Cinnyricinclus leucogaster*	0.05(0.22)	0	0.6(1.1)	0.5(1.27)	M	44
96	Wattled Starling	*Creatophora cinerea*	0	0	0	0.6(1.9)	M	73.05
97	White Bellied Sunbird	*Cinnyris talatala*	0	0.4(0.6)	0.8(1.24)	1.3(1.42)	N	8.1
98	White Helmetshrike	*Prionops plumatus*	0	1.3(3.31)	0.1(0.45)	0	I	33.8
99	White-browed Scrub-Robin	*Cercotrichas leucophrys*	0.45(0.83)	0.45(0.51)	0.6(0.94)	0.1(0.32)	M	16.5
100	White-crowned Shrike	*Eurocephalus anguitimens*	0	0.15(0.67)	0	0	I	69.05
101	White-winged Widowbird	*Euplectes albonotatus*	0	0.1(0.45)	0.35(0.93)	0	M	21.15
102	Willow Warbler	*Phylloscopus trochilus*	0.15(0.37)	0.05(0.22)	0.2(0.7)	0	I	8.7

103	Woodland Kingfisher	*Halcyon senegalensis*	0	0	0	0.8(1.03)	P	74.5
104	Yellow-bellied Eremomela	*Eremomela icteropygialis*	0.15(0.49)	0	0.15(0.49)	0	M	7.55
105	Yellow-fronted Canary	*Crithagra mozambicus*	0.25(0.55)	1.2(1.51)	3.75(2.59)	5(4.37)	G	11.95
106	Yellow-throated Petronia	*Petronia superciliaris*	0	0	0	0.2(0.63)	M	24

Supplementary Appendix S2. Sample statistics and p values for all fourthcorner statistics results as illustrated in Figure 6. L. = Length

Comparison	Q	Statistic	p value	
Abundance / Functional group	F	8.44	0.11	
Abundance / Mass	r	-0.07	0.05	*
Abundance / Tarsus L.	r	-0.05	0.12	
Abundance / Wing L.	r	-0.03	0.29	
Abundance / Culmen L.	r	0.00	0.47	
Abundance / Tail L.	r	0.01	0.45	
Abundance / Clutch size	r	-0.02	0.38	
Abundance / Nest type	F	5.84	0.31	
Abundance / Egg L.	r	-0.01	0.45	
Species richness / Functional group	F	11.28	0.04	*
Species richness / Mass	r	-0.03	0.25	
Species richness / Tarsus L.	r	0.00	0.48	
Species richness / Wing L.	r	0.07	0.14	
Species richness / Culmen L.	r	0.07	0.03	*
Species richness / Tail L.	r	0.16	<0.001	**
Species richness / Clutch size	r	0.02	0.32	
Species richness / Nest type	F	9.76	0.11	
Species richness / Egg L.	r	0.06	0.13	
Land cover type / Functional group	Chi2	126.35	0.02	*
Land cover type / Mass	F	17.69	0.01	*
Land cover type / Tarsus L.	F	20.72	<0.001	**
Land cover type / Wing L.	F	53.35	<0.001	***
Land cover type / Culmen L.	F	23.42	<0.001	***
Land cover type / Tail L.	F	79.25	<0.001	***
Land cover type / Clutch size	F	0.79	0.95	
Land cover type / Nest type	Chi2	197.66	<0.001	***
Land cover type / Egg L.	F	48.40	<0.001	***
Protected status / Functional group	Chi2	61.29	0.03	*
Protected status / Mass	F	9.90	0.21	
Protected status / Tarsus L.	F	4.72	0.35	
Protected status / Wing L.	F	11.24	0.25	
Protected status / Culmen L.	F	6.32	0.15	

Protected status / Tail L.	F	57.04	0.01	*
Protected status / Clutch size	F	1.88	0.59	
Protected status / Nest type	Chi2	83.17	0.01	*
Protected status / Egg L.	F	1.30	0.66	
Protected / Functional group	Chi2	61.29	0.03	*
Protected / Mass	F	9.90	0.21	
Protected / Tarsus L.	F	4.72	0.35	
Protected / Wing L.	F	11.24	0.25	
Protected / Culmen L.	F	6.32	0.15	
Protected / Tail L.	F	57.04	0.01	*
Protected / Clutch size	F	1.88	0.59	
Protected / Nest type	Chi2	83.17	0.01	*
Protected / Egg L.	F	1.30	0.66	
Matrix / Functional group	Chi2	46.63	0.07	.
Matrix / Mass	F	8.48	0.25	
Matrix / Tarsus L.	F	21.83	0.04	*
Matrix / Wing L.	F	28.82	0.06	.
Matrix / Culmen L.	F	28.59	<0.001	**
Matrix / Tail L.	F	53.48	0.01	*
Matrix / Clutch size	F	0.72	0.73	
Matrix / Nest type	Chi2	9.61	0.84	
Matrix / Egg L.	F	27.71	0.03	*
Rural / Functional group	Chi2	35.85	0.16	
Rural / Mass	F	48.01	<0.001	**
Rural / Tarsus L.	F	52.74	<0.001	***
Rural / Wing L.	F	120.39	<0.001	***
Rural / Culmen L.	F	47.66	<0.001	***
Rural / Tail L.	F	118.05	<0.001	***
Rural / Clutch size	F	0.09	0.90	
Rural / Nest type	Chi2	72.93	0.02	*
Rural / Egg L.	F	128.97	<0.001	***
Urban / Functional group	Chi2	19.33	0.43	
Urban / Mass	F	0.60	0.71	
Urban / Tarsus L.	F	0.04	0.92	
Urban / Wing L.	F	46.94	0.02	*
Urban / Culmen L.	F	8.35	0.09	.
Urban / Tail L.	F	67.94	0.01	**
Urban / Clutch size	F	0.28	0.82	
Urban / Nest type	Chi2	99.95	0.01	**
Urban / Egg L.	F	30.54	0.03	*

Significance codes: * = 0.001; ** = 0.01, * = 0.05; . = 0.1**

Supplementary Appendix S3. Sample statistics and p values for all fourthcorner statistics results as illustrated in Supplementary Figure S3. L. = Length; max.h = Maximum height; med.h = median height; freq.oc = Frequency of occurrence.

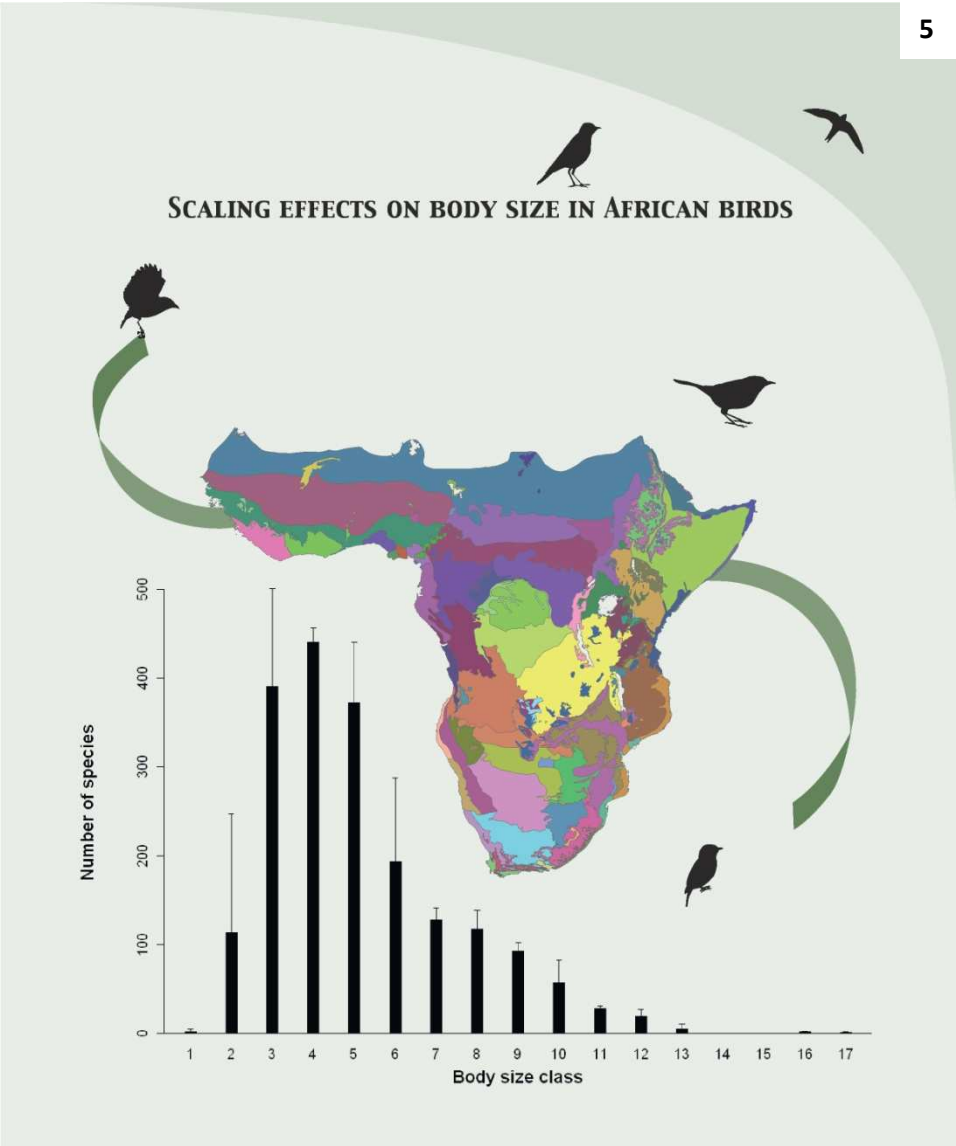
Comparison	Q	Statistic	p value	
Canopy cover / Functional group	F	5.419	0.291	
Canopy cover / Mass	r	0.052	0.202	
Canopy cover / Tarsus L.	r	0.095	0.071	.
Canopy cover / Wing L.	r	0.249	<0.001	***
Canopy cover / Culmen L.	r	0.196	<0.001	***
Canopy cover / Tail L.	r	0.290	<0.001	***
Canopy cover / Cluch size	r	-0.082	0.060	.
Canopy cover / Nest type	F	15.427	0.013	*
Canopy cover / Egg L.	r	0.199	<0.001	***
Grass max.h / Functional group	F	9.534	0.071	.
Grass max.h / Mass	r	0.106	0.055	.
Grass max.h / Tarsus L.	r	0.135	0.012	*
Grass max.h / Wing L.	r	0.076	0.152	
Grass max.h / Culmen L.	r	0.039	0.176	
Grass max.h / Tail L.	r	0.146	0.023	*
Grass max.h / Cluch size	r	0.059	0.192	
Grass max.h / Nest type	F	2.661	0.706	
Grass max.h / Egg L.	r	0.106	0.040	*
Grass med.h / Functional group	F	2.412	0.369	
Grass med.h / Mass	r	-0.028	0.172	
Grass med.h / Tarsus L.	r	-0.013	0.416	
Grass med.h / Wing L.	r	-0.045	0.125	
Grass med.h /Culmen L.	r	-0.026	0.245	
Grass med.h / Tail L.	r	-0.047	0.101	
Grass med.h / Cluch size	r	0.005	0.361	
Grass med.h / Nest type	F	0.650	0.867	
Grass med.h / Egg L.	r	-0.044	0.129	
Tree max.h / Functional group	F	2.047	0.788	
Tree max.h / Mass	r	0.012	0.495	
Tree max.h / Tarsus L.	r	0.018	0.401	
Tree max.h / Wing L.	r	0.198	<0.001	***
Tree max.h / Culmen L.	r	0.122	0.001	***
Tree max.h / Tail L.	r	0.218	0.002	**
Tree max.h / Cluch size	r	-0.099	0.066	.
Tree max.h / Nest type	F	17.912	0.004	**
Tree max.h / Egg L.	r	0.151	0.002	**
Tree med.h / Functional group	F	3.163	0.599	
Tree med.h / Mass	r	0.058	0.205	
Tree med.h / Tarsus L.	r	0.085	0.090	.
Tree med.h / Wing L.	r	0.225	<0.001	***

Tree med.h / Culmen L.	r	0.151	<0.001	***
Tree med.h / Tail L.	r	0.226	<0.001	***
Tree med.h / Cluch size	r	-0.037	0.304	
Tree med.h / Nest type	F	13.281	0.022	*
Tree med.h / Egg L.	r	0.169	0.003	**
Forb max.h / Functional group	F	5.252	0.285	
Forb max.h / Mass	r	-0.008	0.498	
Forb max.h / Tarsus L.	r	0.031	0.277	
Forb max.h / Wing L.	r	0.066	0.173	
Forb max.h / Culmen L.	r	0.097	0.013	*
Forb max.h / Tail L.	r	0.125	0.048	*
Forb max.h / Cluch size	r	-0.004	0.520	
Forb max.h / Nest type	F	2.886	0.597	
Forb max.h / Egg L.	r	0.061	0.151	
Forb med.h / Functional group	F	0.287	0.980	
Forb med.h / Mass	r	-0.010	0.533	
Forb med.h / Tarsus L.	r	-0.006	0.494	
Forb med.h / Wing L.	r	-0.002	0.506	
Forb med.h / Culmen L.	r	-0.013	0.418	
Forb med.h / Tail L.	r	-0.016	0.330	
Forb med.h / Cluch size	r	-0.029	0.205	
Forb med.h / Nest type	F	1.728	0.506	
Forb med.h / Egg L.	r	0.001	0.439	
Grass freq.oc / Functional group	F	1.779	0.825	
Grass freq.oc / Mass	r	0.016	0.418	
Grass freq.oc / Tarsus L.	r	0.018	0.384	
Grass freq.oc / Wing L.	r	-0.107	0.067	.
Grass freq.oc / Culmen L.	r	-0.071	0.039	*
Grass freq.oc / Tail L.	r	-0.119	0.067	.
Grass freq.oc / Cluch size	r	0.027	0.340	
Grass freq.oc / Nest type	F	6.401	0.227	
Grass freq.oc / Egg L.	r	-0.059	0.166	
Tree freq.oc / Functional group	F	4.796	0.351	
Tree freq.oc / Mass	r	0.024	0.325	
Tree freq.oc / Tarsus L.	r	0.076	0.109	
Tree freq.oc / Wing L.	r	0.217	<0.001	***
Tree freq.oc / Culmen L.	r	0.198	<0.001	***
Tree freq.oc / Tail L.	r	0.250	<0.001	***
Tree freq.oc / Cluch size	r	-0.069	0.111	
Tree freq.oc / Nest type	F	14.170	0.018	*
Tree freq.oc / Egg L.	r	0.161	0.004	**
Forb.freq.oc / Functional group	F	7.806	0.141	
Forb.freq.oc / Mass	r	-0.003	0.534	
Forb.freq.oc / Tarsus L.	r	0.038	0.243	
Forb.freq.oc / Wing L.	r	0.015	0.417	
Forb.freq.oc / Culmen L.	r	0.074	0.042	*
Forb.freq.oc / Tail L.	r	0.074	0.172	
Forb.freq.oc / Cluch size	r	-0.008	0.486	

Forb.freq.oc / Nest type	F	2.929	0.568	
Forb.freq.oc / Egg L.	r	0.042	0.237	
Landcover / Functional group	Chi2	126.147	<0.001	***
Landcover / Mass	F	20.868	0.007	**
Landcover / Tarsus L.	F	26.451	0.001	***
Landcover / Wing L.	F	55.959	<0.001	***
Landcover / Culmen L.	F	29.106	<0.001	***
Landcover / Tail L.	F	92.621	<0.001	***
Landcover / Cluch size	F	1.258	0.874	
Landcover / Nest type	Chi2	99.702	0.007	**
Landcover / Egg L.	F	53.684	<0.001	***

Significance codes: * = 0.001; ** = 0.01, * = 0.05; . = 0.1**

Chapter 4 – Scale effects on the body size frequency distributions of African birds: patterns and potential mechanisms[4]



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Introduction

Body size is one of the most striking attributes of an organism. It affects many physiological and ecological traits (Gaston & Blackburn 2000), including species home range size (Haskell et al. 2002), species abundances (Lewis et al. 2008), geographic range size (Gaston & Blackburn 1996) life history strategies (Rohwer et al. 2009) and can mediate invasions (Roy et al. 2002). Species extinction probabilities are also linked to body size (Gaston & Blackburn, 1995; Gaston & Blackburn 1996; Fritz et al. 2009). Therefore, investigations of spatial variation in body size have provided important insights into the ecological and evolutionary processes structuring biological assemblages, with considerable implications for conservation (Brown & Nicoletto 1991; Bakker & Kelt, 2000; Roy et al. 2001; Gaston et al. 2008; Meiri et al. 2009).

Species body size frequency distributions (BSFDs) form a significant means of understanding spatial variation in body size (Gaston & Blackburn 2000). Thus, determining the generality of BSFDs across taxa, regions, and spatial scales, and the mechanisms underlying deviations from general patterns are fundamental questions in macroecology (Gaston & Blackburn 2000). Although much is now known about general patterns in BSFDs at the broadest spatial scales (Blackburn & Gaston 1994; Roy et al. 2000; Smith et al. 2004), at smaller spatial scales the nature of variation in BSFDs and the mechanisms underlying this variation are not as comprehensively understood. At the regional to global scale, BSFDs for birds, mammals, lizards, bivalves and most insects are generally strongly right-skewed on a logarithmic scale (Brown & Nicoletto 1991; Gaston & Blackburn 2000; Roy et al. 2000; Meiri 2008; Chown & Gaston 2010), but bimodal for North American squamates (Cox et al. 2011) and not skewed in snakes (Boback & Guyer 2003), some beetles (Dixon & Hemptinne 2001), or squamates generally (Reed & Boback 2002). At smaller spatial scales BSFDs can also be highly variable, ranging between right-skewed (Gaston et al. 2001), less strongly right-skewed (Brown & Nicoletto 1991; Bakker & Kelt 2000; Smith et al. 2004; Greve et al. 2008; Chown & Gaston 2010), flat (indistinguishable from log-uniform; Marquet & Cofré 1999), or even multimodal (Chown & Gaston 1997; Raffaelli et al. 2000; Cox et al. 2011; Kelt & Meyer 2009).

For smaller spatial scales, a key question is whether BSFDs are merely random subsets from the larger spatial scale assemblages in which they are embedded. If they are not, then some factor must be invoked at that scale to explain observed BSFDs (Gaston & Blackburn, 2001).

In North and South American mammals, smaller spatial scale BSFDs are not random subsets of the larger scale BSFDs (Brown & Nicoletto 1991; Bakker & Kelt 2000). BSFDs of North American mammals are modal and right-skewed, show non-random assembly, and decrease in skewness in assemblages at progressively finer spatial scales. Brown & Nicoletto (1991) ascribed this pattern to three main mechanisms; (i) competition for limited resources means local faunas contain fewer modal-sized species; (ii) large species with small geographic ranges are more extinction prone; (iii) allometric constraints on physiology lead to greater specialisation of modal-sized species. However, Cox et al. (2011) argued that these mechanisms may be of less importance for the squamates of North America, with deep phylogenetic differences among component taxa being more significant. The BSFDs of South American mammals in general are similar to those of North American mammals in showing non-random assembly, but they are multimodal at all spatial scales and do not become indistinguishable from log-normal at the smallest spatial scales (Marquet & Cofré 1999). The additional mode persists at smaller spatial scales, and could be due to habitat specialisation (Bakker & Kelt 2000). The BSFDs of African mammal assemblages are multimodal at all spatial scales. Kelt & Meyer (2009) suggested that the secondary mode could be a consequence of the assemblage not being as adversely affected by anthropogenic Pleistocene extinctions as in other regions, but they did not test if local assemblages were random subsets from the larger species pool.

The global bird BSFD is right-skewed (Blackburn & Gaston, 1994), just as in the Americas (Cardillo 2002). South African birds also have right-skewed BSFDs, and much of the variation in median body size can be predicted by randomly drawing species from the regional distribution (Greve et al. 2008). Therefore, purely stochastic processes also need to be taken into account when explaining BSFDs as they can contribute to observed patterns (Meiri & Thomas 2007). Blackburn & Gaston (2001) showed that in a local assemblage of birds in Britain, a random draw model from the regional bird assemblage accurately predicts most descriptive statistics if the probability that a species is selected is weighted by its geographic range size. However it is unclear how ubiquitous right-skewed BSFDs are for birds, whether BSFDs at smaller scales are indeed non-random subsets of larger scale distributions, and what mechanisms might underlie the scaling effects on BSFDs.

Here, I therefore analyse the BSFDs of avian assemblages at several spatial scales across the Afrotropics. I also test whether the variation in median body size across assemblages at

different spatial scales was related to energy, species richness, and range size, all variables which are known to correlate with the median body size of birds globally (Olson et al. 2009). I also test whether smaller spatial scale distributions are random subsets of the larger spatial scale assemblages in which they are embedded. The influence of stochastic processes on BSFDs is further investigated by comparing observed distributions to three types of null distributions generated by randomly resampling the continental avifauna. Finally, I determine whether energy, species richness, and range size could explain the deviation of the model null distributions from the median observed data, at the local scale.

Methods

Species distribution data

I used the WWF Wildfinder database (Olson et al. 2001) at the ecoregions scale as a template for collating data on all bird species in the Afrotropical bioregion, excluding offshore islands, the Arabian Peninsula and Madagascar. Ecoregions are spatially discrete units that contain geographically distinct assemblages of natural communities that share a large majority of their species, ecological dynamics, and similar environmental conditions (Olson et al. 2001). The taxonomy and distribution of species was comprehensively updated from Sinclair & Ryan (2003). The ranges of species absent from the Wildfinder database (mainly due to taxonomic changes and errors) were digitized in ESRI ArcGIS 9.3 (2011) at the ecoregion scale from Sinclair & Ryan (2003). This study focuses on terrestrial species, excluding vagrants, introduced species and offshore-nesting seabirds. I included migrant species here as their inclusion or exclusion had no significant effect on the BSFD of the South African avifauna (Greve et al. 2008). While in polar and temperate regions small-bodied migratory species are significantly overrepresented (Olson et al. 2009), my study area is not in these regions, further motivating the inclusion of migrants.

Species were assigned to a continental species list, biome species lists, ecoregion species lists and local scale lists. Species lists were generated from the continental species lists for the seven major biomes of sub-Saharan Africa (Deserts and Xeric Scrubland; Mediterranean; Grasslands; Savanna; Flooded Savanna; Moist Broadleaf Rainforests and Dry Broadleaf Rainforests following Olson et al. 2001). A total of 86 ecoregions were used, excluding

mangroves. Local lists were compiled for sites that were historically undisturbed (preferably protected areas), and had been surveyed in at least two seasons or years using multiple techniques. Local scale sites varied in size but averaged approximately 25 km^2. A total of 23 local scale lists were used for analysis, with representation from all biomes (see Supplementary Table S1 and a map of the study region in Supplementary Figure S1).

Body size data

Body mass data for all species was primarily obtained from Dunning (2008), and supplemented with data from Hockey et al. (2005) and Fry et al. (1988) where needed. I accounted for different reporting standards in the data (such as masses for one sex only, masses for few individuals, masses from different locations) using the methods of Greve et al. (2008). Where races differed in body size (as reported in Dunning 2008), but were treated as one species in Sinclair & Ryan (2003), the mean body size across races was used. Since the masses of ten percent of species (200/1967) could not be obtained from the literature, I divided the database into two sets. First, I used all the species with mass data obtained from the literature (N = 1 767). Second, I estimated the mass of species lacking data by averaging the masses of all congeners (N = 1 967). For seven of these species in monotypic genera body masses could not be estimated by this method and these species were omitted from this study (*Coccycolius iris*, *Dryotriorchis spectabilis*, *Pseudoalcippe abyssinica*, *Pseudochelidon eurystomina*, *Tigriornis leucolophus*, *Todirhamphus chloris*, *Zavattariornis stresemanni*). The distribution of bird body sizes from the two datasets did not differ significantly (Kolmogorov-Smirnov [KS] test, $D = 0.0211$, $p > 0.99$) and did not lead to different interpretations from the BSFDs (data not shown) and, therefore, I only report results further including the data calculated from congeners (N = 1 960). Both the Common and Somali Ostriches (*Struthio camelus, S. molybdophanes*) may be outliers in the dataset due to their very large body mass (~70 kg), but omitting them had a negligible impact when comparing the distributions of the two datasets (KS test, $D = 0.0004$; $p > 0.99$), or when interpreting BSFDs histograms (data not shown), so I retained these species at all scales where applicable.

