

Functional importance of snakes in a strandveld ecosystem

by

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Declaration

I, **Juan-Jacques Aiden Forgas**, declare that '**Functional importance of snakes in a strandveld ecosystem**' is my own work and that all the sources I have used or quoted have been indicated and acknowledged by means of complete references.

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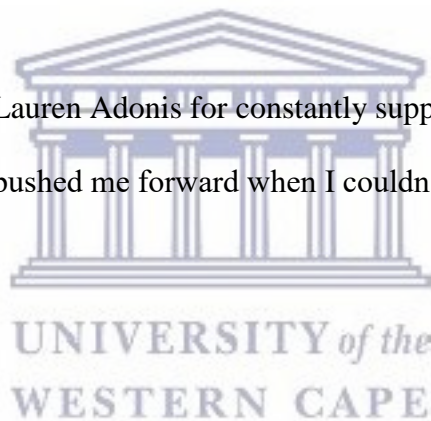
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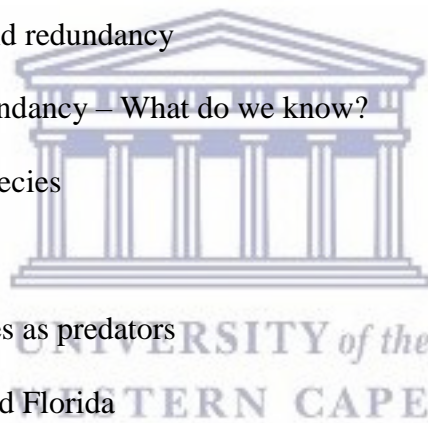
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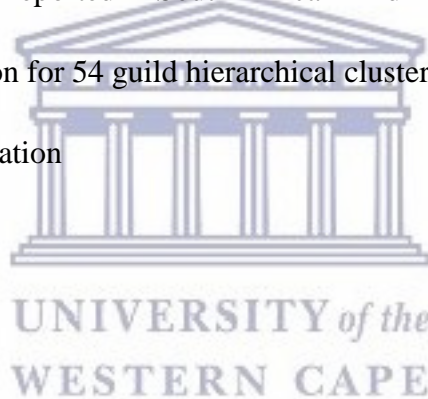
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Abstract

Gaps in our knowledge of the functional roles of snakes within ecosystems limit our ability to predict the potentially cascading effects their removal from an ecosystem might create. Extirpation of snake species could potentially result in losses of ecosystem functionality if those taxa are ecologically unique. I used pitfall and funnel trap arrays, artificial cover object surveys, active searching, and passive camera trapping, as well as pre-existing faunal diversity data to identify terrestrial tetrapod species within the Koeberg Private Nature Reserve. This resulted in a list of 265 species, of which 13 were snakes. I then gathered data on dietary and four additional functional traits for each species from the literature. Next, using hierarchical and partitioning around medoids clustering, I identified ten broad dietary guilds and 54 functional guilds within the terrestrial tetrapod community. Of the dietary guilds *Dasyveltis scabra* was the only snake species that formed a unique single species guild and was one of four snake species (*Pseudaspis cana*, *Homoroselaps lacteus* and *Lamprophis guttatus*) to form four unique single species functional guilds. The remaining snakes clustered together within groups of other vertebrate predators. Functional diversity analysis was then used to simulate losing eight major taxonomic groups (birds, passerines, non-passerines, mammals, reptiles, snakes, non-snake reptiles and amphibians) and gauge the effects of those losses on overall community dietary and functional diversity. Functional diversity analysis revealed that the loss of certain snake species resulted in disproportionate losses of overall community dietary and functional diversity while losing others had negligible effects. These findings provide ambivalent support for the dietary and functional uniqueness of snakes suggesting that certain snake species are fulfilling unique functional roles within the ecosystem. Additionally, it is likely that losing those non-redundant species would result in significant losses of ecosystem functionality.