Statistical analysis

The preliminary analyses broadly followed the methods of others (Brown & Nicoletto 1991; Bakker & Kelt 2000; Cardillo 2002; Greve et al. 2008; Kelt & Meyer 2009). All body masses were converted to $\log_2$ units to reduce heteroscedasticity and for ease of representation. Histograms were used to assess qualitatively the frequency distributions at all spatial scales. Because the analysis of BSFD can be affected by the position of frequency bins, I calculated the BSFD from the mean of three bracketed bins, at 0.5; 1 and 1.5 $\log_2$, respectively, following Kelt & Meyer (2009). Since body size distributions are typically skewed, median body size is a more appropriate measure for analysing body size data of assemblages than the mean (see Meiri & Thomas 2007).

Body size distributions were described using standard metrics; median body size, interquartile range, kurtosis and skew. To test the significance of differences in frequency distributions between successively smaller spatial scales, a Kolmogorov-Smirnoff goodness of fit test was used to compare all distributions and the larger spatial scale assemblages in which they are embedded (e.g. continental BSFD with all biomes' BSFDs, biomes with all their constituent ecoregions etc.). To test if the observed distributions differed significantly from a log-uniform distribution (e.g. Bakker & Kelt 2000), I compared every site to the average of 1 000 randomly generated log-uniform distributions with the same number of species and statistical range of masses as in that site. Since all sites differed highly significantly from a log-uniform distribution at all spatial scales (data not shown), I repeated the test using a random uniform distribution, especially given that the expectation is for such a distribution at the finest spatial scales (Bakker & Kelt 2000).

I also tested if the body masses of species assemblages at smaller scales are a random sub-sample from larger BSFDs. For each of the smaller scale assemblages I randomly drew, without replacement, species' body masses from the larger spatial scale assemblages, drawing the same number of species as was observed at that smaller scale site. Resampling was repeated 10 000 times, after which the median of each resampling was compared with the observed median for that particular site, and the proportion of simulated medians less than or greater than the observed median calculated (following Brown & Nicoletto 1991). Where the proportion of simulations meeting these criteria was less than 0.025 or greater

than 0.975 (i.e. a two-tailed test), the result indicated a significant difference, and therefore non-random local scale assemblage, at the alpha = 0.05 level.

The relationship between the median body size and environmental and spatial explanatory variables was examined at ecoregion and local spatial scales using generalized linear models (GLMs; assuming a Gaussian distribution with a log link function). I did not conduct this analysis at the biome scale due to a small sample size and high colinearity between explanatory variables. For each site, at ecoregion and local scales, explanatory variables were species richness, the mean range size of all species in each site in km^2 of ecoregion area occupied, latitude, longitude and seasonality in primary productivity (as estimated by the absolute difference between January and July NDVI values from 2004-2009, using the SPOT imagery at a 1 km x 1 km spatial resolution; online: www.devcocast.eu). The centroids of all sites were calculated with XTOOLs (online: www.xtoolspro.com) in ESRI ArcGIS 9.3 (2011) for the latitude and longitude coordinates. A small positive constant was added to response variables prior to analyses to ensure that only non-negative values were subject to the log-link function. To account for potential non-linear relationships the quadratic forms of all variables were also included in the models. To avoid multicolinearity among predictor variables, I deleted variables with high colinearity (measured as a Variance Inflation Factor > 10; Quinn & Keough, 2002) in a stepwise manner until colinearity was minimal (the Variance Inflation Factor < 10 for all variables included in the model; following Zuur et al. 2010). A best subsets regression approach was implemented using the 'bestglm' package in R (McLeod & Xu 2010), with all permutations of explanatory variables considered. The models were then ranked by Akaike Information Criterion values (AIC), with the lowest AIC value indicating the best-fit model (Johnson & Omland 2004; McLeod & Xu 2010).

Null models are pattern-generating models based on random sampling from a known distribution (Gotelli & Graves 1996). Three kinds of null models were produced to investigate whether stochastic processes contribute to observed patterns (Meiri & Thomas 2007), and to investigate the influence of geographic range size (Blackburn & Gaston 2001) and energy (Aava 2001; Huston & Wolverton 2009) on structuring BSFDs. First, to assess whether observed BSFDs could be explained by purely random assembly an 'unweighted null model' was produced, where for each site the same numbers of species as occurring at that site were randomly drawn without replacement from the continental species pool, the median body mass calculated across the randomly sampled species, and the resampling process

repeated 10 000 times. For this model all species have an equal probability of being sampled. Second, to account for wide-ranging species being more likely to occur at more sites, a 'range-weighted null model' was produced. For this null model the random draw procedure was repeated, but the probability of a species selection from the continental pool was positively weighted proportional to its range across all ecoregions (in km^2). Thus species with large ranges have a higher probability of being drawn. Third, to assess whether primary productivity structures BSFDs (see Aava 2001; Huston & Wolverton 2009), a 'NDVI-weighted null model' was created by weighting a species probability of selection from the continental pool by the mean NDVI value across its range. I compared each of the three null models calculated medians for each site at all scales to the actual observed median body mass values at that site with a Mann-Whitney U test (Quinn & Keough 2002).

All analyses were conducted in R (R Development Core Team 2010) and MS Excel, MS Access and ESRI ArcGIS 9.3 (2011) were used for data curation.

Results

The African continental avian BSFD is unimodal and significantly right-skewed (Figure 1; Skew = 1.14; $p < 0.0001$) with a mode in size class 3-5 (5.7 g - 45.3 g). BSFDs generally became less skewed and less modal with decreasing spatial scale of the analysis (Figure 2; Figure 3e; Supplementary Table S2). At successively smaller spatial scales, the mean, median and interquartile range of body mass generally increases and the distribution's skew and kurtosis decreases (Supplementary Table S2). Across all the BSFDs from all the three scales investigated, only the Mt. Kupe and the Kibale Forest local scale assemblage were more strongly skewed than the continental BSFD (Supplementary Table S2). Most distributions (95%; 112/117) are significantly right-skewed (skew for 112 distributions: 0.31-1.26; $p < 0.05$), apart from three ecoregions and two local scale distributions which show approximately symmetric distributions (East African montane moorlands, Ethiopian montane moorlands, Eritrean coastal desert, Seekoeivlei, Topoa Region; Supplementary Table S2). Nearly all (97%; 112/116) of the BSFDs showed a decrease in kurtosis by comparison with the continental assemblage (Supplementary Table S2). The majority of distributions (98%; 115/117) differed significantly from a random uniform distribution (means of 1000 iterations; KS tests $0.152 < D < 0.450$; and $p < 0.04$; Supplementary Table S2).

Only two distributions, the East African montane moorlands ecoregion and the Seekoeivlei local scale assemblage, did not differ significantly from a random uniform distribution (means of 1000 iterations; KS tests D = 0.154, p = 0.185 and D = 0.152, p = 0.258, respectively, Supplementary Table S2).

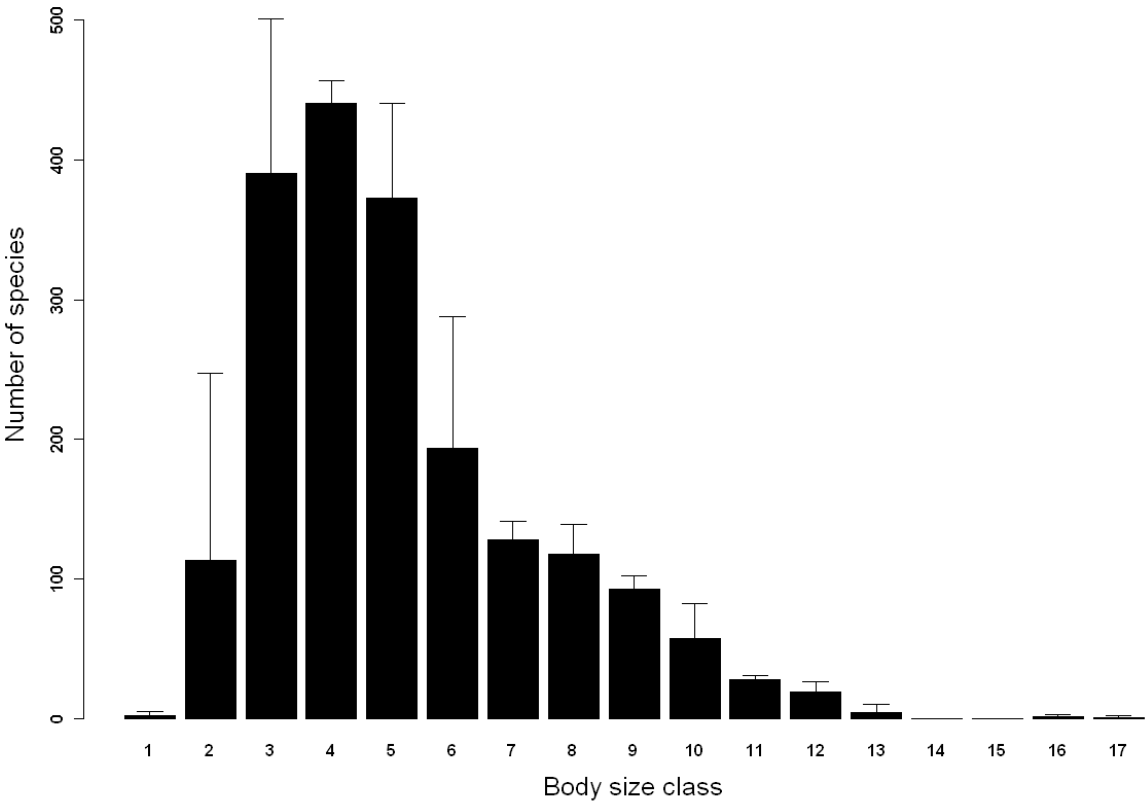

Figure 1. Body size frequency distribution for the avifauna of the continental Afrotropical biogeographic realm (N = 1 960). Avian body masses were $\log_2$ transformed and span body size classes from size class 1 (4.1 g) to 17 (~111 kg). Error bars indicate one standard deviation, as calculated across three size class bins.

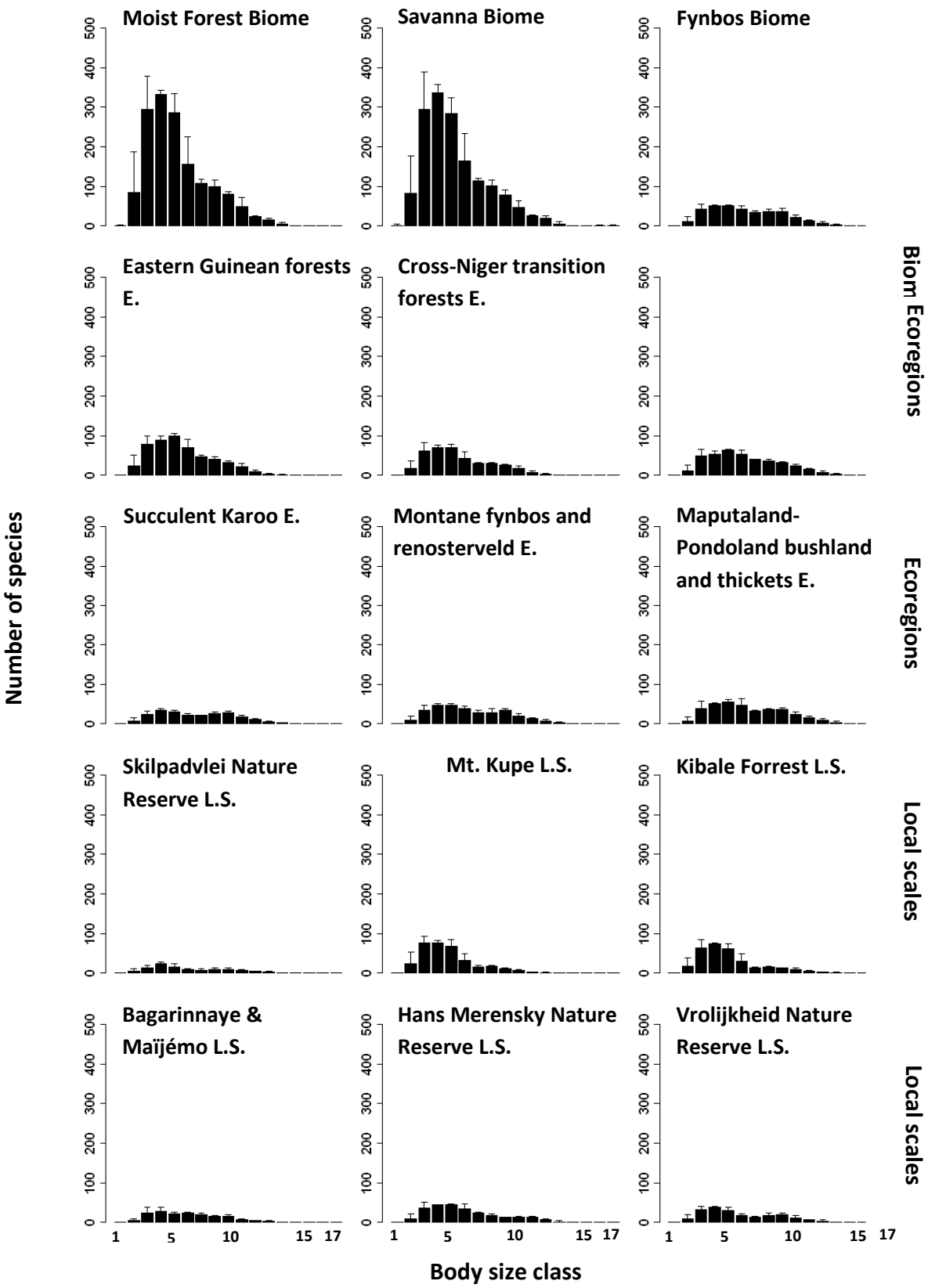

Figure 2. Body size frequency distributions from representative biome (top row), ecoregions (rows 2-3) and local scale sites (rows 4-5). Avian body masses were $\log_2$ transformed and span body size classes from size class 1 (4.1 g) to size class 17 (~111

kg), with the primary mode generally in size class 3-5. Error bars indicate one standard deviation. See Supplementary Table S1 for details of all biomes, ecoregions and local sites, and Supplementary Figure S1 for a map of the study region. (a = Moist Forest; b = Savanna; c = Fynbos; d = Eastern Guinean Forests; e = Cross-Niger Transition Forests; f = Western Zambezian Grasslands; g = Succulent Karoo; h = Montane Fynbos and Renosterveld; i = Maputaland-Pondoland Bushland and Thickets; j = Skilpadvlei Nature Reserve; k = Mt. Kupe; l = Kibale Forrest; m = Bagarinnaye & Maïjémo; n = Hans Merensky Nature Reserve; o = Vrolijkheid Nature Reserve).

The majority of smaller scale distributions are significantly different from their larger scale BSFDs (69%; 80/116; all 81 comparisons: KS tests $0.07 < D < 0.25$; $p < 0.05$; Supplementary Table S4). The Moist Forest and Savanna biomes do not differ significantly from the Continental distributions (KS tests $D = 0.02$, $p = 0.7$ and $D = 0.310$, $p = 0.3$, respectively) and neither do 22 ecoregions and nine local scale distributions differ significantly from the larger scale BSFDs distributions (Supplementary Table S4).

The median body mass of the majority of sites (84%; 97/116) differs significantly from distribution of medians generated through random selection of species from the larger spatial scale assemblages in which they are embedded (Supplementary Table S5). Most sites have significantly higher body mass than expected by chance (71%; 82/116), although 13% of sites have a significantly lower mass than expected (15/116) and some are not significantly different (16%; 19/116; Supplementary Table S5). These results in general are indicative of the non-random assembly of BSFDs at successively smaller spatial scales.

The best-fit GLM model explained 70.82% of the variation in median body mass values at the ecoregion scale and included latitude, latitude^2, longitude, species richness and species range size as significant explanatory variables (Table 1). At the local scale the best-fit model explained 84.98% of variation in median body mass as a function of NDVI, species richness^2 and range (Table 1).

At all spatial scales the median body sizes from all of the three null models were higher than the observed continental median (Figure 3a-d; Mann-Whitney U test, all significantly different; $49 < W < 10211$; $p < 0.05$). The body size predicted by the null models was

generally lower than the observed median values at the biome and ecoregions scales, although this was reversed at the local scales (Figure 3a-d; Supplementary Table S6). Compared with observed data, the unweighted null model produced median masses that are significantly lower at the biome and ecoregion scales, but higher at the local scales.

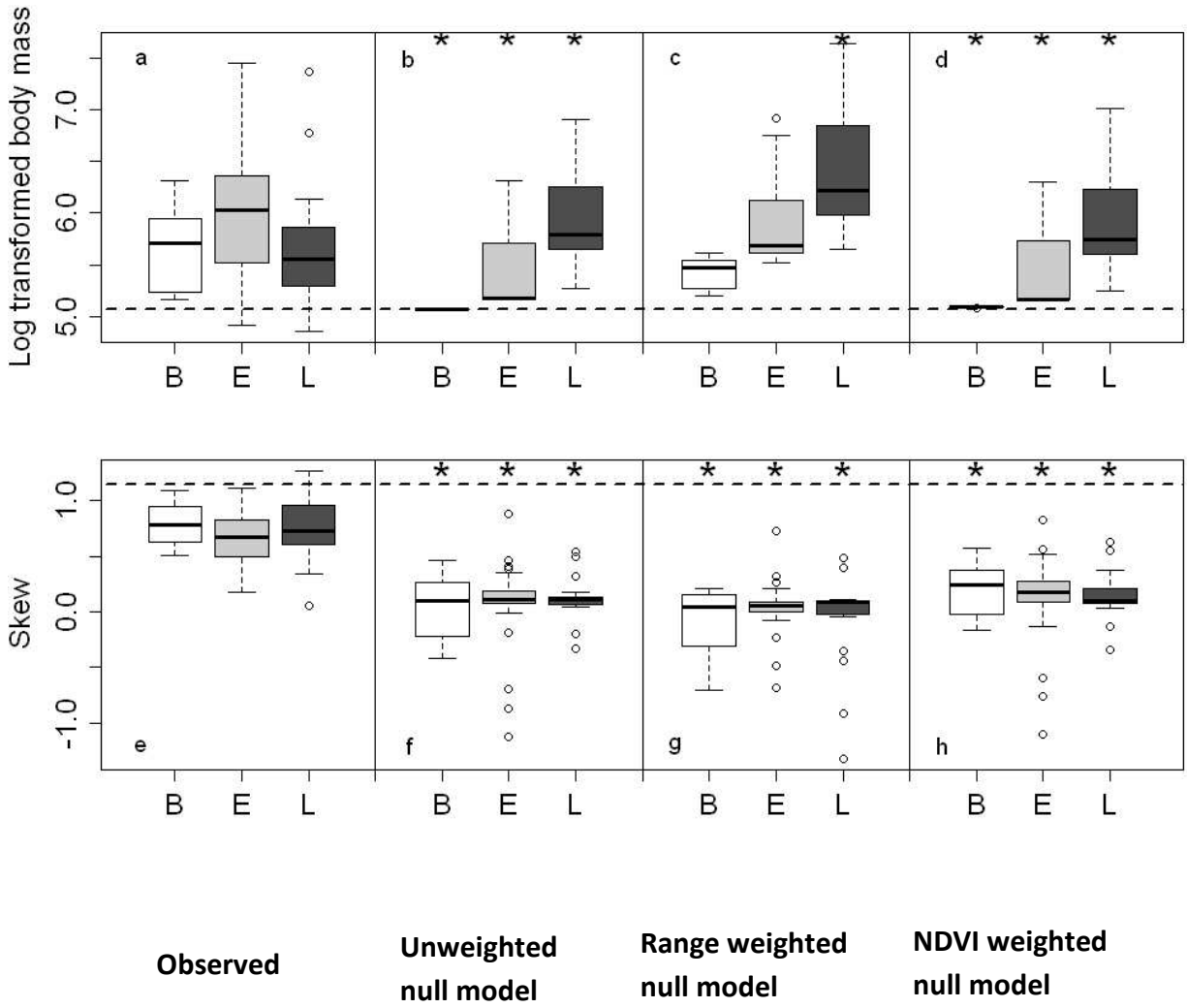

Figure 3. Median body mass and skew for observed data (a,e), the unweighted null model (b,f), the range-weighted null model (c,g), and the NDVI-weighted null model (d,h), at biome, ecoregion and local scales respectively. Dashed lines indicate the observed median body mass (5.07; top row of panels) and observed skew (1.14; bottom panels) at the continental scale. Thick lines indicate median values, boxes indicate the interquartile range, whiskers indicate the non-outlier range, and empty circles indicate outlier values (values more than 1.5 times the interquartile range)

across sites at that scale. B = biome scale; E = ecoregion scale; L = local scale. Null models marked with an asterisk differ significantly from the observed median at that scale (Mann-Whitney U test; 30 < W < 6341.5; p < 0.01). All skew values differ significantly from observed skew (Mann-Whitney U test; 47 < W < 7332; p < 0.002).

Table 1. Best fit multivariate generalized linear models of median body mass in relation to environmental variables.

	Ecoregion scale			**Local scale**		
AIC	51.316			5.821		
AIC weight	0.53			0.39		
N	86			23		
Deviance explained	70.82%			84.98%		
Predictor variable	Slope	SE	P	Slope	SE	P
Intercept	1.485	0.057	****	1.305	0.056	****
Latitude	0.002	0.001	**	n.s.		
Latitude^2	0.001	0.001	****	n.a.		
Longtitude	0.002	0.001	****	n.a.		
Longtitude^2	n.a.			n.s.		
NDVI	n.a.			0.001	0.000	***
NDVI^2	0.001	0.001		n.a.		
Species Richness	0.001	0.001	****	n.a.		
Species Richness^2	n.a.			0.000	0.000	
Range	0.442	0.0645	****	0.615	0.072	****
Range^2	n.a.			n.a.		

Significance codes: ****p <0.0001, ***p < 0.001, **p <0.01, *p < 0.05
n.s. = not significant; n.a. = not applicable (variable with high multicolinearity and was not used; see text for details)

This finding reaffirms that random processes alone cannot explain observed body size frequency distributions (Figure 3b; Supplementary Table S6). The biome and ecoregion scale range-weighted null model medians did not differ significantly from the observed median (Figure 3c; Mann-Whitney U test, $30 < W < 6421$; $p > 0.3$), although at the local scale there was a significant difference. Compared to observed data, the NDVI-weighted null model produced median masses that were significantly lower than expected at the biome and ecoregion scales, but higher at the local scales (Figure 3d; Mann-Whitney U test, all significantly different Mann-Whitney U test; $30 < W < 6341.5$; $p < 0.01$). The skew of all null models at all scales was lower than the observed continental skew, and significantly different at all scales from the observed data (Figure 3e-h; Mann-Whitney U test; $47 < W < 7332$; $p < 0.002$).

While the range-weighted null model provided an indication of the process underlying the observed BSFDs especially at broader scales (see Discussion), none of the null models showed median body masses or distribution skews similar to the local scale observed BSFDs (Figure 3). To test if the difference between observed median and null-modelled medians at the local scale (hereafter termed the null model residuals) could be explained, I used the same generalized linear modelling approach and identical variables as detailed in the above, for analysing the local scale data. Best fit models to explain the null model residuals at the local scale all had significant terms for space (latitude or longitude), NDVI and range, but not for species richness. Deviance explained for the unweighted null model, range-weighted null model, and NDVI-weighted null model, was 76.70%, 81.04% and 75.90%, respectively (Table 2).

Discussion

The continental African avifaunal body size frequency distribution (BSFD) is predominantly right-skewed and unimodal, similar in general to the BSFDs found for many vertebrates (e.g. Brown & Nicoletto 1991; Greenwood et al. 1996; Arita & Figueroa 1999; Polo & Carrascal 1999; Bakker & Kelt 2000; Knouft & Page 2003; Meiri 2008; Griffiths 2011, but see Reed & Boback 2002; Boback & Guyer 2003; Olden et al. 2007; Hu et al. 2011; Cox et al. 2011), for birds in the New World (Cardillo 2002) and for the global avifaunal distribution (Olson et al. 2009). Indeed, this pattern seems general (Gaston & Blackburn 2000; Chown & Gaston 2010;

but see Roy & Martien 2001; Boback & Guyer 2003; Ulrich & Fiera, 2010). Although the median mass of African birds (33.5 g) is only slightly lower than that of global avifauna (37.6 g; Blackburn & Gaston, 1994), the BSFDs for the African avifauna generally become less skewed and less modal with decreasing spatial scale of the analysis, as has been found for mammals elsewhere (e.g. Brown & Nicoletto 1991; Marquet & Cofré 1999; Bakker & Kelt 2000; Smith et al. 2004; Kelt & Meyer 2009). Surprisingly, the change in shape and central position of the BSFD has not been as widely characterized at a variety of spatial scales for birds, as it has been for mammals or reptiles (Cox et al. 2011). Indeed, formal, quantitative investigation of change in the BSFD with spatial scale for birds is typically limited to investigations of two spatial scales (e.g. Blackburn & Gaston 2001; Greve et al. 2008). In consequence, an understanding of the generality of the patterns found here across multiple spatial scales for a major continental landmass must rely on work done mostly on mammals.

Unlike African mammals, the African avifaunal BSFDs are not bimodal at all spatial scales (Kelt & Meyer 2009). Kelt & Meyer (2009) argued that large mammals in Africa coevolved with proto-human hunters and so predominantly escaped the mass extinctions typical of other regions. For birds at least, my data does not support this interpretation, mainly because it requires the presence of an additional mode to vindicate it, and the effect of proto-human hunters in structuring bird assemblages in any case is unclear. Rather, I suggest the difference in BSFDs between African mammals and birds points to substantial differences in various life history traits, body shape, foraging ecology, body architecture and macroecological features among these major taxa (Silva et al. 1997; Speakman 2005; Melo et al. 2009). Such consistent, among-clade trait variation potentially accounts for observed differences in the BSFDs of other taxa, such as the squamate reptiles (Boback & Guyer 2008; Cox et al. 2011). From the perspective of changes in BSFDs with spatial scale, the implications of these differences warrant further analysis. The pronounced additional mode at smaller spatial scales found in South American mammals is also absent in the African avifauna. Bakker & Kelt (2000) posited that Neotropical arboreal mammal species are of a smaller body size and can co-exist due to the addition of the rain forest canopy habitat which contains more and typically larger species, thus inflating local scale species richness and so increasing the number of low to medium mass species in the assemblages (Bakker & Kelt 2000, and see Marquet & Cofré 1999; Polo & Carrascal 1999).

Table 2. Best fit multivariate generalized linear models of unweighted, range-weighted and NDVI-weighted null model residuals (observed median minus calculated null model median), in relation to explanatory environmental variables at the local scale.

	Unweighted			**Range-weighted**			**NDVI-weighted**		
AIC	20.745			20.735			22.333		
AIC weight	0.43			0.54			0.42		
N	23			23			23		
Deviance explained	76.70%			81.04%			75.90%		
Predictor variable	Slope	SE	P	Slope	SE	P	Slope	SE	P
Intercept	-1.340	0.270	***	-1.140	0.267	***	-0.773	0.202	**
Latitude	0.085	0.004	*	n.a.			n.a.		
Latitude^2	n.a.			-0.001	0.001	***	n.s.		
Longtitude	n.a.			n.a.			n.a.		
Longtitude^2	0.001	0.001		n.s.			0.001	0.001	*
NDVI	0.009	0.002	***	n.a.			0.008	0.008	***
NDVI^2	n.a.			0.001	0.001	***	n.a.		
Species Richness	n.s.			n.a.			n.a.		
Species Richness^2	n.a.			n.s.			n.s.		
Range	n.a.			2.250	0.347	***	n.a.		
Range^2	1.855	0.355	***	n.a.			1.712	0.295	***

Significance codes: ****p <0.0001, ***p < 0.001, **p <0.01, *p < 0.05
n.s. = not significant; n.a. = not applicable (variable with high multicolinearity and was not used; see text for details)

Again that interpretation does not seem to apply here, mainly since it requires the addition of a second mode in BSFDs at smaller spatial scales (e.g. in Figure 2; Supplementary Table S2). Nonetheless, a similar mechanism may well apply at local spatial scales (see de Silva & Medellín 2002). Despite these differences with mammalian assemblages, the change in BSFDs from the continental to local scale found here is similar to the limited work on birds

(Gaston & Blackburn 2000; Blackburn & Gaston 2001; Cardillo 2002; Greve et al. 2008), suggesting that patterns found here likely hold for birds generally, as they seem to for many other taxa (e.g. Chown & Gaston 2010), although not for North American squamates (Cox et al. 2011).

In keeping with work on mammals (Brown & Nicoletto 1991; Smith et al. 2004; Bakker & Kelt 2000; Rodríguez et al. 2006) and birds (Blackburn & Gaston 2001; Greve et al. 2008) Afrotropical avian BSFDs at a range of spatial scales show non-random assembly from larger scale assemblages. Several explanations could account for this pattern. First, it has been suggested (Meiri & Thomas 2007) and demonstrated (Greve et al. 2008), that richness is likely to have a substantive effect on assemblage median mass, especially since in low richness sites the modal size is likely to be higher for reasons of sampling alone (Gaston & Blackburn 2000; Meiri & Thomas 2007). Although I found that richness was a significant explanatory variable for median mass at the ecoregion scale, when richness was accounted for in the unweighted null model, it failed to simulate the observed median body size. In consequence, some other mechanistic process must be responsible for the differences between the null and observed assemblages. Two of the primary contenders are energy, given its role in affecting size and size distributions (reviewed most recently by Huston & Wolverton 2011), and range size, given that smaller-bodied species tend to have higher spatial turnover than larger-bodied ones (Brown & Nicoletto 1991; Brown & Lomolino 1998; Melo et al. 2009; Chown & Gaston 2010), leading to the accumulation of more small-bodied species in BSFDs compiled at larger spatial extents.

Median body mass of assemblages in the NDVI-weighted null models differed significantly from the observed values at all spatial scales, and NDVI likewise did not enter as an explanatory variable in the generalized linear models except at the local scale. In consequence, at least at the biome and ecoregion scales variation in energy availability is unlikely a contender for explaining variation in BSFDs. By contrast, not only did range size enter the generalized linear models as a significant term, but at the biome and ecoregion scales, median body mass of the range-weighted null assemblages did not differ significantly from the observed values. In consequence, it appears that, at least at these scales, the change in central tendency of the BSFDs is well-explained by differences in turnover rate among smaller- and larger-bodied species, with the former tending to having the largest turnover rates (as suggested by a triangular range-size body size relationship;

Supplementary Figure S2 and see Brown & Lomolino 1998; Fernández & Vrba 2005; Melo et al. 2009). While it does not seem to apply to squamates (Cox et al. 2011), this explanation for differences in BSFDs at different spatial scales has been mooted for both birds and mammals (Brown & Nicoletto 1991; Blackburn & Gaston 2001), and my work provides further evidence for it.

Although not adequately captured in my null models, energy may still structure BSFDs especially at local scales, as indicated by differences between the NDVI-weighted null model median and observed median and that the observed data at this scale continue to be related to NDVI. While my measure of energy may be too coarse and should have rather been eNPP (Ecologically relevant Net Primary Productivity, defined as net primary production during the growing season; Huston & Wolverton 2011), it is clear that some other process is likely also involved because my models inevitably failed to capture the skew in the observed data. This unexplained mechanism may well be the optimization of size based on the size-dependence of production rates (the difference between energy assimilation and respiration) and mortality rates (Kozłowski & Gawelczyk 2002). Production rates are directly related to energy availability, while mortality may be indirectly related in the sense that mortality from predators, parasites or competitors is likely to increase as diversity increases, which is in turn related to energy availability (Hawkins et al. 2003; Currie et al. 2004). Such varying size optimization, an essentially evolutionary mechanism, is a key process that leads to positively skewed frequency distributions, but one that is not captured by any of the null models here. At larger spatial scales, size-based variation in diversification rates (Maurer et al. 1992; Gaston & Chown 1999; Kozłowski & Gawelczyk 2002), accompanied by variation in dispersal rates, which have a large influence on clade diversity (Phillimore et al. 2006), may be key in determining skewness. The role of productivity therefore clearly deserves further attention for the explanation of changes in size distributions with changing spatial scale.

Several caveats need to be taken into consideration in interpreting my results. First, in common with many other studies of BSFD variation, I was not always able to assess the effects of spatial autocorrelation, and future studies should take the potential effects thereof into consideration (see e.g. Bahn et al. 2006), although given the strength of the results here I do not think that the outcomes will be much affected (see also Bini et al. 2009). Second, due the lack of an appropriate and well resolved molecular phylogeny for the species in my study area, I could not incorporate phylogenetic affects, and future work

incorporating such an approach, especially examining the evolutionary mechanisms underlying the patterns I document, would likely account for much of the unexplained variation. Finally, there is much variation in the actual size of areas within the ecoregion and local scales. The continued presence of modes in body sizes at especially local scales (i.e. Mt. Kupe; Figure 2k) might indicate that the sites are too large or heterogeneous to effectively capture the change in BSFDs with scale. However, there is a consistent dampening of BSFDs across scales (Supplementary Table S2), a consistent low kurtosis of BSFDs within local scales (Supplementary Table S2) and the majority of smaller scale distributions differ from the larger scale distributions within which they are embedded (Supplementary Table S4). Consequently, regardless of the effective area of the sites, it appears that the observed patterns are consistent.

In conclusion, here I have shown that on log scales, the BSFDs in Afrotropical birds are unimodal, right-skewed and become less skewed and less modal with the decreasing spatial scale of the analysis, in keeping with patterns found in other taxa. Much of the pattern in median body size change with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD. However, at smaller spatial scales energy availability may be the most significant determinant of median size, and energy may also play a role in determining the substantial skew of distributions at all spatial scales through species-level optimization of size and the processes that lead to size-biased diversification. Exactly how diversity, size and diversification interact to produce BSFDs across spatial scales remains one of macroecology's largest challenges (see Allen et al. 2006; Smith & Lyons, 2011).

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Suppplementary material

Supplementary Table S1. Size, centroid coordinates and source of all sites analysed.

Abbreviation	Name	Spatial scale	Size (km^2)	Latitude (°N)	Longitude (°E)	"Parent" distribution	Source
cont	Continental	Continent	20291366	-1.49122	21.0831899	n.a.	1
mforest	Moist Forest	Biome	3151748	0.829353	19.2809295	Continental	1
dforest	Dry Forest	Biome	38085	-13.9103	23.6269209	Continental	1
savana	Tropical Savanna	Biome	13926640	1.421852	20.4592051	Continental	1
fsavana	Flooded Savanna	Biome	456066	-1.96939	25.6089879	Continental	1
grassland	Grassland	Biome	858675	-13.6639	29.7953857	Continental	1
fynbos	Fynbos	Biome	95608	-33.3734	21.2239519	Continental	1
desert	Desert	Biome	1764544	-18.9069	23.8332961	Continental	1
AT0101	Albertine Rift montane forests	Ecoregion	103404	-2.24021	29.4609682	Moist Forest	1
AT0102	Atlantic Equatorial coastal forests	Ecoregion	188821	-0.2953	10.7944297	Moist Forest	1
AT0103	Cameroonian Highlands forests	Ecoregion	37879	6.466968	11.0857391	Moist Forest	1
AT0104	Central Congolian lowland forests	Ecoregion	412882	-1.34229	21.779629	Moist Forest	1
AT0106	Cross-Niger transition forests	Ecoregion	20629	5.456205	7.41829952	Moist Forest	1
AT0107	Cross-Sanaga-Bioko coastal forests	Ecoregion	51840	5.189494	9.37155291	Moist Forest	1
AT0108	East African montane forests	Ecoregion	65199	-0.19334	35.6935523	Moist Forest	1
AT0109	Eastern Arc forests	Ecoregion	23556	-6.93058	36.7671439	Moist Forest	1
AT0110	Eastern Congolian swamp forests	Ecoregion	92315	-0.31151	20.4802647	Moist Forest	1
AT0111	Eastern Guinean forests	Ecoregion	188895	6.40246	-3.361625	Moist Forest	1
AT0112	Ethiopian montane forests	Ecoregion	247734	9.629402	38.2491541	Moist Forest	1
AT0114	Guinean montane forests	Ecoregion	30924	10.09664	-10.892088	Moist Forest	1
AT0115	Knysna-Amatole montane forests	Ecoregion	3061	-33.5689	24.2641123	Moist Forest	1
AT0116	KwaZulu-Cape coastal forest mosaic	Ecoregion	17779	-30.7895	29.9764095	Moist Forest	1
AT0119	Maputaland coastal forest mosaic	Ecoregion	30146	-26.3593	32.5347627	Moist Forest	1
AT0121	Mount Cameroon and Bioko montane forests	Ecoregion	1141	4.220224	9.17244005	Moist Forest	1
AT0122	Niger Delta swamp forests	Ecoregion	14343	5.113701	6.38698995	Moist Forest	1
AT0123	Nigerian lowland forests	Ecoregion	67043	6.834145	4.91956388	Moist Forest	1
AT0124	Northeastern Congolian lowland forests	Ecoregion	531067	1.647358	25.2060826	Moist Forest	1
AT0125	Northern Zanzibar-Inhambane coastal	Ecoregion	112151	-4.05068	39.9187777	Moist Forest	1

	forest mosaic						
AT0126	Northwestern Congolian lowland forests	Ecoregion	432190	1.709255	14.1550263	Moist Forest	1
AT0128	Southern Zanzibar-Inhambane coastal forest mosaic	Ecoregion	146463	-16.5641	37.8335378	Moist Forest	1
AT0129	Western Congolian swamp forests	Ecoregion	128060	1.076009	18.0093631	Moist Forest	1
AT0130	Western Guinean lowland forests	Ecoregion	204226	6.990911	-9.4989798	Moist Forest	1
AT0203	Zambezian Cryptosepalum dry forests	Ecoregion	38085	-13.9103	23.6269209	Dry Forest	1
AT0701	Angolan Miombo woodlands	Ecoregion	657515	-12.4747	18.1260003	Tropical Savanna	1
AT0702	Angolan Mopane woodlands	Ecoregion	133028	-17.9383	15.4562122	Tropical Savanna	1
AT0704	Central Zambezian Miombo woodlands	Ecoregion	1179319	-9.57786	28.6361672	Tropical Savanna	1
AT0705	East Sudanian savanna	Ecoregion	913702	8.432142	25.0921135	Tropical Savanna	1
AT0706	Eastern Miombo woodlands	Ecoregion	482013	-12.2385	37.2378148	Tropical Savanna	1
AT0707	Guinean forest-savanna mosaic	Ecoregion	670796	8.868827	-1.4071213	Tropical Savanna	1
AT0708	Itigi-Sumbu thicket	Ecoregion	7809	-7.14583	32.1708244	Tropical Savanna	1
AT0709	Kalahari Acacia-Baikiaea woodlands	Ecoregion	334545	-21.0716	22.9013751	Tropical Savanna	1
AT0710	Mandara Plateau mosaic	Ecoregion	7479	10.51551	13.7001792	Tropical Savanna	1
AT0711	Northern Acacia-Commiphora bushlands and thickets	Ecoregion	324482	0.659337	36.883814	Tropical Savanna	1
AT0712	Northern Congolian forest-savanna mosaic	Ecoregion	705006	5.496271	22.0591898	Tropical Savanna	1
AT0713	Sahelian Acacia savanna	Ecoregion	3042451	14.77224	14.8425903	Tropical Savanna	1
AT0714	Serengeti volcanic grasslands	Ecoregion	17948	-2.96551	35.5757234	Tropical Savanna	1
AT0715	Horn of Africa Acacia Savannas	Ecoregion	1049301	5.896454	43.4990672	Tropical Savanna	1
AT0716	Southern Acacia-Commiphora bushlands and thickets	Ecoregion	226770	-4.40234	35.3313267	Tropical Savanna	1
AT0717	Southern Africa bushveld	Ecoregion	222541	-22.6068	28.5113944	Tropical Savanna	1
AT0718	Southern Congolian forest-savanna mosaic	Ecoregion	567187	-5.72314	21.946612	Tropical Savanna	1
AT0719	Southern Miombo woodlands	Ecoregion	406913	-17.5322	31.337479	Tropical Savanna	1
AT0721	Victoria Basin forest-savanna mosaic	Ecoregion	165042	0.588198	32.1201791	Tropical Savanna	1
AT0722	West Sudanian savanna	Ecoregion	1631860	11.85605	-0.9301734	Tropical Savanna	1
AT0723	Western Congolian forest-savanna mosaic	Ecoregion	411615	-5.32822	15.0455601	Tropical Savanna	1
AT0724	Western Zambezian	Ecoregion	33890	-14.2774	22.9362017	Tropical	1

	grasslands					Savanna	
AT0725	Zambezian and Mopane woodlands	Ecoregion	471874	-19.1371	31.0127403	Tropical Savanna	1
AT0726	Zambezian Baikiaea woodlands	Ecoregion	263554	-17.2735	21.2277961	Tropical Savanna	1
AT0901	East African halophytics	Ecoregion	2626	-3.56569	35.7988699	Flooded Savanna	1
AT0902	Etosha Pan halophytics	Ecoregion	7208	-18.7924	16.3762274	Flooded Savanna	1
AT0903	Inner Niger Delta flooded savanna	Ecoregion	45868	15.50289	-3.641082	Flooded Savanna	1
AT0904	Lake Chad flooded savanna	Ecoregion	18761	13.30218	13.4584333	Flooded Savanna	1
AT0905	Saharan flooded grasslands	Ecoregion	178952	7.812708	31.4812205	Flooded Savanna	1
AT0906	Zambezian coastal flooded savanna	Ecoregion	19484	-18.7404	35.7147989	Flooded Savanna	1
AT0907	Zambezian flooded grasslands	Ecoregion	152878	-13.283	27.7395338	Flooded Savanna	1
AT0908	Zambezian halophytics	Ecoregion	30289	-21.4684	27.604028	Flooded Savanna	1
AT1001	Angolan montane forest-grassland mosaic	Ecoregion	25418	-12.5708	15.053464	Grassland	1
AT1002	Angolan scarp savanna and woodlands	Ecoregion	74055	-9.28066	13.7444781	Grassland	1
AT1003	Drakensberg alti-montane grasslands and woodlands	Ecoregion	11894	-29.7592	28.5947053	Grassland	1
AT1004	Drakensberg montane grasslands, woodlands and forests	Ecoregion	201962	-29.4548	28.9147458	Grassland	1
AT1005	East African montane moorlands	Ecoregion	3273	-1.27377	36.7688962	Grassland	1
AT1006	Eastern Zimbabwe montane forest-grassland mosaic	Ecoregion	7804	-18.9743	32.7679674	Grassland	1
AT1007	Ethiopian montane grasslands and woodlands	Ecoregion	244349	9.791951	38.2894877	Grassland	1
AT1008	Ethiopian montane moorlands	Ecoregion	25049	8.918108	38.9068999	Grassland	1
AT1009	Highveld grasslands	Ecoregion	185863	-27.6306	27.4923215	Grassland	1
AT1010	Jos Plateau forest-grassland mosaic	Ecoregion	13281	9.741702	9.07888345	Grassland	1
AT1012	Maputaland-Pondoland bushland and thickets	Ecoregion	19515	-31.0451	29.0288536	Grassland	1
AT1013	Rwenzori-Virunga montane moorlands	Ecoregion	2661	-0.16104	29.8184661	Grassland	1
AT1014	South Malawi montane forest-grassland mosaic	Ecoregion	10191	-15.7406	35.1070949	Grassland	1
AT1015	Southern Rift montane forest-grassland mosaic	Ecoregion	33360	-10.2588	34.0718509	Grassland	1
AT1201	Albany thickets	Ecoregion	17084	-33.2947	24.5148381	Fynbos	1
AT1202	Lowland fynbos and renosterveld	Ecoregion	32744	-33.7095	20.2250514	Fynbos	1
AT1203	Montane fynbos and renosterveld	Ecoregion	45780	-33.161	20.7129029	Fynbos	1

AT1303	East Saharan montane xeric woodlands	Ecoregion	27775	16.48732	22.9442612	Desert	1
AT1304	Eritrean coastal desert	Ecoregion	4577	12.83454	42.7775856	Desert	1
AT1305	Ethiopian xeric grasslands and shrublands	Ecoregion	152524	12.59552	41.9262444	Desert	1
AT1307	Hobyo grasslands and shrublands	Ecoregion	25454	4.095918	47.2440137	Desert	1
AT1309	Kalahari xeric savanna	Ecoregion	586846	-24.7113	21.2620495	Desert	1
AT1310	Kaokoveld desert	Ecoregion	45585	-17.0324	12.5731922	Desert	1
AT1313	Masai xeric grasslands and shrublands	Ecoregion	100505	2.585553	37.7972949	Desert	1
AT1314	Nama Karoo	Ecoregion	350726	-30.2063	21.8218514	Desert	1
AT1315	Namib desert	Ecoregion	80689	-23.8326	15.0764243	Desert	1
AT1316	Namibian savanna woodlands	Ecoregion	224903	-21.4483	15.346761	Desert	1
AT1319	Somali montane xeric woodlands	Ecoregion	62375	10.30347	49.1537608	Desert	1
AT1322	Succulent Karoo	Ecoregion	102585	-30.5306	18.4123201	Desert	1
Anysberg	Anysberg Nature Reserve	Local scale	465	-33.4762	20.58355	AT1203	2
Bagarin	Bagarinnaye and Maïjémo villages	Local scale	26.5	14.14608	4.951483	AT0713	3
Gola	Gola heights	Local scale	1	7.475966	-10.669205	AT0130	4
Gustav	Gustav Klingbiel Nature Reserve	Local scale	1	-25.0891	30.504401	AT1004	5
Hans	Hans Merensky Nature Reserve	Local scale	527	-23.6977	30.668392	AT0725	2
kibale	Kibale Forest	Local scale	776	0.501507	30.412473	AT0101	7
kifufu	Kifufu Farm	Local scale	0.8	-3.163	37.075264	AT0108	6
kyabobo	Kyabobo National Park	Local scale	360	8.402048	0.620362	AT0722	8
Magangwe	Magangwe, Ruaha National Park	Local scale	0.8	-7.67504	37.919606	AT0125	6
mamala	Malala Lodge	Local scale	1.35	-27.9037	32.283793	AT0119	9
mtkupe	Mt. Kupe	Local scale	50	4.808373	9.710214	AT0103	10
platberg	Platberg Nature Reserve	Local scale	1.5	-28.3614	28.927368	AT1009	2
pugu	Pugu Hills	Local scale	0.8	-6.88515	39.101965	AT0125	6
remhoog	Remhoogte	Local scale	1	-33.3713	21.236378	AT1322	10
seekoei	Seekoeivlei	Local scale	1	-28.072	29.13193	AT1009	11
Sengwa	Sengwa Wildlife Research Area	Local scale	373	-18.1949	28.167161	AT0725	12
Skilpad	Skilpadvlei Nature Reserve	Local scale	400	-30.1603	17.809529	AT1322	2
sokoke	Arabuko Sokoke Forest	Local scale	410	-3.31476	39.875398	AT0125	13
speke	Speke Bay Lodge	Local scale	0.8	2.265217	33.79695	AT0705	6

swartbos	Swartboskloof	Local scale	1	-34.0492	18.955848	AT1203	14
Tapoa	Tapoa Region, W Niger National Park	Local scale	8	12.32231	2.227	AT0722	3
Vrolik	Vrolijkheid Nature Reserve	Local scale	250	-33.9282	19.910543	AT1203	2
yapo	Yapo forest	Local scale	240	5.351895	-4.027552	AT0111	15

Source codes:

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Supplementary Table S2. Summary statistics of species richness and log transformed body mass (grams) for all sites analysed at all scales. Min = minimum, Max = maximum, IQR = inter-quartile range.