Chapter 1: Introduction

Framework and problem identification

In the face of ongoing global species losses, understanding the impacts of anthropogenic activities on ecosystems has never been more pressing an issue. This is due to most losses being attributed to human exploitation of the earth's resources and the large-scale effects thereof. The prospect of global biodiversity loss at rates outpacing those previously seen in the fossil record (Millenium Ecosystem Assessment 2005) has prompted research into the associated effects of those losses. Research of this nature grows increasingly important as evidence continues to mount suggesting that losses in species, via extinction or extirpation, may be altering key ecosystem processes in manners that we are yet to fully understand or predict (Wake and Vredenburg 2008, Hooper et al. 2012).

Ecosystem functioning—defined as the rate, level, or temporal dynamics of one or more ecosystem processes (Tilman 2001)—is maintained partly by biological and physical ecosystem traits as well as the interactions between the organisms living within those ecosystems (Walker 1992, Chapin et al. 1997). Unfortunately, the interplay between species-specific traits and species interactions as well as how they collectively influence ecosystem function aren't clear (Clare et al. 2016). Without a proper understanding of the way species traits determine environmental functionality, we cannot hope to confidently prioritize conservation of those species contributing most significantly to maintaining ecosystem resilience and potentially preventing catastrophic changes. In this context, resilience is broadly defined as “the capacity of a system to absorb disturbance and reorganize so as to retain essentially the same function, structure, identity and feedbacks.” (Folke et al. 2004). Research into the functional ecology of species is crucial for providing insight into managing ecosystems more effectively (Soulé et al. 2005) but current gaps in our understanding of ecosystem

functionality undermines our ability to make confident management decisions. By focussing research on species interactions and functional roles within the community, a more holistic understanding of community structuring and stabilization could be achieved. Achieving this understanding might enable us to better predict the way systems behave in response to various disturbances such as species losses or habitat degradation. Previously, the majority (but see Ricklefs and Travis 1980, Lawton 1991, Keddy 1992) of community ecology research has focused on population dynamics between specific groups or pairs of key species in order to extrapolate into models of communities (McGill et al. 2006). While this approach succeeded in describing species-poor systems, it has rarely provided general principles for understanding species rich communities with a large diversity of organisms and interactions (Lawton 1999, Simberloff 2004)—which is often the case in natural ecosystems.

Studies of functional ecology have traditionally involved three main components: (1) The construction of trait matrices for study species; (2) the exploration of empirical relationships between selected species traits; and (3) investigation of the relationships between traits and the environment (Keddy 1992). This makes knowing the species identities and diversity levels within communities a logical starting point for studies of functional ecology. Despite local systems (study areas less than a few dozen hectares in size for plants or slightly larger for animals) being the most well-studied of all ecological systems (Sax and Gaines 2003), information about changes in diversity through time within these systems is, on a global scale, relatively scarce. Currently, most of our current knowledge originates from systems displaying significant diversity changes, particularly those affected by invasive species or anthropogenic development and land use. For most ecosystems, we do not know which species occur at particular sites at the local scale especially with regard to vertebrate species diversity (Sax and Gaines 2003, Jenkins et al. 2013). This lack of general diversity data for local systems limits our ability to investigate ecosystem functionality as well as identify ecological groupings

within small-scale ecological systems. The use of ecological groupings—classifying species with similar traits into discrete groups—has been applied to various fields within ecology. These include the clarification of relationships between ecological groupings and ecosystem functioning (Du Toit and Cumming 1999, Diaz and Cabido 2001, Brodie et al. 2009), investigating the relationship between species and habitats (Kurosawa 2009), predicting the effects of environmental changes on floral and faunal groupings (Kissling et al. 2008), as well as the importance of landscape management in nature conservation (Todd and Andrews 2008, Barbaro and Van Halder 2009). The majority of research into functional ecology and ecological groupings has focused on floral taxa, their functional traits, and ecosystem services (Moretti and Legg 2009, Blaum et al. 2011, Villéger et al. 2017) with comparatively little investigation into the functional ecology of faunal groups. Since plants represent the basal trophic level of many ecosystems, they tend to be the logical focal point for most studies into ecosystem functioning (Loreau et al. 2001). Inevitably, research into plant communities has made steady progress towards overcoming the associated methodological challenges of functional ecology research (Pillar 1999, Cornelissen et al. 2003, Poschlod et al. 2003). In comparison the functional ecology of animal communities is still considered to be in its infancy displaying a lack of consistent and standardized methodology (Villéger et al. 2017).

Single species and Ecosystem approaches

While the range of various approaches towards the conservation and management of species can be represented as a continuum, they can generally be split into two broad categories. Single/focal species approaches (Simberloff 1998) and ecosystem approaches (Walker and Salt 2006). The former approach refers to the conservation of ‘umbrella’ and/or ‘keystone’ species. Umbrella species are taxa that display demanding and large habitat requirements to thrive. As a result the conservation of habitats they require is thought to automatically conserve a large host of other more vulnerable taxa (Simberloff 1998). Keystone species (Paine 1969), on the

other hand, play a *known*, fundamental role in maintaining ecosystem structure and functionality (Walker 1995). Vertebrate species tend to be designated as targets during these conservation efforts with their conservation possessing the potential to protect taxa at various spatial scales within the associated habitat types. Unfortunately, the consideration of whether or not species qualify as umbrella and/or keystone is often not a primary factor when designating species to be conserved (Walker 1995). Often, more popular and iconic ‘flagship’ species garner public support and become representative taxa for entire conservation campaigns (Walpole and Leader-Williams 2002, Verissimo et al. 2011, Ducarme et al. 2013). Single species approaches can also take the form of research that uses the reactions of specific species to environmental changes as indications of ecosystem health (Simberloff 1998). These species are referred to as bioindicators or indicator species and are defined as “organelles, organisms or groups of organisms suited to determine qualitatively or quantitatively the state of the environment” (Fränze 2006). Various species from plant, invertebrate and vertebrate groups have been used as indicators for a variety of different elements thought to represent ecosystem health. These include air quality, water quality, testing for the presence of environmental contaminants, species population fluctuations and more (Landres et al. 1988). Using indicator species for observing the effect of disturbances on ecosystems and their reactions as a basis for making conservation management decisions is an appealing cost and time efficient approach due to the relative ease associated with observing few species rather than all within a system (Carignan and Villard 2002). Criticisms regarding usage of this approach highlight the fact that single species only respond to a limited range of disturbances and that a range of taxa rather be used to indicate different stresses within ecosystems (Hawkins et al. 1994, Dale and Beyeler 2001). Additionally, the most important factor when designating bioindicators is that they exhibit a direct and measureable response to ecosystem changes, which is often a difficult and time consuming task (Goodsell et al. 2009). Inevitably, the species

approach has its limits, particularly its failure to: (1) prioritise the maintenance of desired ecosystem processes, (2) address key threatening processes within ecosystems, or (3) result in management plans that combat the issue of general ecosystem functionality decline (Lindenmayer et al. 2002, 2007). The benefit of single species approaches is that they tend to yield a detailed understanding of the relationships between a single species and its environment (Lindenmayer et al. 2007) that may add to our understanding of the role similar organisms fulfil. Single species approaches suggest that by investigating the influence of some species on their respective systems, we may improve our ability to identify the most important species and areas to be conserved, which is crucial for conservation research. The ecosystem approach on the other hand focuses on conserving the biota contributing to processes that maintain ecosystem resilience to change, rather than purely conserving important single species (Groom et al. 2005). By shifting the focus to maintaining the general 'health' of an ecosystem rather than just some species within, this approach works towards combatting the issue of large-scale, potentially catastrophic, biodiversity decline. The ecosystem approach has the potential to aid us in ensuring the long-term conservation of the maximum number of functional types possible. When faced with the reality of conservation management using limited resources in the current extinction crisis (Walker 1995) this approach seems like the logical path to pursue. However, the ecosystem approach also has its limitations, including; (1) established patterns as a result of research often being site-specific, (2) the possibility of over/under estimating the value of specialist species and most importantly, (3) its dependence on the specific details of the relationship between species and their environment (Lindenmayer et al. 2007). Considering the limitations of these two types of approaches it seems then that a synergistic approach incorporating the insight obtained from both methods would be best.