			Body mass (g)							
Abbreviation	**Name**	**Total species richness**	**Mean**	**Median**	**Min**	**Max**	**IQR**	**Skew**	**Skew p-value**	**Kurtosis**
cont	Continental	1960	5.623	5.068	2.170	16.760	2.699	1.145	<0.001	4.022
mforest	Moist Forest	1531	5.712	5.170	2.170	13.217	2.958	0.994	<0.001	3.350
dforest	Dry Forest	393	6.571	6.113	2.655	13.217	3.867	0.514	<0.001	2.339
savana	Tropical Savanna	1549	5.748	5.170	2.170	16.760	3.020	1.090	<0.001	3.885
fsavana	Flooded Savanna	781	6.344	5.781	2.379	16.760	3.631	0.751	<0.001	2.962
grassland	Grassland	1118	5.934	5.303	2.406	13.217	3.355	0.899	<0.001	3.019
fynbos	Fynbos	346	6.826	6.308	2.561	16.760	4.078	0.508	<0.001	2.650
desert	Desert	804	6.354	5.714	2.170	16.760	3.668	0.781	<0.001	3.109
AT0101	Albertine Rift montane forests	746	5.801	5.271	2.406	13.217	2.875	1.003	<0.001	3.369
AT0102	Atlantic Equatorial coastal forests	491	5.820	5.276	2.585	13.217	2.898	0.894	<0.001	3.079
AT0103	Cameroonian Highlands forests	578	5.913	5.385	2.511	13.217	3.219	0.888	<0.001	3.098
AT0104	Central Congolian lowland	349	5.955	5.399	2.511	13.217	2.988	0.880	<0.001	3.060

	forests									
AT0106	Cross-Niger transition forests	371	6.029	5.511	2.511	12.589	3.483	0.708	<0.001	2.600
AT0107	Cross-Sanaga-Bioko coastal forests	487	5.761	5.240	2.511	12.589	3.041	0.892	<0.001	3.011
AT0108	East African montane forests	638	6.222	5.552	2.379	13.217	3.728	0.741	<0.001	2.621
AT0109	Eastern Arc forests	557	6.171	5.564	2.561	13.217	3.638	0.738	<0.001	2.684
AT0110	Eastern Congolian swamp forests	356	5.882	5.279	2.511	13.217	3.026	0.920	<0.001	3.124
AT0111	Eastern Guinean forests	513	6.046	5.597	2.511	12.627	3.253	0.675	<0.001	2.720
AT0112	Ethiopian montane forests	496	6.761	6.353	2.585	13.217	4.346	0.405	<0.001	2.156
AT0114	Guinean montane forests	409	6.133	5.585	2.632	12.627	3.355	0.757	<0.001	2.750
AT0115	Knysna-Amatole montane forests	270	7.023	6.791	2.776	13.217	4.149	0.311	0.019	2.188
AT0116	KwaZulu-Cape coastal forest mosaic	374	6.946	6.442	2.621	13.217	4.081	0.410	0.001	2.266
AT0119	Maputaland coastal forest mosaic	397	6.794	6.300	2.621	13.217	3.865	0.429	<0.001	2.266
AT0121	Mount Cameroon and Bioko montane forests	399	5.925	5.498	2.511	12.627	3.098	0.827	<0.001	2.940
AT0122	Niger Delta swamp forests	330	6.057	5.518	2.511	12.589	3.297	0.747	<0.001	2.732
AT0123	Nigerian lowland forests	404	5.931	5.408	2.511	12.627	3.121	0.823	<0.001	2.912
AT0124	Northeastern Congolian lowland forests	560	5.905	5.322	2.511	12.853	3.030	0.885	<0.001	2.969
AT0125	Northern Zanzibar-Inhambane coastal forest mosaic	558	6.201	5.659	2.170	13.217	3.509	0.678	<0.001	2.602
AT0126	Northwestern Congolian lowland forests	532	5.687	5.214	2.511	13.217	2.727	0.978	<0.001	3.333
AT0128	Southern	462	6.411	5.886	2.561	13.217	3.756	0.610	<0.001	2.493

AT0129	Zanzibar-Inhambane coastal forest mosaic	323	6.033	5.505	2.511	13.217	3.282	0.838	<0.001	2.937
AT0130	Western Congolian swamp forests	448	5.984	5.477	2.585	12.627	3.326	0.750	<0.001	2.727
AT0203	Western Guinean lowland forests	393	6.571	6.113	2.655	13.217	3.867	0.514	<0.001	2.339
AT0701	Zambezian Cryptosepalum dry forests	541	6.090	5.476	2.715	16.760	3.466	0.898	<0.001	3.268
AT0702	Angolan Miombo woodlands	390	6.800	6.288	2.722	16.760	3.745	0.654	<0.001	2.840
AT0704	Angolan Mopane woodlands	721	6.049	5.476	2.561	16.760	3.336	0.931	<0.001	3.368
AT0705	Central Zambezian Miombo woodlands	627	6.247	5.650	2.322	16.760	3.815	0.769	<0.001	2.867
AT0706	East Sudanian savanna	472	6.363	5.821	2.561	16.760	3.631	0.752	<0.001	3.019
AT0707	Eastern Miombo woodlands	547	6.211	5.650	2.322	13.217	3.646	0.717	<0.001	2.689
AT0708	Guinean forest-savanna mosaic	361	6.978	6.781	2.776	16.760	3.761	0.468	<0.001	2.714
AT0709	Itigi-Sumbu thicket	478	6.611	6.145	2.561	16.760	3.775	0.655	<0.001	2.797
AT0710	Kalahari Acacia-Baikiaea woodlands	319	6.652	6.192	2.585	16.760	3.953	0.616	<0.001	2.814
AT0711	Mandara Plateau mosaic	710	6.230	5.621	2.170	16.760	3.578	0.860	<0.001	3.247
AT0712	Northern Acacia-Commiphora bushlands and thickets	621	6.056	5.479	2.536	16.760	3.470	0.882	<0.001	3.206
AT0713	Northern Congolian forest-savanna mosaic	548	6.637	6.174	2.536	16.760	4.103	0.579	<0.001	2.584
AT0714	Sahelian Acacia savanna	435	6.811	6.300	2.585	16.760	3.917	0.556	<0.001	2.656
	Serengeti volcanic grasslands									

AT0715	Horn of Africa Acacia Savannas	561	6.442	5.768	2.170	16.760	3.905	0.760	<0.001	3.064
AT0716	Southern Acacia-Commiphora bushlands and thickets	609	6.315	5.697	2.263	16.760	3.688	0.787	<0.001	2.979
AT0717	Southern Africa bushveld	487	6.570	6.066	2.561	16.760	3.822	0.653	<0.001	2.796
AT0718	Southern Congolian forest-savanna mosaic	559	5.931	5.361	2.511	12.627	3.228	0.859	<0.001	2.920
AT0719	Southern Miombo woodlands	524	6.385	5.857	2.561	16.760	3.635	0.793	<0.001	3.051
AT0721	Victoria Basin forest-savanna mosaic	640	6.068	5.468	2.585	16.760	3.526	0.885	<0.001	3.194
AT0722	West Sudanian savanna	553	6.298	5.748	2.322	16.760	3.902	0.721	<0.001	2.892
AT0723	Western Congolian forest-savanna mosaic	558	5.844	5.271	2.511	13.217	3.088	0.933	<0.001	3.126
AT0724	Western Zambezian grasslands	379	6.671	6.214	2.776	13.217	3.744	0.493	<0.001	2.351
AT0725	Zambezian and Mopane woodlands	576	6.348	5.792	2.561	16.760	3.630	0.785	<0.001	3.020
AT0726	Zambezian Baikiaea woodlands	519	6.207	5.618	2.715	16.760	3.607	0.842	<0.001	3.159
AT0901	East African halophytics	225	6.922	6.539	2.916	16.760	3.489	0.653	<0.001	3.184
AT0902	Etosha Pan halophytics	220	6.906	6.409	2.916	16.760	3.657	0.725	<0.001	3.253
AT0903	Inner Niger Delta flooded savanna	295	6.968	6.864	2.632	16.760	4.265	0.489	<0.001	2.693
AT0904	Lake Chad flooded savanna	299	7.091	6.919	2.715	16.760	4.266	0.427	0.001	2.585
AT0905	Saharan flooded grasslands	402	6.696	6.272	2.379	16.760	4.113	0.574	<0.001	2.653
AT0906	Zambezian coastal flooded savanna	313	7.139	6.781	2.561	16.760	3.983	0.455	0.001	2.673
AT0907	Zambezian flooded	519	6.511	5.921	2.561	16.760	3.754	0.728	<0.001	2.890

	grasslands									
AT0908	Zambezian halophytics	267	6.836	6.366	2.776	16.760	3.572	0.723	<0.001	3.250
AT1001	Angolan montane forest-grassland mosaic	364	6.102	5.476	2.744	13.217	3.493	0.810	<0.001	2.770
AT1002	Angolan scarp savanna and woodlands	388	6.281	5.696	2.632	13.217	3.444	0.688	<0.001	2.581
AT1003	Drakensberg alti-montane grasslands and woodlands	294	7.036	6.684	2.561	13.217	4.479	0.341	0.009	2.079
AT1004	Drakensberg montane grasslands, woodlands and forests	467	6.533	5.865	2.561	13.217	3.976	0.625	<0.001	2.385
AT1005	East African montane moorlands	122	7.107	6.955	2.744	12.853	4.837	0.241	0.140	1.914
AT1006	Eastern Zimbabwe montane forest-grassland mosaic	403	6.584	6.098	2.561	13.217	3.921	0.556	<0.001	2.353
AT1007	Ethiopian montane grasslands and woodlands	526	6.669	6.168	2.585	13.217	4.193	0.501	<0.001	2.261
AT1008	Ethiopian montane moorlands	349	7.392	7.304	2.776	13.217	4.045	0.178	0.088	2.121
AT1009	Highveld grasslands	405	6.690	6.209	2.561	13.217	4.109	0.500	<0.001	2.218
AT1010	Jos Plateau forest-grassland mosaic	63	5.333	4.912	2.744	11.454	2.546	1.116	<0.001	3.672
AT1012	Maputaland-Pondoland bushland and thickets	354	6.949	6.378	2.776	13.217	4.139	0.420	0.001	2.228
AT1013	Rwenzori-Virunga montane moorlands	181	6.752	6.178	2.406	12.627	4.285	0.354	0.027	2.073
AT1014	South Malawi montane forest-grassland mosaic	418	6.600	6.090	2.561	13.217	3.774	0.548	<0.001	2.382
AT1015	Southern Rift montane forest-	505	6.367	5.817	2.715	13.217	3.677	0.667	0.000	2.540

	grassland mosaic									
AT1201	Albany thickets	275	6.951	6.700	2.722	13.217	4.218	0.257	0.042	2.110
AT1202	Lowland fynbos and renosterveld	292	6.922	6.511	2.561	13.217	4.222	0.324	0.012	2.116
AT1203	Montane fynbos and renosterveld	307	6.891	6.304	2.561	16.760	4.244	0.531	<0.001	2.631
AT1303	East Saharan montane xeric woodlands	307	6.891	6.304	2.561	16.760	4.244	0.531	<0.001	2.631
AT1304	Eritrean coastal desert	206	7.488	7.451	2.715	16.760	4.252	0.266	0.060	2.409
AT1305	Ethiopian xeric grasslands and shrublands	363	6.891	6.391	2.700	16.760	4.518	0.460	<0.001	2.522
AT1307	Hobyo grasslands and shrublands	147	6.524	6.001	2.170	16.760	3.692	1.078	<0.001	5.252
AT1309	Kalahari xeric savanna	342	6.866	6.378	2.561	16.760	4.079	0.587	<0.001	2.694
AT1310	Kaokoveld desert	228	7.180	7.087	2.722	16.760	4.383	0.385	0.009	2.606
AT1313	Masai xeric grasslands and shrublands	341	6.954	6.408	2.170	16.760	4.708	0.508	<0.001	2.725
AT1314	Nama Karoo	305	6.792	6.269	2.561	16.760	4.225	0.593	<0.001	2.613
AT1315	Namib desert	185	7.069	7.129	2.722	16.760	4.299	0.364	0.022	2.854
AT1316	Namibian savanna woodlands	308	6.845	6.317	2.561	16.760	4.200	0.569	<0.001	2.618
AT1319	Somali montane xeric woodlands	162	6.392	5.745	2.170	16.760	3.537	1.018	<0.001	4.744
AT1322	Succulent Karoo	224	7.061	6.857	2.561	16.760	4.505	0.401	0.008	2.568
yapo	Yapo forest	219	5.389	5.138	2.511	11.830	2.190	0.970	<0.001	3.444
mtkupe	Mt. Kupe	328	5.220	4.863	2.511	12.408	2.218	1.183	<0.001	4.105
sengwa	Sengwa Wildlife Research Area	259	6.597	6.113	2.897	16.760	3.274	0.841	<0.001	3.333
remhoog	Remhoogte	151	6.251	5.548	2.561	12.034	4.588	0.550	0.003	2.066
swartbos	Swartboskloof	76	6.090	5.389	2.954	12.034	3.426	0.706	0.007	2.460
gustav	Gustav Klingbiel Nature Reserve	270	6.299	5.597	2.711	12.997	3.801	0.703	<0.001	2.475
seekoei	Seekoeivlei	107	7.519	7.366	2.897	12.997	4.382	0.055	0.408	1.990
gola	Gola heights	243	5.617	5.186	2.511	11.830	2.415	0.965	<0.001	3.180
kyabobo	Kyabobo National Park	229	5.457	5.053	2.632	11.988	2.445	0.956	<0.001	3.304
vrolik	Vrolijkheid Nature Reserve	196	6.428	5.616	2.561	16.760	4.276	0.722	<0.001	2.920

kibale	Kibale Forest	305	5.473	4.940	2.511	13.217	2.233	1.264	<0.001	4.111
platberg	Platberg Nature Reserve	131	6.631	6.118	2.561	12.997	4.571	0.415	0.027	2.035
skilpad	Skilpadvlei Nature Reserve	103	6.331	5.379	2.561	12.034	4.191	0.609	0.007	2.218
hans	Hans Merensky Nature Reserve	249	6.377	5.817	2.776	12.997	3.352	0.782	<0.001	2.727
anysberg	Anysberg Nature Reserve	157	6.326	5.555	2.561	16.760	4.046	0.823	<0.001	3.323
mamala	Malala Lodge	268	6.247	5.628	2.776	13.217	3.960	0.715	<0.001	2.525
tapoa	Tapoa Region, W Niger National Park	130	6.815	6.781	2.744	12.589	3.523	0.337	0.059	2.307
sokoke	Arabuko Sokoke Forest	139	5.560	5.343	2.585	11.830	2.247	0.953	<0.001	3.790
bagarin	Bagarinnaye and Maïjémo villages	164	6.451	6.135	2.744	12.592	3.974	0.514	0.004	2.427
kifufu	Kifufu Farm	332	6.041	5.299	2.715	12.853	3.551	0.815	<0.001	2.628
magangwe	Magangwe, Ruaha National Park	306	6.366	5.921	2.715	12.853	3.752	0.611	<0.001	2.468
pugu	Pugu Hills	168	5.789	5.284	2.585	12.408	2.412	1.034	<0.001	3.390
speke	Speke Bay Lodge	289	6.329	5.748	2.585	13.217	3.528	0.689	<0.001	2.610

Supplementary Table S3. Summary of comparison of observed data to a randomly generated uniform distributions with the maximum and minimum body mass values taken from the continental species pool, using a Kolmogorov-Smirnoff goodness of fit test and repeated 1000 times.

Name	Mean of 1000 D statistics	Mean of 1000 p-values	Count of p-values p> 0.05 at each of 1000 iterations
Continental	0.450	<0.001	0
Moist Forrest	0.333	<0.001	0
Dry Forrest	0.222	<0.001	0
Tropical Savanna	0.432	<0.001	0
Flooded Savanna	0.389	<0.001	0

Grassland	0.310	<0.001	0
Fynbos	0.365	<0.001	0
Desert	0.378	<0.001	0
Albertine Rift montane forests	0.347	<0.001	0
Atlantic Equatorial coastal forests	0.351	<0.001	0
Cameroonian Highlands forests	0.316	<0.001	0
Central Congolian lowland forests	0.325	<0.001	0
Cross-Niger transition forests	0.274	<0.001	0
Cross-Sanaga-Bioko coastal forests	0.328	<0.001	0
East African montane forests	0.257	<0.001	0
Eastern Arc forests	0.276	<0.001	0
Eastern Congolian swamp forests	0.335	<0.001	0
Eastern Guinean forests	0.273	<0.001	0
Ethiopian montane forests	0.190	<0.001	0
Guinean montane forests	0.274	<0.001	0
Knysna-Amatole montane forests	0.193	0.001	2
KwaZulu-Cape coastal forest mosaic	0.188	<0.001	0
Maputaland coastal forest mosaic	0.199	<0.001	0
Mount Cameroon and Bioko montane forests	0.302	<0.001	0
Niger Delta swamp forests	0.278	<0.001	0
Nigerian lowland forests	0.299	<0.001	0
Northeastern Congolian lowland forests	0.319	<0.001	0
Northern Zanzibar-Inhambane coastal forest mosaic	0.256	<0.001	0
Northwestern Congolian lowland forests	0.370	<0.001	0
Southern Zanzibar-Inhambane coastal forest mosaic	0.243	<0.001	0
Western Congolian swamp forests	0.310	<0.001	0
Western Guinean lowland forests	0.289	<0.001	0
Zambezian Cryptosepalum dry forests	0.223	<0.001	0
Angolan Miombo woodlands	0.418	<0.001	0
Angolan Mopane woodlands	0.367	<0.001	0
Central Zambezian Miombo woodlands	0.420	<0.001	0
East Sudanian savanna	0.378	<0.001	0
Eastern Miombo woodlands	0.390	<0.001	0
Guinean forest-savanna mosaic	0.258	<0.001	0
Itigi-Sumbu thicket	0.365	<0.001	0
Kalahari Acacia-Baikiaea woodlands	0.372	<0.001	0
Mandara Plateau mosaic	0.369	<0.001	0
Northern Acacia-Commiphora bushlands and thickets	0.378	<0.001	0
Northern Congolian forest-savanna mosaic	0.411	<0.001	0

Sahelian Acacia savanna	0.364	<0.001	0
Serengeti volcanic grasslands	0.362	<0.001	0
Horn of Africa Acacia Savannas	0.363	<0.001	0
Southern Acacia-Commiphora bushlands and thickets	0.381	<0.001	0
Southern Africa bushveld	0.373	<0.001	0
Southern Congolian forest-savanna mosaic	0.300	<0.001	0
Southern Miombo woodlands	0.388	<0.001	0
Victoria Basin forest-savanna mosaic	0.411	<0.001	0
West Sudanian savanna	0.385	<0.001	0
Western Congolian forest-savanna mosaic	0.344	<0.001	0
Western Zambezian grasslands	0.223	<0.001	0
Zambezian and Mopane woodlands	0.389	<0.001	0
Zambezian Baikiaea woodlands	0.410	<0.001	0
East African halophytics	0.382	<0.001	0
Etosha Pan halophytics	0.390	<0.001	0
Inner Niger Delta flooded savanna	0.360	<0.001	0
Lake Chad flooded savanna	0.347	<0.001	0
Saharan flooded grasslands	0.359	<0.001	0
Zambezian coastal flooded savanna	0.340	<0.001	0
Zambezian flooded grasslands	0.376	<0.001	0
Zambezian halophytics	0.385	<0.001	0
Angolan montane forest-grassland mosaic	0.309	<0.001	0
Angolan scarp savanna and woodlands	0.276	<0.001	0
Drakensberg alti-montane grasslands and woodlands	0.164	0.006	20
Drakensberg montane grasslands, woodlands and forests	0.229	<0.001	0
East African montane moorlands	0.154	0.185	731
Eastern Zimbabwe montane forest-grassland mosaic	0.217	<0.001	0
Ethiopian montane grasslands and woodlands	0.201	<0.001	0
Ethiopian montane moorlands	0.164	0.002	2
Highveld grasslands	0.203	<0.001	0
Jos Plateau forest-grassland mosaic	0.381	0.003	8
Maputaland-Pondoland bushland and thickets	0.189	<0.001	0
Rwenzori-Virunga montane moorlands	0.173	0.028	161
South Malawi montane forest-grassland mosaic	0.221	<0.001	0
Southern Rift montane forest-grassland mosaic	0.256	<0.001	0
Albany thickets	0.196	0.001	0

Lowland fynbos and renosterveld	0.190	0.001	1
Montane fynbos and renosterveld	0.354	<0.001	0
East Saharan montane xeric woodlands	0.354	<0.001	0
Eritrean coastal desert	0.317	<0.001	0
Ethiopian xeric grasslands and shrublands	0.362	<0.001	0
Hobyo grasslands and shrublands	0.413	<0.001	0
Kalahari xeric savanna	0.352	<0.001	0
Kaokoveld desert	0.349	<0.001	0
Masai xeric grasslands and shrublands	0.334	<0.001	0
Nama Karoo	0.347	<0.001	0
Namib desert	0.381	<0.001	0
Namibian savanna woodlands	0.345	<0.001	0
Somali montane xeric woodlands	0.407	<0.001	0
Succulent Karoo	0.352	<0.001	0
Yapo forrest	0.373	<0.001	0
Mt. Kupe	0.419	<0.001	0
Sengwa Wildlife Research Area	0.398	<0.001	0
Remhoogte	0.226	0.007	26
Swartboskloof	0.288	0.018	82
Gustav Klingbiel Nature Reserve	0.277	<0.001	0
Seekoeivlei	0.152	0.258	781
Gola heights	0.341	<0.001	0
Kyabobo National Park	0.368	<0.001	0
Vrolijkheid Nature Reserve	0.382	<0.001	0
Kibale Forrest	0.423	<0.001	0
Platberg Nature Reserve	0.209	0.024	111
Skilpadvlei Nature Reserve	0.233	0.030	157
Hans Merensky Nature Reserve	0.282	<0.001	0
Anysberg Nature Reserve	0.392	<0.001	0
Malala Lodge	0.301	<0.001	0
Tapoa Region, W Niger National Park	0.205	0.035	157
Arabuko Sokoke Forrest	0.374	<0.001	0
Bagarinnaye and Maïjémo villages	0.232	0.003	9
Kifufu Farm	0.301	<0.001	0
Magangwe, Ruaha National Park	0.245	<0.001	0
Pugu Hills	0.364	<0.001	0
Speke Bay Lodge	0.266	<0.001	0

Supplementary Table S4. Kolmogorov-Smirnoff goodness of fit test between all nested distributions (continental BSFDs with the BSFDs of all biomes, biome BSFDs with all their constituent ecoregions' BSFDs, etc.). See Supplementary Table S1 for abbreviations.

Name	D Statistic	p-value
cont_mforest	0.024	0.702
cont_dforest	0.213	< 0.001
cont_savana	0.033	0.305
cont_fsavana	0.157	< 0.001
cont_grassland	0.066	0.004
cont_fynbos	0.251	< 0.001
cont_desert	0.155	< 0.001
mforest_AT0101	0.038	0.456
mforest_AT0102	0.059	0.147
mforest_AT0103	0.049	0.264
mforest_AT0104	0.069	0.129
mforest_AT0106	0.080	0.045
mforest_AT0107	0.039	0.613
mforest_AT0108	0.102	< 0.001
mforest_AT0109	0.104	< 0.001
mforest_AT0110	0.048	0.529
mforest_AT0111	0.103	0.001
mforest_AT0112	0.217	< 0.001
mforest_AT0114	0.107	0.001
mforest_AT0115	0.281	< 0.001
mforest_AT0116	0.252	< 0.001
mforest_AT0119	0.226	< 0.001
mforest_AT0121	0.079	0.039
mforest_AT0122	0.096	0.014
mforest_AT0123	0.069	0.094
mforest_AT0124	0.054	0.191
mforest_AT0125	0.116	< 0.001
mforest_AT0126	0.038	0.631
mforest_AT0128	0.154	< 0.001
mforest_AT0129	0.085	0.044
mforest_AT0130	0.078	0.030
dforest_AT0203	<0.001	1.000
savana_AT0701	0.080	0.011
savana_AT0702	0.225	< 0.001
savana_AT0704	0.065	0.030
savana_AT0705	0.112	< 0.001
savana_AT0706	0.136	< 0.001

savana_AT0707	0.109	< 0.001
savana_AT0708	0.272	< 0.001
savana_AT0709	0.182	< 0.001
savana_AT0710	0.207	< 0.001
savana_AT0711	0.092	0.001
savana_AT0712	0.070	0.027
savana_AT0713	0.188	< 0.001
savana_AT0714	0.215	< 0.001
savana_AT0715	0.140	< 0.001
savana_AT0716	0.114	< 0.001
savana_AT0717	0.170	< 0.001
savana_AT0718	0.053	0.202
savana_AT0719	0.142	< 0.001
savana_AT0721	0.068	0.030
savana_AT0722	0.128	< 0.001
savana_AT0723	0.044	0.412
savana_AT0724	0.201	< 0.001
savana_AT0725	0.130	< 0.001
savana_AT0726	0.109	< 0.001
fsavana_AT0901	0.146	0.001
fsavana_AT0902	0.136	0.003
fsavana_AT0903	0.134	0.001
fsavana_AT0904	0.150	< 0.001
fsavana_AT0905	0.083	0.052
fsavana_AT0906	0.170	< 0.001
fsavana_AT0907	0.032	0.910
fsavana_AT0908	0.126	0.004
grassland_AT1001	0.055	0.367
grassland_AT1002	0.086	0.027
grassland_AT1003	0.209	< 0.001
grassland_AT1004	0.113	< 0.001
grassland_AT1005	0.242	< 0.001
grassland_AT1006	0.143	< 0.001
grassland_AT1007	0.150	< 0.001
grassland_AT1008	0.294	< 0.001
grassland_AT1009	0.158	< 0.001
grassland_AT1010	0.131	0.257
grassland_AT1012	0.207	< 0.001
grassland_AT1013	0.192	< 0.001
grassland_AT1014	0.146	< 0.001
grassland_AT1015	0.097	0.003
fynbos_AT1201	0.048	0.880
fynbos_AT1202	0.029	0.999
fynbos_AT1203	0.019	1.000
desert_AT1303	0.102	0.020

desert_AT1304	0.200	< 0.001
desert_AT1305	0.112	0.004
desert_AT1307	0.095	0.213
desert_AT1309	0.114	0.004
desert_AT1310	0.164	< 0.001
desert_AT1313	0.116	0.003
desert_AT1314	0.083	0.092
desert_AT1315	0.176	< 0.001
desert_AT1316	0.096	0.034
desert_AT1319	0.103	0.594
desert_AT1322	0.142	0.002
AT0101_kibale	0.100	0.027
AT0103_mtkupe	0.145	< 0.001
AT0108_kifufu	0.057	0.467
AT0111_yapo	0.160	0.001
AT0119_mamala	0.128	0.011
AT0125_sokoke	0.159	0.007
AT0125_sokoke	0.159	0.007
AT0125_magangwe	0.055	0.595
AT0125_pugu	0.133	0.021
AT0130_gola	0.096	0.112
AT0107_speke	0.142	0.001
AT0713_bagarin	0.061	0.729
AT0722_kyabobo	0.184	< 0.001
AT0722_tapoa	0.149	0.018
AT0722_hans	0.058	0.614
AT0722_sengwa	0.104	0.043
AT1004_gustav	0.053	0.720
AT1009_seekoei	0.190	0.004
AT1009_platberg	0.048	0.975
AT1203_anysberg	0.140	0.034
AT1203_swartbos	0.165	0.073
AT1203_vrolik	0.121	0.061
AT1322_skilpad	0.168	0.037
AT1322_remhoog	0.153	0.029

Supplementary Table S5. Results of simulations to evaluate if body size frequency distributions of smaller scale are randomly drawn subsets from the larger spatial scale assemblages in which they are embedded. "Simulated median" = mean of 10 000 simulated medians. "Proportion" = proportion of the 10000 of simulated medians greater or smaller than the observed median body mass, with proportions less than 0.025 or greater than 0.975 indicating a larger difference than expected by change alone (significant difference at the alpha = 0.05 level, in a two- tailed comparison). Non-significant values are in bold.