Functional traits and ecosystem functionality

Functional traits are well-defined, measurable properties of organisms that strongly influence the role and performance of species within an ecosystem (McGill et al. 2006, Violle et al. 2007). They are used to compare the extent to which organisms contribute toward ecosystem processes and provide a powerful tool for investigating the effect multiple species have on the system they inhabit. A species' traits tend to dictate how they are involved with ecosystem processes and include measures such as basal metabolic rates, seed or egg sizes, adult body masses and so on (McGill et al. 2006).

The notion that losing taxa that provide similar traits and fulfil similar roles in communities would not result in any loss of ecosystem functionality is referred to as functional redundancy (Rosenfeld 2002b, Fetzner et al. 2015). Functional redundancy is closely related to research that organizes species into ecological groupings (Blaum et al. 2011), food web theory (Reserits and Chalcraft 2007), as well as investigations into functional diversity within ecosystems (Hooper and Vitousek 1997) and stems from the understanding that organisms evolve to do similar things when forced to make use of similar resources (Rosenfeld 2002b). The presence of functional redundancy increases an ecosystem's resilience to perturbation (Walker 1995) since the fulfilment of functional roles and the maintenance of ecosystem stability is not dependent on single species within a given system. This makes research into the redundancy of taxa crucial when attempting to prioritise conservation efforts due to resources for conservation often being limited, making policies that place equal conservation priority on every species being impractical and unachievable (Walker 1992).

In the face of global biodiversity declines (Reaka-Kudla et al. 1997), the loss of species could devastate the functionality of various ecosystems around the globe. The loss of non-redundant taxa has the potential to induce cascading instability in ecosystems with varied effects on

ecosystem functionality (Schlapfer and Schmid 1999, Schmitz et al. 2000, Rosenfeld 2002b, Baum and Worm 2009). These losses could potentially result in further species declines (Donohue et al. 2017), and it is crucial that further research into accurately evaluating functional redundancy be conducted for the sake of predicting the effects that losing ecologically unique species could bring about (Walker 1992).

Functional diversity and redundancy

Functional diversity (FD) can be defined as “the value and range of those species and organismal traits that influence ecosystem functioning” (Tilman 2001). Studies of FD were initially conducted to explore two main topics; (1) the influence of species on ecosystem functioning and (2) the responses of species to environmental change (Hooper et al. 2002). The applicability of FD research has since been expanded into fields such as community assembly rules, interspecific competition, and biodiversity conservation (Laureto et al. 2015). The past two decades have seen a rise in research investigating the quantification of FD, resulting in the development of a plethora of FD indices (Petchey et al. 2009, Mouchet et al. 2010). Currently, no consensus exists on the ‘best’ measure of FD due to the different aspects measured by each as well as the suitability of each when attempting to answer different research questions.

Functional redundancy is assessed by observing the relationship between community FD and species richness (Diaz and Cabido 2001, Petchey et al. 2007) due to the close relationship between these three ecological phenomena (Diaz and Cabido 2001, Luck et al. 2013, Laureto et al. 2015). Considering that measures of FD are based on the various functional traits that species display, functional redundancy occurs when species richness is high and FD is low as a result of overlapping species traits within a community (Luck et al. 2013). Various biotic and abiotic factors influence the resilience of ecosystem properties and by investigating the influence of functional traits on functional diversity within various communities it is possible

to maintain ecosystem processes by conserving those species displaying complementary traits aiding in maintaining ecosystem properties and processes (Hooper et al. 2005).

Faunal functional redundancy – What do we know?

While previous studies into ecological guilds and functional redundancy have mostly focussed on plant taxa, the number of investigations into the functional redundancy of vertebrates are beginning to increase. Chalcraft and Resetarits (2003) investigated the impact of six different predator species (three fish and three salamander) on a common set of prey species (larval anurans) and discovered that the degree of redundancy among the investigated predators depended largely on the scale of response variables used to characterise predator trophic levels. They also noted that simply grouping species together into discrete guilds runs the risk of overestimating the redundancy of individual species. A more recent study tested for functional redundancy within the avian assemblages of Great Britain (Petchey et al. 2007). This study indicated that on average, changes in functional diversity over time were proportional to changes in species richness over time indicating a low level of functional redundancy in the temporal dynamics of the bird assemblages of Britain. They also noted that perceived levels of functional redundancy were highly dependent on the traits selected for measuring functional diversity and emphasized a pragmatic *a priori* decision regarding trait selection. Examples of similar studies have also been conducted on taxa such as New World bat assemblages (Stevens et al. 2003), vertebrate predators such as birds and foxes (Jaksic et al. 1996), and fish species (Resetarits and Chalcraft 2007). While these studies made use of a variety of methods and produced differing findings, the common trend seen throughout is the relatively limited taxonomic scope of species forming the communities under study. The purpose of community ecology, as a research discipline, is to attempt to find generality in the functioning of diverse communities (McGill et al. 2006). Interactions between animal and plant species, such as parasitism and pollination, play important roles in the maintenance of biodiversity (Gómez et

al. 2010) with predation, as an interaction, displaying a strong influence on ecosystem functioning (Duffy 2002, Schmitz 2009). Faunal species within communities do not function and coexist in taxonomically isolated guilds, but rather display complex networks of interactions across multiple trophic levels. By limiting our investigations of faunal functional redundancy to within taxonomic groups and assemblages rather than entire faunal communities, we run the risk of drawing misleading conclusions that may fail to consider the diverse influence faunal taxa have on taxa belonging to other guilds as well as general ecosystem functionality.

Strongly interacting species

With advances in biodiversity and ecosystem functioning research it is widely understood that the removal of strongly interactive species from ecosystems has the potential to change those systems fundamentally (Soulé and Terborgh 1999, Oksanen and Oksanen 2000, Soulé et al. 2003, 2005). Keystone species are known to contribute significantly to ecosystem structuring, resource composition, and diversity providing a stabilizing role in various ecosystems (Soulé and Terborgh 1999, Oksanen and Oksanen 2000, Soulé et al. 2005). Species involvement occurs via a variety of interactions within their habitats including competition, habitat enrichment, ecosystem engineering, as well as predation (Soulé et al. 2005). Inevitably these species serve as focal points when justifying biodiversity protection and prioritizing conservation efforts for the communities they inhabit (Mills et al. 1993) further demonstrating their importance in the field of conservation ecology.

Predator influence

Predators have the ability to alter ecosystem structure, fulfil important functional roles, perform ecosystem services, and potentially influence ecosystem processes within various ecosystems around the globe (Estes and Duggins 1995, Dobson et al. 2006, Griffin et al. 2008, Beschta and

Ripple 2016). Examples range from the provisioning of recreational and aesthetic ecotourism attractions (Dobson et al. 2006)—along with the associated socio-economic benefits thereof (Cumming and Maciejewski 2017)—to the more pertinent (and less obvious) sustaining of plant and kelp communities via the regulation of grazer populations (Beschta and Ripple 2009, Estes and Duggins 1995). The presence of predators within ecosystems results in trophic cascades that play a structuring role in both the biotic and abiotic components of ecosystems via top down control. The most notable example being the extensive recovery of riparian vegetation in Yellowstone National Park as a result of the reintroduction of Gray wolves (*Canis lupus*) after a seven decade absence (Ripple and Beschta 2012, Beschta and Ripple 2016). The importance of predators as keystone species in both terrestrial and marine ecosystem structuring and functioning is relatively well documented (Chase 2000).