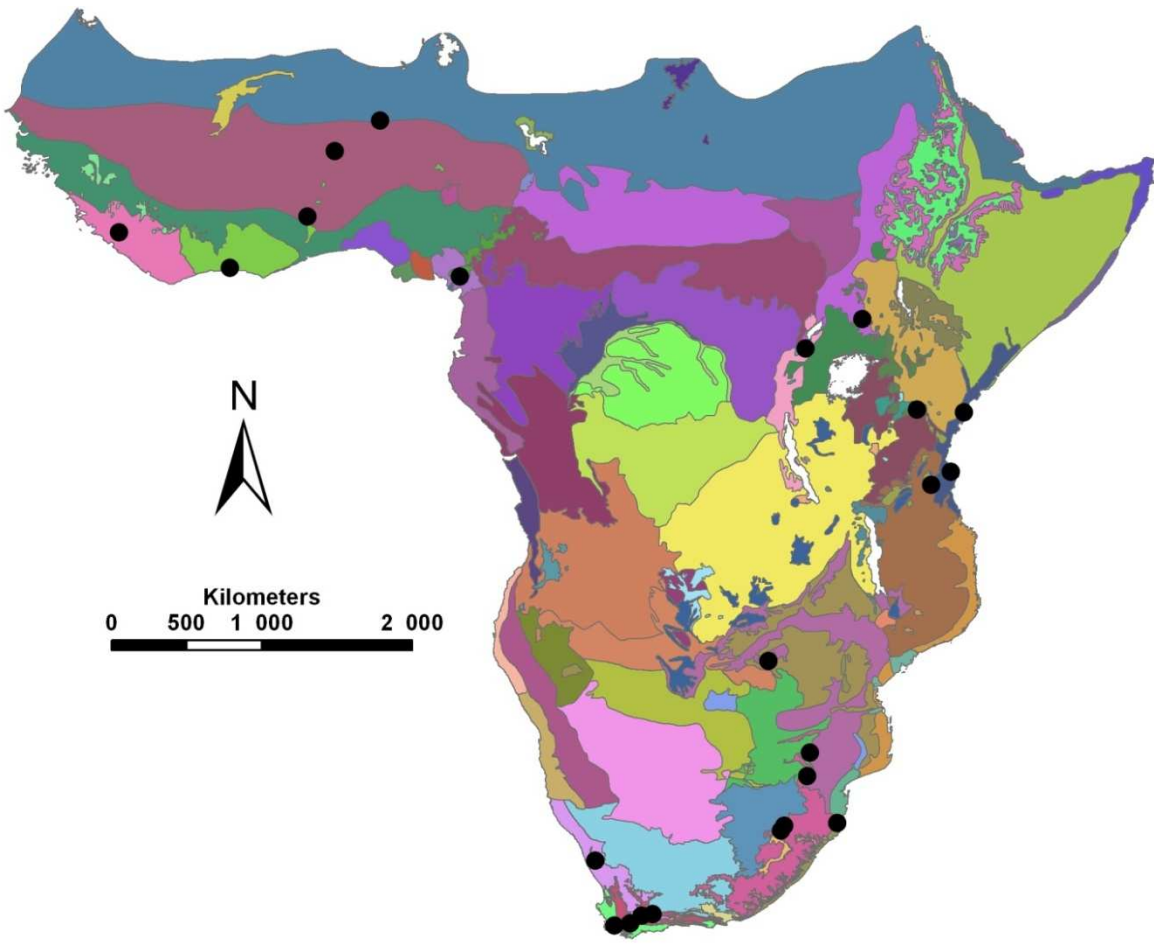
Name	Observed Median	Simulated Median	Proportion
Continental	5.068	5.068	0
Moist Forest	5.170	5.070	0.999
Dry Forest	6.113	5.066	1
Tropical Savanna	5.170	5.070	1
Flooded Savanna	5.781	5.066	1
Grassland	5.303	5.068	1
Fynbos	6.308	5.073	1
Desert	5.714	5.068	1
Zambezian Cryptosepalum dry forests	5.476	5.170	0.999
Angolan Miombo woodlands	6.288	5.174	1
Angolan Mopane woodlands	5.476	5.170	1
Central Zambezian Miombo woodlands	5.650	5.170	1
East Sudanian savanna	5.821	5.173	1
Eastern Miombo woodlands	5.650	5.170	1
Guinean forest-savanna mosaic	6.781	5.170	1
Itigi-Sumbu thicket	6.145	5.171	1
Kalahari Acacia-Baikiaea woodlands	6.192	5.177	1
Mandara Plateau mosaic	5.621	5.173	1
Northern Acacia-Commiphora bushlands and thickets	5.479	5.177	0.999
Northern Congolian forest-savanna mosaic	6.174	5.174	1
Sahelian Acacia savanna	6.300	5.177	1
Serengeti volcanic grasslands	5.768	5.170	1
Horn of Africa Acacia Savannas	5.697	5.170	1
Southern Acacia-Commiphora bushlands and thickets	6.066	5.170	1
Southern Africa bushveld	5.361	5.170	0.986
Southern Congolian forest-savanna mosaic	5.857	5.173	1
Southern Miombo woodlands	5.468	5.173	0.999
Victoria Basin forest-savanna mosaic	5.748	5.170	1
West Sudanian savanna	**5.271**	**5.173**	**0.880**
Western Congolian forest-savanna mosaic	6.214	5.170	1

Western Zambezian grasslands	5.792	5.174	1
Zambezian and Mopane woodlands	5.618	5.170	1
Albertine Rift montane forests	**5.271**	**5.168**	**0.969**
Atlantic Equatorial coastal forests	**5.276**	**5.170**	**0.916**
Cameroonian Highlands forests	5.385	5.168	0.998
Central Congolian lowland forests	5.399	5.170	0.987
Cross-Niger transition forests	5.511	5.170	0.999
Cross-Sanaga-Bioko coastal forests	**5.240**	**5.170**	**0.859**
East African montane forests	5.552	5.168	1
Eastern Arc forests	5.564	5.170	1
Eastern Congolian swamp forests	**5.279**	**5.168**	**0.876**
Eastern Guinean forests	5.597	5.170	1
Ethiopian montane forests	6.353	5.167	1
Guinean montane forests	5.585	5.170	1
Knysna-Amatole montane forests	6.791	5.164	1
KwaZulu-Cape coastal forest mosaic	6.442	5.168	1
Maputaland coastal forest mosaic	6.300	5.170	1
Mount Cameroon and Bioko montane forests	5.498	5.170	0.999
Niger Delta swamp forests	5.518	5.168	0.998
Nigerian lowland forests	5.408	5.167	0.994
Northeastern Congolian lowland forests	5.322	5.168	0.988
Northern Zanzibar-Inhambane coastal forest mosaic	5.659	5.168	1
Northwestern Congolian lowland forests	**5.214**	**5.168**	**0.741**
Southern Zanzibar-Inhambane coastal forest mosaic	5.886	5.168	1
Western Congolian swamp forests	5.505	5.170	0.998
Western Guinean lowland forests	5.477	5.168	0.999
Zambezian halophytics	**5.476**	**5.301**	**0.917**
Angolan montane forest-grassland mosaic	5.696	5.303	0.999
Angolan scarp savanna and woodlands	6.684	5.301	1
Drakensberg alti-montane grasslands and woodlands	5.865	5.304	1
Drakensberg montane grasslands, woodlands and forests	6.955	5.300	1
East African montane moorlands	6.098	5.302	1
Eastern Zimbabwe montane forest-grassland mosaic	6.168	5.303	1
Ethiopian montane grasslands and woodlands	7.304	5.302	1
Ethiopian montane moorlands	6.209	5.304	1
Highveld grasslands	**4.912**	**5.302**	**0.096**
Jos Plateau forest-grassland mosaic	6.378	5.302	1
Maputaland-Pondoland bushland and thickets	6.178	5.304	1
Rwenzori-Virunga montane moorlands	6.090	5.302	1
South Malawi montane forest-grassland mosaic	5.817	5.304	1
Southern Rift montane forest-grassland mosaic	6.700	6.304	0.996
Albany thickets	**6.511**	**6.308**	**0.947**
Lowland fynbos and renosterveld	**6.304**	**6.313**	**0.270**
Zambezian Baikiaea woodlands	6.539	5.788	1
East African halophytics	6.409	5.783	0.999

Etosha Pan halophytics	6.864	5.781	1
Inner Niger Delta flooded savanna	6.919	5.781	1
Lake Chad flooded savanna	6.272	5.785	1
Saharan flooded grasslands	6.781	5.781	1
Zambezian coastal flooded savanna	**5.921**	**5.781**	**0.914**
Zambezian flooded grasslands	6.366	5.781	0.999
Montane fynbos and renosterveld	6.304	5.714	0.999
East Saharan montane xeric woodlands	7.451	5.713	1
Eritrean coastal desert	6.391	5.714	1
Ethiopian xeric grasslands and shrublands	**6.001**	**5.714**	**0.826**
Hobyo grasslands and shrublands	6.378	5.714	1
Kalahari xeric savanna	7.087	5.716	1
Kaokoveld desert	6.408	5.714	1
Masai xeric grasslands and shrublands	6.269	5.714	0.999
Nama Karoo	7.129	5.714	1
Namib desert	6.317	5.714	1
Namibian savanna woodlands	**6.276**	**5.726**	**0.890**
Succulent Karoo	6.857	5.714	1
Somali montane xeric woodlands	6.857	6.857	0
Remhoogte	5.548	6.807	0
Skilpadvlei Nature Reserve	5.379	6.907	0
Swartboskloof	5.389	6.308	0.002
Vrolijkheid Nature Reserve	5.616	6.308	0
Anysberg Nature Reserve	5.555	6.304	0
Seekoeivlei	7.366	6.209	0.999
Platberg Nature Reserve	**6.118**	**6.209**	**0.324**
Gustav Klingbiel Nature Reserve	5.597	5.882	0.013
Sengwa Wildlife Research Area	6.113	5.797	0.987
Hans Merensky Nature Reserve	**5.817**	**5.797**	**0.518**
Kyabobo National Park	5.053	5.748	0
Tapoa Region, W Niger National Park	6.781	5.750	0.999
Bagarinnaye and Maïjémo villages	**6.135**	**6.189**	**0.408**
Speke Bay Lodge	**5.748**	**5.650**	**0.757**
Gola heights	5.186	5.476	0.001
Arabuko Sokoke Forest	**5.343**	**5.655**	**0.048**
Magangwe, Ruaha National Park	**5.921**	**5.659**	**0.97**
Pugu Hills	5.284	5.659	0.009
Malala Lodge	5.628	6.301	0
Yapo forest	5.138	5.597	0
Kifufu Farm	5.299	5.552	0.016
Mt. Kupe	4.863	5.385	0
Kibale Forest	4.940	5.267	3.00E-04

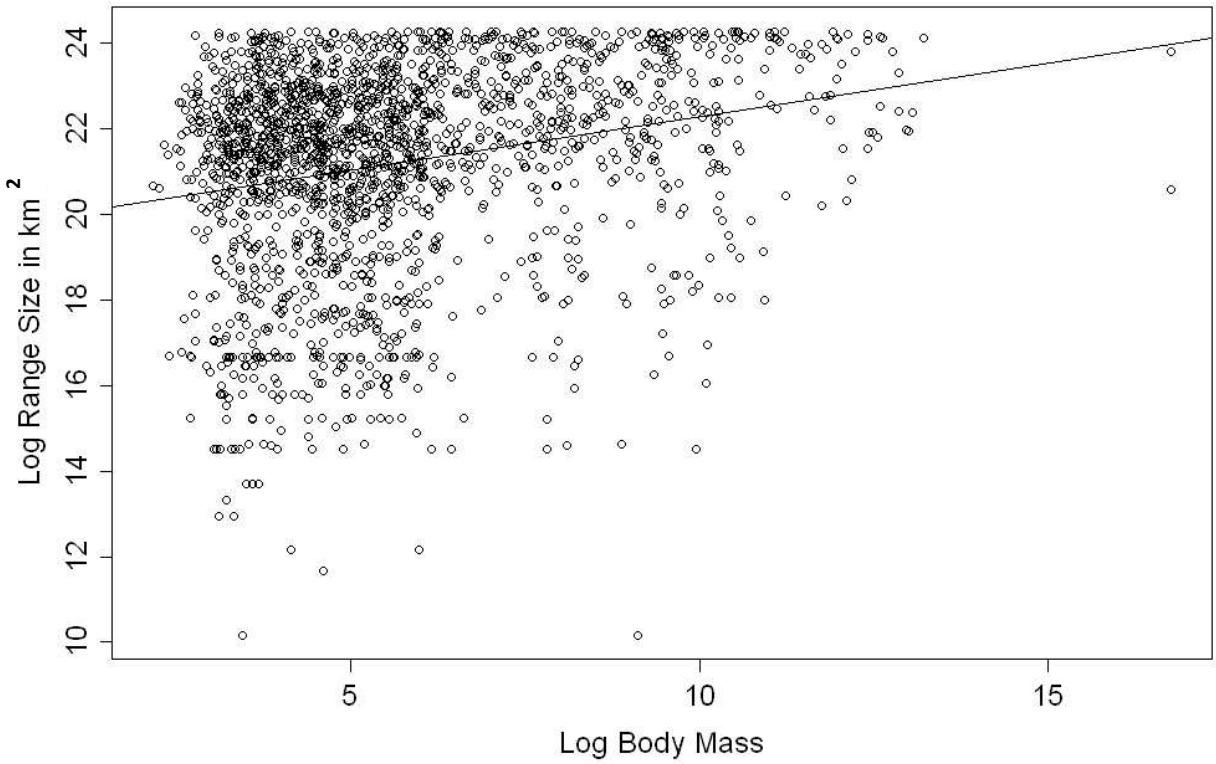
Supplementary Table S6. Percentage of all null models greater than, less than, or equal to observed median mass for all sites at the biome, ecoregion and local scales.

Null model	Scale	Null > Observed	Null < Observed	Null = Observed
Unweighted	Biome	0	100	0
	Ecoregion	2.3	96.5	1.2
	Local	73.9	26.1	0
Range weighted	Biome	42.9	57.1	0
	Ecoregion	41.8	56.9	1.3
	Local	91.3	8.7	0
NDVI weighted	Biome	0	100	0
	Ecoregion	1.2	96.5	2.3
	Local	73.9	26.1	0



Supplementary Figure S1. Map of the study area, the Afrotropical biogeographic region, excluding Madagascar and the Arabian Peninsula. Detailed here are the African terrestrial ecoregions, excluding mangroves (N = 86). Centroids of local scale lists indicated by black circles (N = 23). See Supplementary Table S1 for site details.

Source: Wildfinder Database. [Online](27 July 2011) (http://www.worldwildlife.org/science/data/item1873.html).



Supplementary Figure S2. Range size at the ecoregion scale and body mass relationships for African terrestrial avifauna. Pearson's r = 0.23; p < 0.001; N = 1960.

Chapter 5 – Conclusion

Masorini hill in the Kruger National Park, on the road towards Letaba, the major route through the study site detailed in Chapter 3.

Protected area efficacy

On the 1st of March 1872, United States president Ulysses S. Grant established Yellowstone National Park, widely considered the world's first protected area (PA; USS 1872). Since then, the concept has steadily permeated society and is now one of the major global strategies to conserve nature (Jenkins & Joppa 2009). Importantly, it is a widely accepted conservation tool across various facets of society. Large support for PA designation has come from international donors, non-governmental organizations, national and international political frameworks and the private sector (Jenkins & Joppa 2009). Perhaps the most lasting contribution of Pres. Grant's action was creating the political will and impetus to designate PAs. More recently, it has continued with similar efforts worldwide, and the trend is perhaps best illustrated by the establishment of multinational transboundary PAs (Sandwith et al. 2001). In this context, the continued establishment and maintenance of PAs is, undoubtedly, a conservation success story.

Given its history of application, large support and continued political use, it may seem unusual then to question the efficacy of this conservation approach as I have done in this thesis. The global conservation movement, however, is hampered by its systematic and continued failure to report comprehensively on its successes and failures, and in evaluating the efficacy of conservation investments (Ferraro & Pattanayak 2006; Rodrigues 2006 and see McDonald-Madden et al. 2009). Where there is reporting, the global standard is to report gains and successes, but not the losses and failures of conservation interventions (Possingham 2001). In other sectors, such as finance and the corporate world, not reporting on progress or indeed the lack of doing so is consider bad practice, if not criminal (Possingham 2001; McDonald-Madden et al. 2009). The lack of reporting standards would not be such a concern where it not that by the most sophisticated measures and indicators, the conservation movement is failing to halt the biodiversity extinction crisis (Butchart et al. 2010; Lalasz et al. 2011). As a consequence, from local to global scales, an empirical understanding of the ecological effectiveness of PAs, and the mechanisms giving rise to observed patterns remains almost entirely absent (Gaston et al. 2008). The realisation that the conservation movement needs clear and transparent reporting standards has led to a revolution in establishing conservation evidence, such as the "Collaboration for Environmental Evidence" (CEE 2012), and the establishment of the Intergovernmental

Platform on Biodiversity and Ecosystem Services (IPBES 2012). However, while commendable, these initiatives are still in their infancy.

In this thesis, using names-based architecture, a technique rooted in ecoinformatics, I studied species assembly patterns and PA efficacy to help address this fundamental shortfall. I quantitatively analysed the ecological effectiveness of PAs, and so contributed to testing our assumptions about the efficacy of this conservation intervention. In Chapter 2, the global meta-analysis showed that the establishment of PAs do indeed lead to significant conservation outcomes measured as higher biodiversity values compared with alternative land covers. However, it also showed that results from studies on PAs ecological performance is context-specific and can be influenced by a variety of local factors (Gaston et al. 2006; Gaston et al. 2008; Laurance et al. 2012). This finding was independently confirmed in the third chapter which tested the efficacy of the Kruger National Park, a bastion for conservation. It showed that species richness and abundance are not necessarily higher inside PAs, and that other land covers can contribute to a regions conservation portfolio in predictable ways. The work also indicated that species with certain traits, in this case large-bodied bird species, and those with ground nesting behaviour, are at particular risk outside reserves. However, some species traits clearly benefit, mainly generalists and smaller bodied species, as a consequences of the altered vegetation via water provisioning in the urban land cover area (see Chapter 3). While the generality of trait changes are emerging (Clergeau et al. 1998; Woodroffe & Ginsberg 1998; Herremans & Herremans-Tonnoeyr 2000; McKinney 2006; Kark et al. 2007; van Rensburg et al. 2009; Evans et al. 2011; Greve et al. 2011; Pautasso et al. 2011), a better understanding is required to relate species traits to land cover changes, if we are to model the global consequences of PA efficacy.

Considerations in the use of meta-analysis

Substantive concerns have been raised as to the utility of meta-analysis in ecology and conservation. These broadly fall into four categories:

- (i) It is inappropriate to combine results from different studies (i.e. meta-analysis ‘mixes apples and oranges’; Whittaker 2010; Borenstein et al. 2009).

- (ii) Due to the file drawer problem (that findings of high treatment effects are more likely to be published in the first place) the meta-analysis is biased to begin with (Borenstein et al. 2009)
- (iii) Pairwise comparisons such as used here might not be fully comparable? (R.A. Fuller *pers. comm*.).
- (iv) The meta-analysis in Chapter 2 cannot establish counterfactual causality (R.A. Fuller *pers. comm*.).

I will briefly discuss each criticism in turn:

(i) It is inappropriate to combine results from different studies.

Whittaker (2010) recently concluded that "we should be wary of trying to crunch (analyze) chalk and cheese data sets together, and we should be circumspect in regard to the use of meta-analysis in ecology". The main argument of this typical concern for the use of meta-analysis is that the summary effect can ignore important differences across studies. This may seem to be a reasonable concern, as inevitably, the studies that are combined will differ in at least some characteristics. Ecological studies in particular typically differ in study design, analytical techniques, and a host of both biotic and abiotic factors that could potentially influence the effect under consideration. Ultimately however, meta-analyses are trying to answer broad, overarching questions. To use the oft quoted metaphor, apples and oranges may be combined if our aim to make inferences at the level of fruit (Borenstein et al. 2009). In the conservation context addressed here, the perhaps larger remaining concern is whether conservation interventions, in this case PAs, are effective. I have adopted a meta-analytical approach primarily for baseline establishment of conservation evidence, and at a minimum it now provides a departure point for further research into this most fundamental of conservation questions.

(ii) Due to the file drawer problem the meta-analysis is biased to begin with.

Published studies are more likely to be included in a meta-analysis than unpublished studies, and studies with significant effects are also more likely to be published in the first place. This legitimate concern has been met with a range of analytical methods to assess the objectivity, transparency and reproducibility of findings in meta-analyses (Rothstein et al. 2005; Borenstein et al. 2009). In so doing, meta-analysis tackles the problem head on and attempts to quantify bias, and so is explicit about such bias influencing interpretations from the study, unlike a traditional review. We may never be able to avoid the influence of publication bias, but we are now in a position to test and control for its influence, as has been done here.

(iii) Are pairwise comparisons such as used here indeed comparable?

In the meta-analysis presented here, a concern may be on how comparable the pairwise comparisons inside and outside PAs themselves are. As discussed in Chapter 2, changes in biodiversity may be observed for a variety of reasons, including their spatial position and their management intensity (Gaston et al. 2008). In addition, differences between pairwise comparisons could be due to the spatial attributes of points themselves or the abiotic attributes of habitats in which the measurements where made influencing local biodiversity, such as slope, altitude or vegetation types and/or structure. They may also experience anthropogenic alterations at different levels of intensity. Chapter 3 showed that such local scale variance can be accounted for by testing the relationships between species assemblages inside and outside PA. In that case study, I was able to account for the variation in the response and showed that it was mainly the addition of resources that changed species assemblages, as consistent with the more individual hypothesis (Gaston 2000). As a consequence, the meta-analysis in Chapter 2 indicated the general positive signal in determining PAs efficacy, and the local scale analysis in Chapter 3 could in part account for a mechanism structuring variance in the study.

A larger scale approach to account for the variance in PA efficacy is a so called match pair analysis, which pairs data points in control versus experimental groups on the basis of

matching factors (Andam et al. 2008). In the case of the meta-analysis here, such matched pairings may be based on, for instance, habitat condition, altitude, slope, elevation or vegetation type etc., and has been used to calculate deforestation rates inside and outside PAs in Costa Rica (Andam et al. 2008). Matched-pair analysis is one of the possible ways to minimize the effect of extraneous variables. Three lines of evidences suggest that the pairwise comparisons in Chapter 3 are valid, and that a match pair analysis would not necessarily provide an improvement in the study presented here.

(a) Both the distance among comparison sites and their distance to the PA boundary explain little of the variation in effect size for studies included the meta-analysis. Furthermore, the small amount of deviance explained when the geographic context of the PAs is used to explore effect size variation is likewise supportive that a match pair design would not necessarily improve inference.

(b) A significant concern with a match pairing approach with the global data used is that it could produce spurious comparisons, especially using geographic data, for instance matching sites may occur across countries or even continents. Even when constrained to continental comparisons, such match pairs designs could potentially inflate uncertainty. One of the major strengths of my analysis is that the pairwise comparisons are indeed local in scale, and so essentially, differences in biodiversity value are driven by local scale effects, in this case, the influence of PA designation.

(c) Finally, in the context of testing PA efficacy, whether significant bias exists due to incomparable pairwise comparisons may be irrelevant in the context of conservation. The primary aim of Chapter 2 was to establish if a conservation intervention had the desired outcome, in this case, increased biodiversity benefits. Of primary importance then is the direction of the effect, rather than the variance in the measure (which in this case is argued to be introduced through a paired design). Given the strength of the positive effect and its consistency across different measure of biodiversity, I can have confidence that the positive effect is not an artefact of the pairwise design, and that the primary goal of the analysis was achieved, that is, establishing if PAs achieve positive conservation outcomes.

(iv) The analysis cannot establish counterfactual causality

A remaining concern in the use of meta-analysis, more deeply rooted in philosophy of science, is that the meta-analytical approach adopted in Chapter 2 could be considered to be arguing for non-counterfactual causality (R.A. Fuller *pers. comm.*). Counterfactual dependence is a philosophical approach to causation as an explanation of causal facts: for example, event 'c' (the cause) and 'e' (the effect) both occur, but had 'c' not occurred, 'e' would not have occurred either (Collins et al. 2004). In the context of my study, the implication of this position is that in the absence of PA designation, would the same effect be observed? Or more generally, how can I be sure that PA establishment confers a net benefit to biodiversity?

As I pointed out, many factors that could potentially produce biodiversity benefit are proximally related to the establishment of PAs. They fall in three classes (for a review see Gaston et al. 2008): (a) spatial difference in biodiversity persist after establishment, so that the measured benefit is simply a result of historical contingency (b) either by chance, complex socio-economic factors, or design, lower threatening processes persist in PA and so lead to biodiversity benefit and/or (c) active management leads to biodiversity benefit. In comparisons inside and outside PAs it is indeed difficult to infer what the influence on biodiversity would be had the PA not been established, as I am trying to analyse the influence of a landscape management activity which differs vastly between regions. However, the 623 pairwise comparisons inside PAs only present the view of change in biodiversity only under one overarching management regime and an anthropogenic disturbance under PA establishment. The overall effect size from pairwise comparisons inside PAs is lower than that of the inside and outside comparisons only (their 95% confidence intervals do not overlap), suggesting that PAs offset negative anthropogenic influences within their borders to a greater degree than no PA designation (see Chapter 3). Whatever the mechanism driving changes in biodiversity between pristine habitat and exploited land covers, PA establishment itself seems to confer a net benefit to biodiversity, as it lessens or at least slows negative anthropogenic influences to biodiversity features. Since the effect is greater outside PAs, I suggest we can infer an at least correlative link that PA itself causes a net benefit to biodiversity conservation.

Policy implications

The Convention of Biological Diversity is an international legally binding treaty consisting of 193 parties (countries), tasked with the conservation of biodiversity and the sustainable and equitable use of its components (CBD 2012). It has recently become clear however, using a variety of indicators, that the convention has failed on its primary goal "to achieve a significant reduction in the rate of biodiversity loss by 2010" (Butchart et al. 2010). This led the political leaders of the world to commit to new, so called "Aichi targets", ratified in Nagoya, Japan, with the overarching aims of again committing to the conservation of global biodiversity (ABT 2012).

Only one overarching target concerns PAs in terms of biodiversity conservation. Strategic Goal C; Target 11, aims that "By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of PAs…" (ABT 2012). Unlike much of the generally vague language for most strategies in the Aichi framework, Target 11 contains relatively clear targets and indicators - although is not accompanied by any guidelines on how countries should best go about achieving it.

However, this target is only a proxy measurement of conservation. Area targets convey little information, if any, about their actual efficacy at conserving biodiversity features (Gaston et al. 2008). Essentially then at the global policy level, there can remain substantive doubts whether the expense dedicated to PA designation and management is indeed justified in terms of biodiversity conservation. However, the meta-analysis in Chapter 2 provided a comprehensive and evidence-based analysis that PA perform positively, at least in terms of containing a higher inventory of biodiversity features that alternative land covers, and can hopefully contribute to political impetus to reach Aichi Target 11. Protected areas establishment is of course only a component of an effective conservation strategy. But armed with the evidence that establishing PAs produce a net benefit to biodiversity, policymakers can and should continue to employ sound conservation planning to maximize benefits to biodiversity with the maintenance and further establishment of PAs (Margules & Pressey 2000; Fuller et al. 2010; Laurance et al. 2012; Gaston et al. 2008; Ricketts et al.

2011), and to maximize the many benefits they provide (Arcese & Sinclair 1997; Balmford et al. 2002; MA 2005; Chown 2010; Craigie et al. 2010; TEEB 2010). The results in Chapter 3 also suggest that areas under moderate extraction retain much bird diversity and preventing their further destruction can fundamentally contribute to a landscape conservation approach (Dobson et al. 1997; Cowling et al. 2003; Scholes & Biggs 2005).

The latest round of policy negotiations at Rio+20 Earth Summit delivered poor outcomes in terms of biodiversity conservation (Carrière et al. 2012). However, given the convincing evidence in favour of PA benefits, and prospects for their useful expansion provided here, I have every confidence that this work will help to invigorate global policy on how biodiversity conservation can be achieved through interventions that have a well-established history and legal framework in most countries. Humanity is not reacting to the biodiversity extinction crisis with the same intensity as it is to, for instance, climate change. While the scientific consensus on the biodiversity crisis is indeed damningly negative, it would seem not to be inspiring a coherent response and most reporting in the media is similarly negative. Here, however, using an analytical technique pioneered in psychology and medicine, we can for the first time demonstrate globally that establishing PAs is having a positive influence on the world's species. Battles in conservation remain and there is no reason for complacency, but there is now demonstrable hope that this conservation intervention is having a quantitatively measurable positive impact.

Future directions

Species traits and predictive ecology

Species trait research is particularly mature in plant ecology, but to a lesser extent so in vertebrate ecology. A more coherent theoretical framework is needed to support hypothesis generation, methodological methods and prediction in traits-based ecology. Webb et al. (2010) suggest that such a framework should consist of three parts (i) the underlying trait distribution (ii) the fitness responses of traits to different environments (be they natural or altered) (iii) a dynamic projection of such responses. Such a framework is particularly important because conceptual models also suggest that traits, rather than

species, are at the centre of structuring species community assembly (Mayfield et al. 2010) and consequently, greatly effects ecosystem functioning (Norberg et al. 2001). If we are to predict the consequences of biodiversity change and the relationship between biodiversity and ecosystem functioning, a greater focus is needed on the interactions between species traits and community assembly and the implications of anthropogenic alterations.

Furthermore, rather than analysing the correlations and/or differences between species traits and environmental variables (Gaston & Blackburn 2000; Hawkins et al. 2005; Diniz-Filho et al. 2007), a direct functional analysis where species data, environmental data, and species-trait data are analyzed simultaneously may represent a more optimal solution (Dray & Legendre 2008). An eloquent, but poorly explored method to combine spatially explicit environmental data and species traits are species by sites matrices (Legendre et al. 1997; Dray & Legendre 2008; Gaston et al. 2008; Chown et al. 2010), as used in Chapter 3. Traditionally these matrices are populated with environmental, species presence/ absence or species population data and data on species traits. However, the approach can take into account any trait under consideration and may be the key to synthesising patterns between species, environmental and biological variables (Gaston et al. 2008; Chown et al. 2010). The approach can identify positive or negative associations between the biological or other traits of organisms, and the environmental characteristics of the locations at which they are found, much in the same way as correlation coefficients do in traditional data analysis (Legendre et al. 1997). Surprisingly, although the technique was introduced over a decade ago (Legendre et al. 1997), it has not been widely used in ecological studies and despite its potential utility, it is often widely misinterpreted and misapplied (Dray & Legendre 2008). Importantly, such an approach also has potential utility at a range of spatial scales within both biogeographic and community ecological realms, and may lead to better integration of the two (see Pennings & Silliman 2005; Cavender-Bares et al. 2009).

Conservation biogeography

The fourth chapter in the thesis tested hypotheses on the body size frequency distribution (BSFD) of African birds, linking disparate databases by virtue of species names. It showed that much of the change in median body size with spatial scale in species assemblages can

be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD.

The work also showed that unlike African mammals, the African avifaunal BSFDs are not bimodal at all spatial scales (Kelt & Meyer 2009). Kelt & Meyer (2009) suggested that bimodality in large mammals is due to their co-evolution with proto-human hunters, and so they were able to escape the mass extinctions typical of other regions. For birds at least, my study did not support this interpretation, as it requires the presence of an additional mode to vindicate it. The effect of proto-human hunters in structuring bird assemblages is unclear, and I suggested that the difference in BSFDs between African mammals and birds rather points to differences in various life history traits, body shape, foraging ecology, body architecture and macroecological features among these major taxa (Silva et al. 1997; Speakman 2005; Melo et al. 2009). However, the point does illustrate some of the difficulties in separating "natural" historical and contemporary patterns and mechanisms structuring species assemblages, from those caused by anthropogenic processes. Historical anthropogenic influence on contemporary biodiversity patterns may in fact be more prevalent than we think (Alroy 2001; Roberts 2007). While I aimed to document natural BSFD patterns in this study, it is important to disentangle the role of natural versus anthropogenic influences in structuring contemporary biodiversity patterns, if and where it may be applicable. Such impacts were illustrated across the land cover types investigated in Chapter 3, and clearly will play a role at smaller spatial scales (see also discussion in Chown et al. 2010).

Despite the long standing application of biogeographic principles in conservation biology, the emergence of "*Conservation biogeography*" as a discipline is still in its infancy (Whittaker & Ladle 2011). Both Richardson & Whittaker (2010) and Ladle & Whittaker (2011) recently reviewed prominent areas of current and potential future areas of research in conservation biogeography. I would add that in terms of studying species assembly patterns, which was the focus here, of critical concern is the implications of species assembly and disassembly on ecosystem function. In particular, I suggest the consequence of community disassembly due to anthropogenic disturbance on the provisioning of ecosystem services is a prominent research area (e.g. Lomolino & Perault 2000; Gonzalez &

Chaneton 2002; Sanders et al. 2003; Larsen et al. 2008; Okie & Brown 2009; Cardinale et al. 2012). This is particularly relevant with the realisation that biodiversity loss reduces the efficiency by which ecological communities capture resources and that ecosystem process change accelerates as biodiversity loss increases (Cardinale et al. 2012). While understanding the processes responsible for structuring assemblages is a fruitful research field, it is perhaps best combined with investigations into the consequences of disassembly. The role of additional traits above body size analysed here, like a suite of life history characteristics and especially phylogenetic information in a trait-based framework as discussed above, may be of particular use.

Protected area efficacy

Protected area performance can broadly be assessed in two ways. One can either assess the inventory of biodiversity, or one can assess the condition of biodiversity, in terms of changes in trends over time (Gaston et al. 2008). In context of the work presented in this thesis which documented species inventory, consider two hypothetical scenarios of the change of biodiversity condition over time in PAs, both inside and outside their borders (Figure 1). In Model one, consistent with global trends in biodiversity, in general biodiversity is declining outside of PA borders, but the establishment of PAs, either by effective management or positive ecological attributes, is leading to increases in biodiversity.

I hypothesize however that the reality is closer to Model two, where despite the establishment of PAs a decline in biodiversity is nonetheless occurring. While this could be due to poor management and continued exploitation (Gaston et al. 2008; Craigie et al. 2010; Laurance et al. 2012), more insidious ecological factors such as extinction debt also play a role (Carroll et al. 2004). The analysis in Chapter 2, however, is the first global quantitative synthesis to show that on average and despite context-specificity, biodiversity values are higher inside PAs, so ultimately PAs achieve significant conservation outcomes. What the analyses in Chapters 2 and 3 cannot differentiate, is both the initial conditions of the trends, and also the change of the trends over time. In other words, it cannot differentiate between the two Model scenarios (Figure 1).

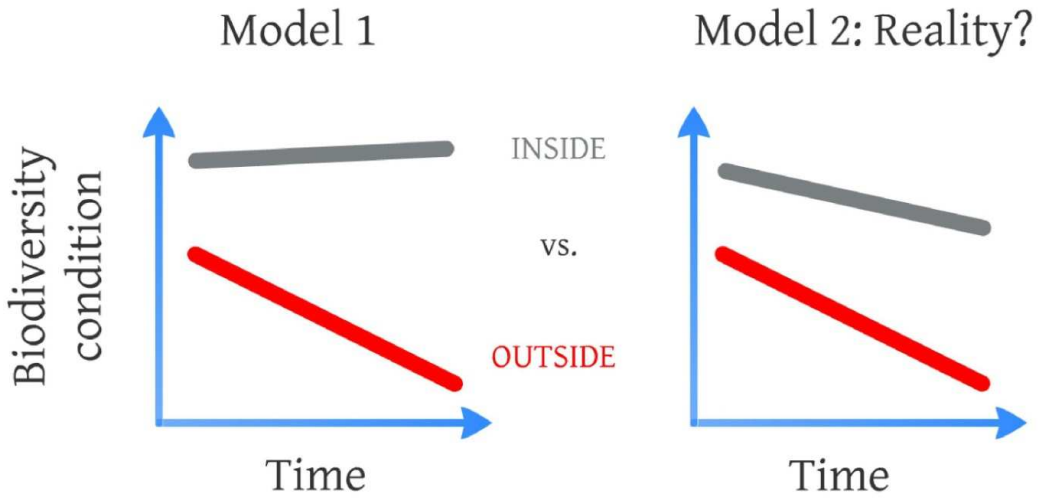


Figure 1. Hypothetical status of an index of biodiversity condition over time both inside (grey) and outside (red) protected areas. Due to intrinsic factors of PAs like extinction debt and continued exploitation, model two more likely provides an approximation of the influence of protected areas.

A key area for future research then is documenting the trends in biodiversity condition over time both inside and outside PAs. Time series data to do so inside PAs exist, at least regionally (Craigie et al. 2010), but of critical importance is monitoring the changes in trends relative to the outside of PAs (see also Lindenmayer et al. 2011; Lindenmayer et al. 2012). In this way, the continued efficacy of PAs can be measured and the implications of not establishing PAs can be projected. Given that PA efficacy is context specific, such existing datasets and monitoring protocols to generate them, would ultimately need wide geographic and taxonomic scope if we are to comprehensively understand, model and predict global PA efficacy.

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Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change

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Recent greenhouse gas emissions exceed the highest IPCC SRES scenario (Raupach et al. 2007); global warming this century is thus on track to exceed the 1.5°C lower limit cited by the IPCC Fourth Assessment Report as resulting in increasingly high extinction risk for 20–30% of Earth's biodiversity (Parry et al. 2007). Minimising negative impacts on biodiversity requires effective conservation strategies that will enhance species' opportunities to adapt to climatic change, especially as their capacity for natural adaptation very likely will be exceeded this century (Parry et al. 2007). Developing and applying such strategies requires insight into species' responses and an integrated approach to identifying vulnerable species and regions (Williams et al. 2008). Robust predictive models of species' and community responses to climatic change are essential to this approach, and vital to inform policy and management (Barnard and Thuiller 2008).

Species exhibit a variety of responses to climatic changes, the magnitude and rate of change determining which response type predominates (Fig. 1). Apart from macro-evolution, that is elicited by relatively slow, larger-magnitude changes, species have exhibited all these generic responses to the climatic changes of the past half century (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006). Behavioural and micro-evolutionary changes offer limited scope for adaptation, however, being constrained by species' inherent plasticity and/or genetic variance (Huntley 2007). Local abundance changes are principally precursors to, or symptoms of, spatial responses. Extinction results from a species' inability to achieve a sufficient response of any other type. As the Quaternary record shows (Huntley and Webb 1989), geographical distribution changes are species' predominant response to relatively rapid, large-magnitude climatic changes, such as are projected for this century. Our aim in this paper is to outline a strategy for developing robust predictive models of species' spatial responses and the associated changes in abundance patterns.

Current state of the art

To-date, bioclimatic envelope models have been the principal approach used to project potential species' distribution changes resulting from climatic change (Midgley et al. 2002, Araújo and Guisan 2006, Thuiller et al. 2006, Huntley et al. 2008). Although their underlying assumptions and inherent simplifications have been debated (Gaston 2003, Pearson and Dawson 2003) and their reliability questioned (Davis et al. 1998, Beale et al. 2008), several studies have demonstrated their general robustness. They can successfully simulate species' distributions for regions (Beerling et al. 1995) or times (Hijmans and

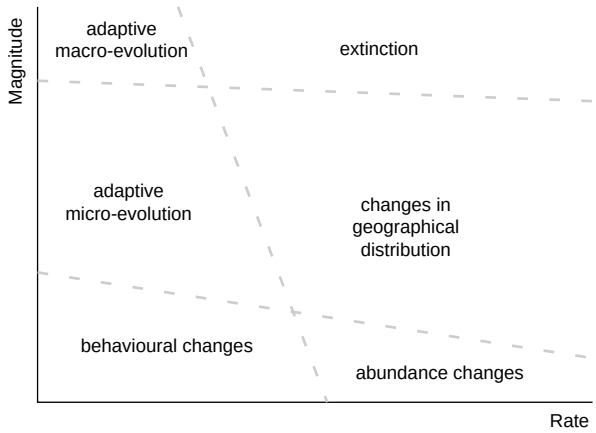

Figure 1. Schematic representation of species' responses to climatic changes. Species' predominant response to climatic changes depends upon the combination of the magnitude and the rate of those changes. Spatial responses, i.e. changes in geographical distribution, predominate for relatively large magnitude and relatively rapid changes, such as those projected for the present century.

Graham 2006) independent of those from which data were used in model construction, and retrodict species' abundance changes both near range margins (Green et al. 2008) and throughout sub-continental regions (Gregory et al. 2009). Their application has highlighted the potential magnitude of climatic change impacts upon species' distributions (Thomas et al. 2004, Fitzpatrick et al. 2008, Huntley et al. 2008), and potential species' losses from protected areas (Hannah et al. 2007, Hole et al. 2009, Coetzee et al. 2009).

However, these static models may give an unrealistically optimistic impression of species' capacities to adapt to climatic change because dispersal and colonisation rates will limit realisation of potential range shifts (Huntley et al. 1995, Midgley et al. 2006), as may barriers to dispersal. Efforts to address this have focused mostly on dispersal limitations, especially of plants (Neilson et al. 2005), relative mobility of animals (Warren et al. 2001) and habitat availability and/or fragmentation (Collingham and Huntley 2000, Hill et al. 2001). Demographic processes, however, especially intrinsic rates of population increase, are also fundamentally important determinants of species' rates of range expansion (Willis et al. 2009). Climatic change may also de-couple existing relationships between species' range extents and abundances, because of changes in relative range quality (Wilson et al. 2004). Demographic processes thus affect species' ability to achieve range expansions from source populations and to persist under less favourable climatic conditions. Only by developing dynamic models of species' potential range shifts, that incorporate population and dispersal processes, as well as ecological processes that influence habitat suitability (e.g. disturbance), can we move beyond simply simulating species' potential range changes (Guisan and Thuiller 2005). This is critical to our ability to assess climatic change impacts upon species' relative extinction risks (Thomas et al. 2004, Schwartz et al. 2006) and to develop climatic change-adapted conservation management strategies (Hannah et al. 2002) that will enhance species' likelihood of persistence.

The next generation – fully integrated models

Addressing this challenge requires integrated models that bring together the necessary component sub-models as modules within a unified framework. We envisage such models as grid-based, operating on discrete, normally annual, time steps, and with modules to simulate: 1) climatic suitability; 2) habitat availability/suitability; 3) population dynamics; and 4) dispersal. Although candidate models are available for all four components, integrated models are still in the early stages of development (Keith et al. 2008, Anderson et al. 2009). There are three core challenges in developing such models: 1) integrating across different spatial and temporal scales at which their components operate. For example, climatic suitability operates principally at extensive spatial scales to determine species' overall potential geographical ranges, whereas habitat availability/suitability is more relevant when considering where in a local landscape a species may occur, and in what numbers. 2) Providing realistic uncertainty estimates for model outputs. As with other complex models, analytical statistical approaches to assessing uncertainty are unlikely to be possible. 3) Balancing a desire for biologically "realistic" process representation with model complexity, data requirements and computational demands. It is likely that, as with earth system models (ESMs), there will be a need for complementary models differing in their degree of complexity. Much can be learned by developing and applying models of intermediate complexity, as the application of ESMs of intermediate complexity has shown (Claussen et al. 2002, Sánchez-Goñi et al. 2005).

1. Climatic suitability module

This module will be needed for most species, although in a minority of cases it will be redundant. The latter will be the case where: 1) the species' inherent physiological limits are known; 2) available data allow the species' growth, performance, survival and reproduction to be modelled mechanistically, including the effects of climate; or 3) a physiologically mechanistic approach is possible (Kearney and Porter 2009). The module will usually be based primarily upon observed correlations between the species' present distribution and present climate, and the necessary assumption that the species' distribution is at least approximately in equilibrium with that climate. The approach is thus precluded for those, usually rare, species that violate this assumption. It is essential that variables used, whether acting directly or indirectly, have plausible, preferably known, mechanistic roles in determining species' range limits. These bioclimatic variables generally are not solely those recorded in meteorological data, but are derived from these. It also is important that the implicit and/or explicit assumptions of the modelling approach are consistent with observations, especially with respect to the form

of the relationships between species' occurrence probability and bioclimatic variables.

2. Habitat availability/suitability module

This module may be simple or quite complex. At its simplest, it may be a binary mask (Midgley et al. 2010), with areas categorised either as suitable or unsuitable for the species. Such masks often will be derived from earth observation data, usually using a classified land-cover data product. Where the data product has a finer grain than that of the model, habitat availability within each model cell can be quantified (Hill et al. 2001). At the opposite extreme, complex niche models may include many habitat dimensions (Catling et al. 1998, Franco et al. 2000). Such models may be fitted using many different approaches, some more appropriate in their assumptions than others (Austin 2007). Although recent emphasis has been on applying more complex functions, and thereby more realistically relating species' responses to environmental predictors (Austin 2007), such approaches are limited by data availability. Generally, the more complex the responses, the more data are needed to construct a reliable model (Barry and Elith 2006) whilst avoiding over-fitting (Araújo and Guisan 2006). In practice, data limitations will preclude use of more complex models for most species.

Whichever approach is adopted, a key issue is how to incorporate changes in habitat availability and/or suitability arising mainly from three processes: 1) disturbance, whether natural (e.g. wildfire, extreme weather events) or anthropogenic (e.g. forest harvesting, burning), triggers episodic regeneration of vegetation. This leads to rapid changes in both the nature and extent of habitats available at spatial scales from landscapes to regions. 2) Vegetation structure and composition determine habitat suitability for most terrestrial animals and sub-dominant plants. Climatic change and increasing atmospheric CO_2 concentration are expected to lead to changes in these vegetation attributes over most of the global land surface, through shifts in plant species' distributions, CO_2 fertilisation and differential benefits to C3 vs C4 plants (Woodward and Kelly 2008) and to woody vs herbaceous plants (Bond et al. 2003). These changes will take place across a range of temporal scales, depending upon disturbance frequency and the rates at which individual species' responses are realised. 3) Changes in human land use resulting from both climatic change and socio-economic factors will result in loss and/or fragmentation of many species' habitats.

Sub-modules to simulate some of these processes, including disturbance and related vegetation dynamics, and vegetation structural responses to climatic change and increasing CO_2 concentration (Keith et al. 2008, Midgley et al. 2010), could be incorporated into the habitat module. Careful consideration of temporal and spatial scale differences between vegetation dynamics and species' range changes is necessary, as well as the need to balance complexity with computational efficiency. Alternatively, land-cover scenario series could be simulated using an ESM that includes a coupled dynamic global vegetation model (Cox et al. 2000, Sitch et al. 2003), although scale mismatches between the ESM grid and that needed to model species' range and abundance dynamics require consideration. Land-cover scenarios, therefore, might better be derived from offline runs of a vegetation dynamics model, driven by the changing climatic conditions simulated by an ESM, for the grid used in the integrated model. Potential human land-use changes could be incorporated using scenarios derived from models of societal and economic processes, and their impacts on land use (Alcamo et al. 1996).

3. Population dynamics module

This module too may have various levels of complexity. Where data describing the influence of climate on life-history (e.g. age-specific survival, reproduction) are available for a species, the climatic suitability module may be redundant. Instead, the population dynamics module can simulate how climatic changes affect key demographic processes that determine a species' range and abundance. In practice, such data are rarely available and then only from intensive, localised studies. It is unclear whether relationships between weather and fitness observed in such local studies apply also to longer-term climatic changes and, if so, how they lead to distribution changes at the extensive spatial scales at which ranges are limited principally by climate (Schwager et al. 2008). If such relationships do apply at extensive spatial scales, demographic parameters should vary with climatic gradients. Although demographic parameters do vary geographically (Frederiksen et al. 2005), we know of no study clearly relating this to climate. Ample evidence for local adaptation of life-history characteristics (e.g. counter-gradient variation, Laugen et al. 2003) suggests extrapolations from local studies to overall ranges require care. Nonetheless, where basic demographic data are available, a simple population dynamics module could simulate population changes. In a grid-based model, this module would simulate population changes in each grid cell, the maximum population each cell can support being determined by its climatic suitability and habitat availability/suitability (Hill et al. 2001, Keith et al. 2008). Where demographic data are not available for a species, generic estimates based upon similar species may suffice (Anderson et al. 2009). Sensitivity analysis of the demographic module will reveal which fitness components must be estimated most accurately to maximise reliability of the predictions. Minimally, data enabling estimation of the maximum population density and maximum intrinsic rate of population increase in optimal habitat and climate can provide a basis for simulating abundance changes as climate and habitat change.

4. Dispersal module

At its simplest, this module would, at each time step, take the propagules/offspring simulated for each grid cell by the population dynamics module and disperse them stochastically according to a function representing the species' dispersal characteristics. Whilst this may be adequate for passive dispersers, mobile organisms capable of directed dispersal and habitat selection may require more sophisticated treatment. For example, an offspring's eventual

destination may be simulated by a combination of a stochastic process, determining distance and direction of initial dispersal, and a subsequent directed movement if that grid cell is unsuitable. This allows occupation of the nearest suitable and/or not yet fully occupied grid cell within some maximum distance of that to which it initially dispersed (Hill et al. 2001). Density-dependent dispersal also requires consideration (Sutherland et al. 2002). Animals capable of strongly directed dispersal and habitat selection may disperse according to the rules of an ideal free distribution, electing to settle in the optimal reachable patch, as determined by habitat quality and population density. This can lead to a balanced dispersal process in which propensity to disperse is negatively correlated with local carrying capacity (McPeek and Holt 1992, Diffendorfer 1998). Dispersal of strongly territorial species, however, may accord with an ideal despotic distribution (Zimmerman et al. 2003). If dispersal propensity is unrelated to local population density, source–sink dynamics will dominate population dynamics at the range edge (Pulliam 1988), with more suitable areas supporting higher population densities and producing more emigrants than marginal areas. The module must be able to simulate these various dispersal modes. In addition, many mobile species disperse more than once during their life, often in age- and sex-specific ways (Greenwood and Harvey 1982), and the module also must accommodate these cases.

A practical challenge for simulating dispersal is that of obtaining reliable data from which to estimate the distribution of dispersal distances (Paradis et al. 1998, Clark et al. 2003). Suitable propagule dispersal data are available for only very few plant species (Schurr et al. 2005). Dispersal of mobile animal offspring is often easier to observe than plant propagule dispersal, especially where offspring can be individually marked at their natal site and observed or recaptured later. A key difficulty with such data, however, is how to account for varying detection probabilities (Bennetts et al. 2001, Tufto et al. 2005). Faced with these challenges, some authors have used arbitrary migration rates (Fitzpatrick et al. 2008) or simple rule-based dispersal models (Williams et al. 2005, Midgley et al. 2006) to simulate plant species' range expansion. Reliable estimates of dispersal characteristics are important, however, because the distribution of dispersal distances can critically affect species' rates of range shift (Anderson et al. 2009). In particular, much evidence indicates that species' occupation of newly suitable areas following an environmental change depends not upon relatively local, easily observed and more measurable dispersal of the majority of propagules/offspring, but upon inherently rare and difficult to detect long-distance dispersal of a very small minority of propagules/offspring (Clark 1998, Cain et al. 2000). Furthermore, such long-distance dispersal may depend upon mechanisms different from those involved in local dispersal (Wilkinson 1997, Higgins et al. 2003). Where possible, therefore, the form of the species' long-distance dispersal function should be estimated, including, where relevant, the maximum distance attainable by active dispersal. An estimate of the proportion of long-distance dispersed propagules/offspring also is desirable. When faced with a shortage of data upon which to base such estimates, however, simpler approaches to modelling long-distance dispersal will be necessary.

Discussion

Development of integrated models requires careful balancing of model complexity with data availability. For a few species, available data may permit a mechanistic approach to simulating all key processes; more likely, such an approach will be possible for only one or two processes. For most species, the data requirements of fully mechanistic approaches cannot be satisfied and various simplifications are necessary, such as using a binary habitat mask rather than a quantitative habitat suitability sub-model. Even simple integrated models (Keith et al. 2008, Anderson et al. 2009), however, represent an important advance upon climatic envelope models. Integrated model development should be pursued urgently for species that satisfy the necessary assumptions, and especially those for which at least minimum data requirements are met. Initially, these models will be valuable research tools, enabling hypothesis testing and sensitivity analyses to investigate, for example, how habitat availability and/or fragmentation limit species' realisation of their potential responses to climatic change. Development of these models will also highlight areas of critical data deficiency, whilst sensitivity analyses can help prioritise efforts to fill data gaps. Ultimately, and most importantly, these models will provide more and better policy-relevant information on species' responses to climatic change within a dynamic community and habitat context, and thus a sounder basis for decisions about how and where to allocate scarce conservation resources.

The data requirements of such models emphasise the vital contribution made by amateurs and the general public. It is often they who have provided most of the species' distribution and abundance data over extensive regions. Furthermore, model validation requires datasets from repeated mapping/atlas schemes and schemes recording long-term abundance or demographic data. Continuity of financial support for such activities is essential for future assessments of the success of biodiversity conservation strategies and for identifying needs for their adaptive modification (Sutherland et al. 2004). In addition, long-term detailed datasets collected by researchers for individual species are essential for development of the more complete and mechanistic models required to assess simpler models' performances. Although maintaining such long-term studies is unfashionable and difficult, the value of the data they provide in guiding climatic change adaptation options must be recognised by scientific funding agencies worldwide and appropriate resources provided to ensure their future continuity.

The development of integrated range–abundance dynamics models is an urgent research priority, although only the next step towards more realistic simulations of species' responses to climatic change (Barnard and Thuiller 2008). As such models are developed, an important challenge is provision of realistic uncertainty assessments for their outputs; these, in turn, require uncertainty assessments for the inputs. One potential approach to assessing uncertainties is to develop simplified models, often formulated using a Bayesian framework (Wynn et al. 2001), that emulate the behaviour of complex models but can be run many thousands of times to provide uncertainty estimates. In

the longer term, models able jointly to simulate the range and abundance dynamics of two or more interacting species can be envisaged. Such models can test competing hypotheses about the importance of species' interactions in determining geographical distributions (Heikkinen et al. 2007, Preston et al. 2008), and about assembly and dynamics of communities as climate changes (Guisan et al. 2006). They would also contribute to further improvements in robustness of range-change projections upon which conservation policy, planning and management decisions must be made.

In summary, bioclimatic envelope models produce valuable, first-order assessments of potential climatic change impacts on biodiversity. However, their limitations, together with the urgent need to provide more robust information to policy-makers and conservation practitioners, demand the development of integrated models with at least the components we outline here. Because data constraints will inevitably prevent use of complex, fully-mechanistic models for most species of conservation concern, however, we advocate development of models of intermediate complexity (Keith et al. 2008, Anderson et al. 2009) as a means to bridge the knowledge gap and provide more realistic projections of species' responses to climatic change.

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RESEARCH PAPER

Scale effects on the body size frequency distributions of African birds: patterns and potential mechanisms

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ABSTRACT

Aim To describe and analyse the body size frequency distributions (BSFDs) of avian assemblages at several spatial scales in the Afrotropics. We also tested if the variation in median body size across assemblages at different spatial scales was related to environmental variables and whether purely stochastic processes could explain BSFDs.

Location The Afrotropical biogeographic realm.

Methods Avian body masses for 1960 species where analysed at continental, biome, ecoregion and local spatial scales with standard metrics. Variation in median assemblage body size was modelled as a function of environmental and spatial explanatory variables to assess non-random assemblage structure. We tested if BSFDs of smaller spatial scale distributions are random subsets of the larger spatial scale assemblages in which they are embedded, and used three different null model randomizations to investigate the influence of stochastic processes on BSFDs.

Results The African avifauna's continental BSFD is unimodal and right-skewed. BSFDs generally become less skewed and less modal with decreasing spatial scale. The best-fit model explained 71% of median body size values at the ecoregion scale as a function of latitude, latitude^2, longitude, species richness and species range size. BSFDs at smaller scales show non-random assembly from larger scale BSFDs distributions.

Main conclusion African avifaunal BSFDs are quantitatively dissimilar to African mammal BSFDs, which are bimodal at all spatial scales. Much of the change in median body size with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD. At the local scale, energy may well contribute to structuring BSFDs, but this pattern is less pronounced at larger spatial scales.

Keywords
African avifauna, African birds, body mass, body size, range size, scaling effects.

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INTRODUCTION

Body size is one of the most striking attributes of an organism. It affects many physiological and ecological traits (Gaston & Blackburn, 2000), including species home range size (Haskell *et al.*, 2002), species abundances (Lewis *et al.*, 2008), geographic range size (Gaston & Blackburn, 1996) life-history strategies (Rohwer *et al.*, 2009) and can mediate invasions (Roy *et al.*, 2002). Species extinction probabilities are also linked to body size (Gaston & Blackburn, 1995, 1996; Fritz *et al.*, 2009). Therefore, investigations of spatial variation in body size have provided important insights into the ecological and evolutionary processes structuring biological assemblages, with considerable implications for conservation (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Roy *et al.*, 2001; Gaston *et al.*, 2008; Meiri *et al.*, 2009).

Species body size frequency distributions (BSFDs) form a significant means of understanding spatial variation in body size

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(Gaston & Blackburn, 2000). Thus, determining the generality of BSFDs across taxa, regions and spatial scales, and the mechanisms underlying deviations from general patterns are fundamental questions in macroecology (Gaston & Blackburn, 2000). Although much is now known about general patterns in BSFDs at the broadest spatial scales (Blackburn & Gaston, 1994; Roy *et al.*, 2000; Smith *et al.,* 2004), at smaller spatial scales the nature of variation in BSFDs and the mechanisms underlying this variation are not as comprehensively understood. At the regional to global scale, BSFDs for birds, mammals, lizards, bivalves and most insects are generally strongly right-skewed on a logarithmic scale (Brown & Nicoletto, 1991; Gaston & Blackburn, 2000; Roy *et al.*, 2000; Meiri, 2008; Chown & Gaston, 2010), but bimodal for North American squamates (Cox *et al.,* 2011) and not skewed in snakes (Boback & Guyer, 2003), some beetles (Dixon & Hemptinne, 2001), or squamates generally (Reed & Boback, 2002). At smaller spatial scales BSFDs can also be highly variable, ranging between right-skewed (Gaston *et al.,* 2001), less strongly right-skewed (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Smith *et al.,* 2004; Greve *et al.,* 2008; Chown & Gaston, 2010), flat (indistinguishable from log-uniform) (Marquet & Cofré, 1999), or even multimodal (Chown & Gaston, 1997; Raffaelli *et al.*, 2000; Kelt & Meyer, 2009; Cox *et al.,* 2011).

For smaller spatial scales, a key question is whether BSFDs are merely random subsets from the larger spatial scale assemblages in which they are embedded. If they are not, then some factor must be invoked at that scale to explain observed BSFDs (Gaston & Blackburn, 2000). In North and South American mammals, smaller spatial scale BSFDs are not random subsets of the larger scale BSFDs (Brown & Nicoletto, 1991; Bakker & Kelt, 2000). BSFDs of North American mammals are modal and right-skewed, show non-random assembly, and decrease in skewness in assemblages at progressively finer spatial scales. Brown & Nicoletto (1991) ascribed this pattern to three main mechanisms: (1) competition for limited resources means local faunas contain fewer modal-sized species; (2) large species with small geographic ranges are more extinction prone; and (3) allometric constraints on physiology lead to greater specialization of modal-sized species. However, Cox *et al.* (2011) argued that these mechanisms may be of less importance for the squamates of North America, with deep phylogenetic differences among component taxa being more significant. The BSFDs of South American mammals in general are similar to those of North American mammals in showing non-random assembly, but they are multimodal at all spatial scales and do not become indistinguishable from log-normal at the smallest spatial scales (Marquet & Cofré, 1999). The additional mode persists at smaller spatial scales, and could be due to habitat specialization (Bakker & Kelt, 2000). The BSFDs of African mammal assemblages are multimodal at all spatial scales. Kelt & Meyer (2009) suggested that the secondary mode could be a consequence of the assemblage not being as adversely affected by anthropogenic Pleistocene extinctions as in other regions, but they did not test if local assemblages were random subsets from the larger species pool.

The global bird BSFD is right-skewed (Blackburn & Gaston, 1994), just as in the Americas (Cardillo, 2002). South African birds also have right-skewed BSFDs, and much of the variation in median body size can be predicted by randomly drawing species from the regional distribution (Greve *et al.,* 2008). Therefore, purely stochastic processes also need to be taken into account when explaining BSFDs as they can contribute to observed patterns (Meiri & Thomas, 2007). Blackburn & Gaston (2001) showed that in a local assemblage of birds in Britain, a random draw model from the regional bird assemblage accurately predicts most descriptive statistics if the probability that a species is selected is weighted by its geographic range size. However it is unclear how ubiquitous right-skewed BSFDs are for birds, whether BSFDs at smaller scales are indeed non-random subsets of larger scale distributions, and what mechanisms might underlie the scaling effects on BSFDs.

Here, we therefore analyse the BSFDs of avian assemblages at several spatial scales across the Afrotropics. We test whether the variation in median body size across assemblages at different spatial scales was related to energy, species richness and range size, all variables which are known to correlate with the median body size of birds globally (Olson *et al.,* 2009). We also test whether smaller spatial scale distributions are random subsets of the larger spatial scale assemblages in which they are embedded. The influence of stochastic processes on BSFDs is further investigated by comparing observed distributions to three types of null distributions generated by randomly resampling the continental avifauna. Finally, we determine whether energy, species richness and range size could explain the deviation of the model null distributions from the median observed data, at the local scale.

METHODS

Species distribution data

We used the WWF Wildfinder database (Olson *et al.,* 2001) at the ecoregions scale as a template for collating data on all bird species in the Afrotropical bioregion, excluding offshore islands, the Arabian Peninsula and Madagascar. Ecoregions are spatially discrete units that contain geographically distinct assemblages of natural communities that share a large majority of their species, ecological dynamics and similar environmental conditions (Olson *et al.,* 2001). The taxonomy and distribution of species was comprehensively updated from Sinclair & Ryan (2003). The ranges of species absent from the Wildfinder database (mainly due to taxonomic changes and errors) were digitized in ESRI ArcGIS 9.3 (2011) at the ecoregion scale from Sinclair & Ryan (2003). This study focuses on terrestrial species, excluding vagrants, introduced species and offshore-nesting seabirds. We included migrant species here as their inclusion or exclusion had no significant effect on the BSFD of the South African avifauna (Greve *et al.,* 2008). While in polar and temperate regions small-bodied migratory species are significantly overrepresented (Olson *et al.,* 2009), our study area is not in these regions, further motivating the inclusion of migrants.

Species were assigned to a continental species list, biome species lists, ecoregion species lists and local scale lists. Species lists were generated from the continental species lists for the seven major biomes of sub-Saharan Africa (Deserts and Xeric Scrubland, Mediterranean, Grasslands, Savanna, Flooded Savanna, Moist Broadleaf Rainforests, and Dry Broadleaf Rainforests following Olson *et al.,* 2001). A total of 86 ecoregions were used, excluding mangroves. Local lists were compiled for sites that were historically undisturbed (preferably Protected Areas), and had been surveyed in at least two seasons or years using multiple techniques. Local scale sites varied in size but averaged approximately 25 km^2. A total of 23 local scale lists were used for analysis, with representation from all biomes (see Supporting Information Appendix S1 and a map of the study region in Appendix S2).

Body size data

Body mass data for all species was primarily obtained from Dunning (2008), and supplemented with data from Hockey *et al.* (2005) and Fry *et al.* (1988) where needed. We accounted for different reporting standards in the data (such as masses for one sex only, masses for few individuals, and masses from different locations) using the methods of Greve *et al.* (2008). Where races differed in body size (as reported in Dunning, 2008), but were treated as one species in Sinclair & Ryan (2003), the mean body size across races was used. Since the masses of 10% of species (200/1967) could not be obtained from the literature, we divided the database into two sets. First, we used all the species with mass data obtained from the literature (n = 1767). Second, we estimated the mass of species lacking data by averaging the masses of all congeners (n = 1967). For seven of these species in monotypic genera body masses could not be estimated by this method and these species were omitted from this study (*Coccycolius iris*, *Dryotriorchis spectabilis*, *Pseudoalcippe abyssinica*, *Pseudochelidon eurystomina*, *Tigriornis leucolophus*, *Todirhamphus chloris* and *Zavattariornis stresemanni*). The distribution of bird body sizes from the two datasets did not differ significantly (Kolmogorov–Smirnov (KS) test, $D = 0.0211$, $P > 0.99$) and did not lead to different interpretations from the BSFDs (data not shown) and, therefore, we only report results further including the data calculated from congeners ($n = 1960$). Both the common and Somali ostriches (*Struthio camelus* and *S. molybdophanes*, respectively) may be outliers in the dataset due to their very large body mass (*c.* 70 kg), but omitting them had a negligible impact when comparing the distributions of the two datasets (KS test, $D = 0.0004$; $P > 0.99$), or when interpreting BSFDs histograms (data not shown), so we retained these species at all scales where applicable.

Statistical analysis

General

The preliminary analyses broadly followed the methods of others (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Cardillo, 2002; Greve *et al.,* 2008; Kelt & Meyer, 2009). All body masses were converted to $\log_2$ units to reduce heteroscedasticity and for ease of representation. Histograms were used to assess qualitatively the frequency distributions at all spatial scales. Because the analysis of BSFD can be affected by the position of frequency bins, we calculated the BSFD from the mean of three bracketed bins, at 0.5, 1 and 1.5 $\log_2$, respectively, following Kelt & Meyer (2009). Since body size distributions are typically skewed, median body size is a more appropriate measure for analysing body size data of assemblages than the mean (see Meiri & Thomas, 2007).

Body size distributions were described using standard metrics: median body size, interquartile range, kurtosis and skew. To test the significance of differences in frequency distributions between successively smaller spatial scales, a Kolmogorov–Smirnoff goodness-of-fit test was used to compare all distributions and the larger spatial scale assemblages in which they are embedded (e.g. continental BSFD with all biomes' BSFDs and biomes with all their constituent ecoregions). To test if the observed distributions differed significantly from a log-uniform distribution (e.g. Bakker & Kelt, 2000), we compared every site to the average of 1000 randomly generated log-uniform distributions with the same number of species and statistical range of masses as in that site. Since all sites differed highly significantly from a log-uniform distribution at all spatial scales (data not shown), we repeated the test using a random uniform distribution, especially given that the expectation is for such a distribution at the finest spatial scales (Bakker & Kelt, 2000).

We also tested if the body masses of species assemblages at smaller scales are a random sub-sample from larger BSFDs. For each of the smaller scale assemblages we randomly drew, without replacement, species' body masses from the larger spatial scale assemblages, drawing the same number of species as was observed at that smaller scale site. Resampling was repeated 10,000 times, after which the median of each resampling was compared with the observed median for that particular site, and the proportion of simulated medians less than or greater than the observed median calculated (following Brown & Nicoletto, 1991). Where the proportion of simulations meeting these criteria was less than 0.025 or greater than 0.975 (i.e. a two-tailed test), the result indicated a significant difference, and therefore non-random local scale assemblage, at the alpha = 0.05 level.

Generalized linear models

The relationship between the median body size and environmental and spatial explanatory variables was examined at ecoregion and local spatial scales using generalized linear models (GLMs; assuming a Gaussian distribution with a log-link function). We did not conduct this analysis at the biome scale due to a small sample size and high collinearity between explanatory variables. For each site, at ecoregion and local scales, explanatory variables were species richness, the mean range size of all species in each site in km^2 of ecoregion area occupied, latitude, longitude and seasonality in primary productivity (as estimated by

the absolute difference between January and July NDVI values from 2004–2009, using the SPOT imagery at a 1 km × 1 km spatial resolution; http://www.devcocast.eu). The centroids of all sites were calculated with XTOOLs (http://www.xtoolspro.com) in ESRI ArcGIS 9.3 (2011) for the latitude and longitude coordinates. A small positive constant was added to response variables prior to analyses to ensure that only non-negative values were subject to the log-link function. To account for potential non-linear relationships the quadratic forms of all variables were also included in the models. To avoid multicollinearity among predictor variables, we deleted variables with high collinearity (measured as a Variance Inflation Factor > 10; Quinn & Keough, 2002) in a stepwise manner until collinearity was minimal (the Variance Inflation Factor < 10 for all variables included in the model; following Zuur *et al.,* 2010). A best subsets regression approach was implemented using the 'bestglm' package in R (McLeod & Xu, 2010), with all permutations of explanatory variables considered. The models were then ranked by Akaike Information Criterion (AIC) values, with the lowest AIC value indicating the best-fit model (Johnson & Omland, 2004; McLeod & Xu, 2010).

Null models

Null models are pattern-generating models based on random sampling from a known distribution (Gotelli & Graves, 1996). Three kinds of null models were produced to investigate whether stochastic processes contribute to observed patterns (Meiri & Thomas, 2007), and to investigate the influence of geographic range size (Blackburn & Gaston, 2001) and energy (Aava, 2001; Huston & Wolverton, 2009) on structuring BSFDs. First, to assess whether observed BSFDs could be explained by purely random assembly an 'unweighted null model' was produced, where for each site the same numbers of species as occurring at that site were randomly drawn without replacement from the continental species pool, the median body mass calculated across the randomly sampled species, and the resampling process repeated 10,000 times. For this model all species have an equal probability of being sampled. Second, to account for wide-ranging species being more likely to occur at more sites, a 'range-weighted null model' was produced. For this null model the random draw procedure was repeated, but the probability of a species selection from the continental pool was positively weighted proportional to its range across all ecoregions (in km^2). Thus species with large ranges have a higher probability of being drawn. Third, to assess whether primary productivity structures BSFDs (see Aava, 2001 and Huston & Wolverton, 2009), a 'NDVI-weighted null model' was created by weighting a species probability of selection from the continental pool by the mean NDVI value across its range. We compared each of the three null models calculated medians for each site at all scales to the actual observed median body mass values at that site with a Mann–Whitney *U*-test (Quinn & Keough, 2002).

All analyses were conducted in R (R Development Core Team, 2010) and Microsoft Excel, Microsoft Access and ESRI ArcGIS 9.3 (2011) were used for data curation.

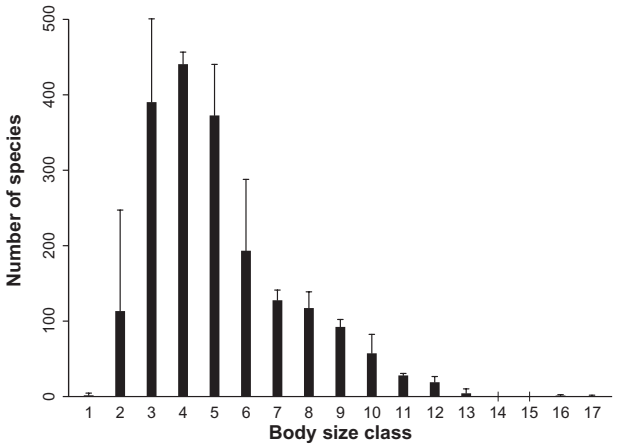

Figure 1 Body size frequency distribution for the avifauna of the continental Afrotropical biogeographic realm (n = 1960). Avian body masses were $\log_2$ transformed and span body size classes from size class 1 (4.1 g) to 17 (*c.* 111 kg). Error bars indicate one standard deviation, as calculated across three size class bins.

RESULTS

The African continental avian BSFD is unimodal and significantly right-skewed (Fig. 1; Skew = 1.14; $P < 0.0001$) with a mode in size class 3–5 (5.7–45.3 g). BSFDs generally became less skewed and less modal with decreasing spatial scale of the analysis (Figs 2 & 3e; Appendix S3). At successively smaller spatial scales, the mean, median and interquartile range of body mass generally increases and the distribution's skew and kurtosis decreases (Appendix S3). Across all the BSFDs from all the three scales investigated, only the Mt Kupe and the Kibale Forest local scale assemblage were more strongly skewed than the continental BSFD (Appendix S3). Most distributions (95%; 112/117) are significantly right-skewed (skew for 112 distributions: 0.31–1.26; $P < 0.05$), apart from three ecoregions and two local scale distributions which show approximately symmetric distributions (East African montane moorlands, Ethiopian montane moorlands, Eritrean coastal desert, Seekoeivlei, Topoa Region; Appendix S3). Nearly all (97%; 112/116) of the BSFDs showed a decrease in kurtosis by comparison with the continental assemblage (Appendix S3).

The majority of distributions (98%; 115/117) differed significantly from a random uniform distribution (means of 1000 iterations; KS tests $0.152 < D < 0.450$; and $P < 0.04$; Appendix S4). Only two distributions, the East African montane moorlands ecoregion and the Seekoeivlei local scale assemblage, did not differ significantly from a random uniform distribution (means of 1000 iterations; KS tests $D = 0.154$, $P = 0.185$ and $D = 0.152$, $P = 0.258$, respectively, Appendix S4).

The majority of smaller scale distributions are significantly different from their larger scale BSFDs (69%; 80/116; all 81 comparisons: KS tests $0.07 < D < 0.25$; $P < 0.05$; Appendix S5). The Moist Forest and Savanna biomes do not differ significantly from the Continental distributions (KS tests $D = 0.02$, $P = 0.7$ and $D = 0.310$, $P = 0.3$, respectively) and neither do 22 ecore-

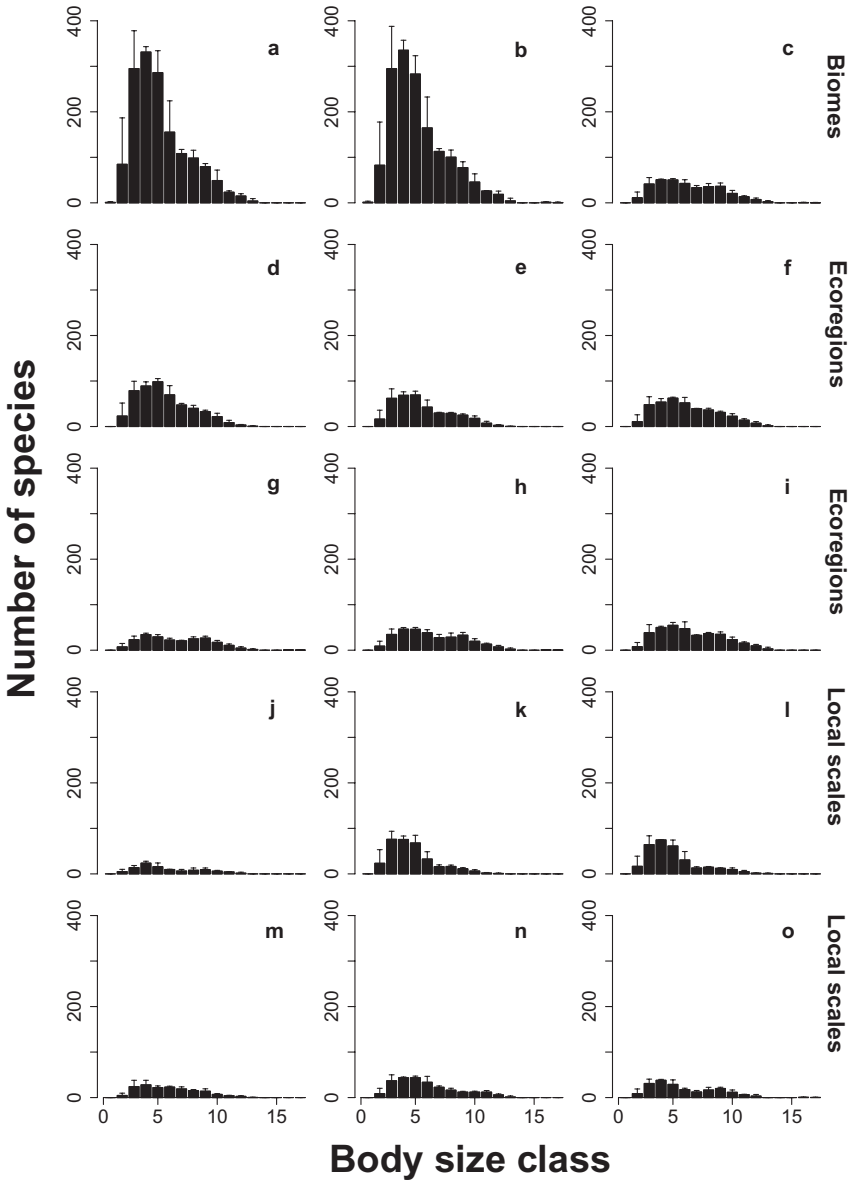

Figure 2 Body size frequency distributions from representative biome (top row), ecoregions (rows 2–3) and local scale sites (rows 4–5). Avian body masses were $\log_2$ transformed and span body size classes from size class 1 (4.1 g) to size class 17 (*c.* 111 kg), with the primary mode generally in size class 3–5. Error bars indicate one standard deviation. See Appendix S1 for details of all biomes, ecoregions and local sites, and Appendix S2 for a map of the study region. (a = Moist Forest; b = Savanna; c = Fynbos; d = Eastern Guinean Forests; e = Cross-Niger Transition Forests; f = Western Zambezian Grasslands; g = Succulent Karoo; h = Montane Fynbos and Renosterveld; i = Maputaland-Pondoland Bushland and Thickets; j = Skilpadvlei Nature Reserve; k = Mt Kupe; l = Kibale Forrest; m = Bagarinnaye and Maïjémo; n = Hans Merensky Nature Reserve; o = Vrolijkheid Nature Reserve).

gions and nine local scale distributions differ significantly from the larger scale BSFDs distributions (Appendix S5). The median body mass of the majority of sites (84%; 97/116) differs significantly from distribution of medians generated through random selection of species from the larger spatial scale assemblages in which they are embedded (Appendix S6). Most sites have significantly higher body mass than expected by chance (71%; 82/116), although 13% of sites have a significantly lower mass than expected (15/116) and some are not significantly different (16%; 19/116; Appendix S6). These results in general are indicative of the non-random assembly of BSFDs at successively smaller spatial scales.

The best-fit GLM model explained 70.82% of the variation in median body mass values at the ecoregion scale and included latitude, latitude^2, longitude, species richness and species range size as significant explanatory variables (Table 1). At the local scale the best-fit model explained 84.98% of variation in median body mass as a function of NDVI, species richness^2 and range (Table 1).

At all spatial scales the median body sizes from all of the three null models were higher than the observed continental median (Fig. 3a–d; Mann–Whitney *U*-test, all significantly different; $49 < W < 10{,}211$; $P < 0.05$). The body size predicted by the null models was generally lower than the observed median values at the biome and ecoregions scales, although this was reversed at the local scales (Fig. 3a–d; Appendix S7). Compared with observed data, the unweighted null model produced median masses that are significantly lower at the biome and ecoregion scales, but higher at the local scales. This finding reaffirms that random processes alone cannot explain observed body size frequency distributions (Fig. 3b; Appendix S7). The biome and ecoregion scale range-weighted null model medians did not

Table 1 Best fit multivariate generalised linear models of median body mass in relation to environmental variables.

	Ecoregion scale			Local scale		
AIC	51.316			5.821		
AIC weight	0.53			0.39		
N	86			23		
Deviance explained	70.82%			84.98%		
Predictor variable	Slope	SE	*P*	Slope	SE	*P*
Intercept	1.485	0.057	****	1.305	0.056	****
Latitude	0.002	0.001	**	n.s.		
Latitude^2	0.001	0.001	****	n.a.		
Longitude	0.002	0.001	****	n.a.		
Longtitude^2	n.a.			n.s.		
NDVI	n.a.			0.001	0.000	***
NDVI^2	0.001	0.001		n.a.		
Species Richness	0.001	0.001	****	n.a.		
Species Richness^2	n.a.			0.000	0.000	
Range	0.442	0.0645	****	0.615	0.072	****
Range^2	n.a.			n.a.		

Significance codes: ****$P < 0.0001$, ***$P < 0.001$, **$P < 0.01$, n.s. = not significant; n.a. = not applicable (variable with high multicollinearity and was not used; see text for details).

differ significantly from the observed median (Fig. 3c; Mann–Whitney *U*-test, $30 < W < 6421$; $P > 0.3$), although at the local scale there was a significant difference. Compared to observed data, the NDVI-weighted null model produced median masses that were significantly lower than expected at the biome and ecoregion scales, but higher at the local scales (Fig. 3d; Mann–Whitney *U*-test, all significantly different Mann–Whitney *U*-test; $30 < W < 6341.5$; $P < 0.01$). The skew of all null models at all scales was lower than the observed continental skew, and significantly different at all scales from the observed data (Fig. 3e–h; Mann–Whitney *U*-test; $47 < W < 7332$; $P < 0.002$).

While the range-weighted null model provided an indication of the process underlying the observed BSFDs especially at broader scales (see Discussion), none of the null models showed median body masses or distribution skews similar to the local scale observed BSFDs (Fig. 3). To test if the difference between observed median and null-modelled medians at the local scale (hereafter termed the null model residuals) could be explained, we used the same generalised linear modelling approach and identical variables as detailed in the above, for analysing the local scale data. Best fit models to explain the null model residuals at the local scale all had significant terms for space (latitude or longitude), NDVI and range, but not for species richness. Deviance explained for the unweighted null model, range-weighted null model, and NDVI-weighted null model, was 76.70%, 81.04% and 75.90%, respectively (Table 2).

DISCUSSION

The continental African avifaunal body size frequency distribution (BSFD) is predominantly right-skewed and unimodal, similar in general to the BSFDs found for many vertebrates (e.g. Brown & Nicoletto, 1991; Greenwood *et al.*, 1996; Arita & Figueroa, 1999; Polo & Carrascal, 1999; Bakker & Kelt, 2000; Knouft & Page, 2003; Meiri, 2008; Griffiths, 2011; but see Reed & Boback, 2002; Boback & Guyer, 2003; Olden *et al.*, 2007; Cox *et al.*, 2011; Hu *et al.*, 2011), for birds in the New World (Cardillo, 2002) and for the global avifaunal distribution (Olson *et al.*, 2009). Indeed, this pattern seems general (Gaston & Blackburn, 2000; Chown & Gaston, 2010; but see Roy & Martien, 2001; Boback & Guyer, 2003; Ulrich & Fiera, 2010). Although the median mass of African birds (33.5 g) is only slightly lower than that of global avifauna (37.6 g; Blackburn & Gaston, 1994), the BSFDs for the African avifauna generally become less skewed and less modal with decreasing spatial scale of the analysis, as has been found for mammals elsewhere (e.g. Brown & Nicoletto, 1991; Marquet & Cofré, 1999; Bakker & Kelt, 2000; Smith *et al.*, 2004; Kelt & Meyer, 2009). Surprisingly, the change in shape and central position of the BSFD has not been as widely characterized at a variety of spatial scales for birds, as it has been for mammals or reptiles (Cox *et al.*, 2011). Indeed, formal, quantitative investigation of change in the BSFD with spatial scale for birds is typically limited to investigations of two spatial scales (e.g. Blackburn & Gaston, 2001; Greve *et al.*, 2008). In consequence, an understanding of the generality of the patterns found here across multiple spatial scales for a major continental landmass must rely on work done mostly on mammals.

Unlike African mammals, the African avifaunal BSFDs are not bimodal at all spatial scales (Kelt & Meyer, 2009). Kelt & Meyer (2009) argued that large mammals in Africa coevolved with proto-human hunters and so predominantly escaped the mass extinctions typical of other regions. For birds at least, our data does not support this interpretation, mainly because it requires the presence of an additional mode to vindicate it, and the effect of proto-human hunters in structuring bird assemblages in any case is unclear. Rather, we suggest the difference in BSFDs between African mammals and birds points to substantial differences in various life history traits, body shape, foraging ecology, body architecture and macroecological features among these major taxa (Silva *et al.*, 1997; Speakman, 2005; Melo *et al.*, 2009). Such consistent, among-clade trait variation potentially accounts for observed differences in the BSFDs of other taxa, such as the squamate reptiles (Boback & Guyer, 2008; Cox *et al.*, 2011). From the perspective of changes in BSFDs with spatial scale, the implications of these differences warrant further analysis. The pronounced additional mode at smaller spatial scales found in South American mammals is also absent in the African avifauna. Bakker & Kelt (2000) posited that Neotropical arboreal mammal species are of a smaller body size and can co-exist due to the addition of the rain forest canopy habitat which contains more and typically larger species, thus inflating local scale species richness and so increasing the number of low to medium mass species in the assemblages (Bakker & Kelt, 2000, and see Marquet & Cofré, 1999; Polo & Carrascal, 1999). Again that interpretation does not seem to apply here, mainly since it requires the addition of a second mode in BSFDs at smaller spatial scales (e.g. in Fig. 2; Appendix S3). Nonetheless, a

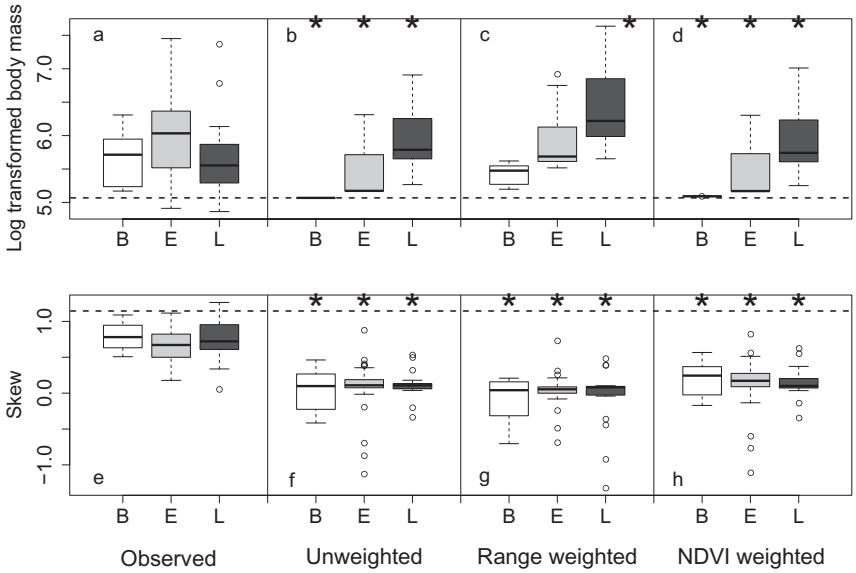

Figure 3 Median body mass and skew for observed data (a,e), the unweighted null model (b,f), the range-weighted null model (c,g), and the NDVI-weighted null model (d,h), at biome, ecoregion and local scales respectively. Dashed lines indicate the observed median body mass (5.07; top row of panels) and observed skew (1.14; bottom panels) at the continental scale. Thick lines indicate median values, boxes indicate the interquartile range, whiskers indicate the non-outlier range, and empty circles indicate outlier values (values more than 1.5 times the interquartile range) across sites at that scale. B = biome scale; E = ecoregion scale; L = local scale. Null models marked with an asterisk differ significantly from the observed median at that scale (Mann–Whitney *U*-test; $30 < W < 6341.5$; $P < 0.01$). All skew values differ significantly from observed skew (Mann–Whitney *U*-test; $47 < W < 7332$; $P < 0.002$).

Table 2 Best fit multivariate generalised linear models of unweighted, range-weighted and NDVI-weighted null model residuals (observed median minus calculated null model median), in relation to explanatory environmental variables at the local scale.

	Unweighted			Range-weighted			NDVI-weighted		
AIC	20.745			20.735			22.333		
AIC weight	0.43			0.54			0.42		
N	23			23			23		
Deviance explained	76.70%			81.04%			75.90%		
Predictor variable	Slope	SE	*P*	Slope	SE	*P*	Slope	SE	*P*
Intercept	−1.340	0.270	***	−1.140	0.267	***	−0.773	0.202	**
Latitude	0.085	0.004	*	n.a.			n.a.		
Latitude^2	n.a.			−0.001	0.001	***	n.s.		
Longitude	n.a.			n.a.			n.a.		
Longtitude^2	0.001	0.001		n.s.			0.001	0.001	*
NDVI	0.009	0.002	***	n.a.			0.008	0.008	***
NDVI^2	n.a.			0.001	0.001	***	n.a.		
Species Richness	n.s.			n.a.			n.a.		
Species Richness^2	n.a.			n.s.			n.s.		
Range	n.a.			2.250	0.347	***	n.a.		
Range^2	1.855	0.355	***	n.a.			1.712	0.295	***

Significance codes: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. = not significant; n.a. = not applicable (variable with high multicollinearity and was not used; see text for details)

similar mechanism may well apply at local spatial scales (see Gómez de Silva & Medellín, 2002). Despite these differences with mammalian assemblages, the change in BSFDs from the continental to local scale found here is similar to the limited work on birds (Gaston & Blackburn, 2000; Blackburn & Gaston, 2001; Cardillo, 2002; Greve *et al.*, 2008), suggesting that patterns found here likely hold for birds generally, as they seem to for many other taxa (e.g. Chown & Gaston, 2010), although not for North American squamates (Cox *et al.*, 2011).

In keeping with work on mammals (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Smith *et al.*, 2004; Rodríguez *et al.*, 2006) and birds (Blackburn & Gaston, 2001; Greve *et al.*, 2008),

Afrotropical avian BSFDs at a range of spatial scales show non-random assembly from larger scale assemblages. Several explanations could account for this pattern. First, it has been suggested (Meiri & Thomas, 2007) and demonstrated (Greve *et al.*, 2008) that richness is likely to have a substantive effect on assemblage median mass, especially since in low richness sites the modal size is likely to be higher for reasons of sampling alone (Gaston & Blackburn, 2000; Meiri & Thomas, 2007). Although we found that richness was a significant explanatory variable for median mass at the ecoregion scale, when richness was accounted for in the unweighted null model, it failed to simulate the observed median body size. In consequence, some other mechanistic process must be responsible for the differences between the null and observed assemblages. Two of the primary contenders are energy, given its role in affecting size and size distributions (reviewed most recently by Huston & Wolverton, 2011), and range size, given that smaller-bodied species tend to have higher spatial turnover than larger-bodied ones (Brown & Nicoletto, 1991; Brown & Lomolino, 1998; Melo *et al.*, 2009; Chown & Gaston, 2010), leading to the accumulation of more small-bodied species in BSFDs compiled at larger spatial extents.

Median body mass of assemblages in the NDVI-weighted null models differed significantly from the observed values at all spatial scales, and NDVI likewise did not enter as an explanatory variable in the generalized linear models except at the local scale. In consequence, at least at the biome and ecoregion scales variation in energy availability is unlikely a contender for explaining variation in BSFDs. By contrast, not only did range size enter the generalized linear models as a significant term, but at the biome and ecoregion scales, median body mass of the range-weighted null assemblages did not differ significantly from the observed values. In consequence, it appears that, at least at these scales, the change in central tendency of the BSFDs is well-explained by differences in turnover rate among smaller- and larger-bodied species, with the former tending to have the largest turnover rates (as suggested by a triangular range-size body size relationship; Appendix S8 and see Brown & Lomolino, 1998; Fernández & Vrba, 2005; Melo *et al.*, 2009). While it does not seem to apply to squamates (Cox *et al.,* 2011), this explanation for differences in BSFDs at different spatial scales has been mooted for both birds and mammals (Brown & Nicoletto, 1991; Blackburn & Gaston, 2001), and our work provides further evidence for it.

Although not adequately captured in our null models, energy may still structure BSFDs especially at local scales, as indicated by differences between the NDVI-weighted null model median and observed median and that the observed data at this scale continue to be related to NDVI. While our measure of energy may be too coarse and should have rather been eNPP (Ecologically relevant Net Primary Productivity, defined as net primary production during the growing season; Huston & Wolverton, 2011), it is clear that some other process is likely also involved because our models inevitably failed to capture the skew in the observed data. This unexplained mechanism may well be the optimization of size based on the size-dependence of production rates (the difference between energy assimilation and respiration) and mortality rates (Kozłowski & Gawelczyk, 2002). Production rates are directly related to energy availability, while mortality may be indirectly related in the sense that mortality from predators, parasites or competitors is likely to increase as diversity increases, which is in turn related to energy availability (Hawkins *et al.*, 2003; Currie *et al.*, 2004). Such varying size optimization, an essentially evolutionary mechanism, is a key process that leads to positively skewed frequency distributions, but one that is not captured by any of the null models here. At larger spatial scales, size-based variation in diversification rates (Maurer *et al.*, 1992; Gaston & Chown, 1999; Kozłowski & Gawelczyk, 2002), accompanied by variation in dispersal rates, which have a large influence on clade diversity (Phillimore *et al.*, 2006), may be key in determining skewness. The role of productivity therefore clearly deserves further attention for the explanation of changes in size distributions with changing spatial scale.

Several caveats need to be taken into consideration in interpreting our results. First, in common with many other studies of BSFD variation, we were not always able to assess the effects of spatial autocorrelation, and future studies should take the potential effects thereof into consideration (see, e.g., Bahn *et al.*, 2006), although given the strength of the results here we do not think that the outcomes will be much affected (see also Bini *et al.*, 2009). Second, due the lack of an appropriate and well resolved molecular phylogeny for the species in our study area, we could not incorporate phylogenetic affects, and future work incorporating such an approach, especially examining the evolutionary mechanisms underlying the patterns we document, would likely account for much of the unexplained variation. Finally, there is much variation in the actual size of areas within the ecoregion and local scales. The continued presence of modes in body sizes at especially local scales (i.e. Mt Kupe; Fig. 2k) might indicate that our sites are too large or heterogeneous to effectively capture the change in BSFDs with scale. However, there is a consistent dampening of BSFDs across scales (Appendix S3), a consistent low kurtosis of BSFDs *within* local scales (Appendix S3) and the majority of smaller scale distributions differ from the larger scale distributions within which they are embedded (Appendix S5). Consequently, regardless of the effective area of our sites, it appears that the observed patterns are consistent.

In conclusion, here we have shown that on log scales, the BSFDs in Afrotropical birds are unimodal, right-skewed and become less skewed and less modal with the decreasing spatial scale of the analysis, in keeping with patterns found in other taxa. Much of the pattern in median body size change with spatial scale can be captured by a range-weighted null model, suggesting that differential turnover between smaller- and larger-bodied species might explain the shift in the central tendency of the BSFD. However, at smaller spatial scales energy availability may be the most significant determinant of median size, and energy may also play a role in determining the substantial skew of distributions at all spatial scales through species-level optimization of size and the processes that lead to size-biased diversification. Exactly how diversity, size and diversification interact to produce BSFDs across spatial scales

remains one of macroecology's largest challenges (see Allen *et al.*, 2006; Smith & Lyons, 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Size, centroid coordinates and origin of all sites analysed.

Appendix S2 Map of the study area.

Appendix S3 Summary statistics for all sites analysed.

Appendix S4 Kolmogorov–Smirnoff tests between random uniform distributions and observed data.

Appendix S5 Kolmogorov–Smirnoff tests between all nested distributions at all scales.

Appendix S6 Simulations and statistics of body size frequency distributions drawn from the larger spatial scale assemblages in which they are embedded.

Appendix S7 Percentage of all null models greater than, less than, or equal to observed.

Appendix S8 Range size and body mass relationship for 1960 African birds.

BIOSKETCHES

Bernard W.T. Coetzee has a range of interests in biogeography and conservation science, with a focus on Protected Areas and global change drivers. He is also interested in science policy and science–public interfaces.

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