Taxa of interest: snakes as predators

Snakes are a diverse group of organisms that includes upwards of 3600 species within approximately 25 families (Uetz 2017). Apart from the polar regions, they inhabit all of earth's biomes with some even occurring within the Arctic circle (Carlsson and Tegelström 2002, Mullin and Seigel 2009). Snakes exhibit adaptations that allow them to thrive in most habitats ranging from aquatic to arboreal, despite sharing the same limbless and elongated body plan. They are exclusively predatory, feeding on a variety of prey including invertebrate, fish, amphibian, avian (eggs as well), mammalian, and reptilian taxa, with certain species specialising on fellow serpents of equal or greater length than their own (Greene 1997, Jackson et al. 2004). Consuming such a diversity of prey species, each with their own differences in physiology, morphology and behavioural patterns, required snakes to evolve advanced physiological and behavioural traits and strategies in order to capture and consume prey. A few of the well-known adaptations include advanced venom delivery systems (Jackson 2003), the ability to track prey chemical trails (Halpern 1987), highly modified jaws allowing

consumption of prey items with diameters greater than that of the snakes heads (Hampton and Moon 2013), as well as the iconic constricting behaviour exhibited by a large diversity of snakes (Greene 1997). Some species display more subtle adaptations as well, an example being members of the snail-eating genus *Pareas* developing more teeth on one side of their jaw versus the other enabling more effective predation of dextral (clockwise-coiled) shelled individuals (Danaisawadi et al. 2016).

With a nearly global distribution, a myriad of predatory adaptations and an opportunistic tendency (in certain species) to consume essentially any faunal protein source (Rodda et al. 1999), characterising all the predatory (morphological and behavioural) adaptations of snakes as a group is no menial task (Greene, 1997). Despite the challenges associated with characterising all of their adaptations, researchers have provided evidence displaying the effects of their presence within ecosystems. Snakes have the ability to alter faunal communities fundamentally via predation and top down control. The most notable examples are the decimation of local bird diversity by the invasive Brown tree snake (*Boiga irregularis*) on Guam (Rodda et al. 1999, Rodda and Savidge 2007), and the severe mammal population declines within the Florida everglades by invasive Burmese pythons (*Python bivittatus*) (Dorcas et al. 2012).

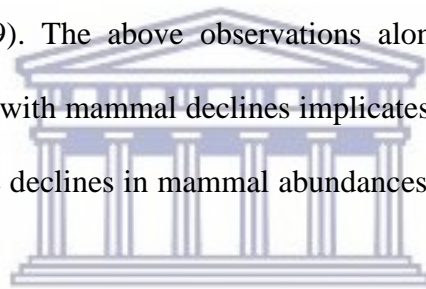
Case studies: Guam and Florida

The Brown Tree Snake (*Boiga irregularis*) is a rear fanged, mainly arboreal snake species belonging to the family Colubridae. It has an Indo-Pacific distribution and is native to eastern Indonesia, Papua New Guinea, Melanesia, and the eastern and northern coasts of Australia (Rodda et al. 1999). It is a predominantly nocturnal species that exhibits a generalist diet feeding on a variety of vertebrates, including carrion (Rodda et al. 1999). This species garnered the attention of the biological science community when it was discovered to be the leading

cause of mammalian and avifaunal population declines on the island of Guam after being accidentally introduced during the 1940s (Marshall 1985, Rodda et al. 1997). Prior to this discovery, there were no notable examples of any snake taxa having such a dramatic impact on any ecosystem (Savidge 1987). The impact was so dramatic that the initial hypothesis that snakes were responsible for the declines in prey populations was met with scepticism and disbelief (Rodda et al. 1997). Scepticism to such an extent that a commentator dedicated an entire article to promoting an alternate hypothesis that suggested unrestricted use of pesticide as the cause rather than predation by snakes (Diamond 1984). The devastating effect that the introduction of *Boiga irregularis* had on the avian diversity of Guam is still observable half a century later. The extirpation of such a large component of Guam's vertebrate taxa also resulted in a host of secondary ecological impacts. These included the disruption of forest tree seed dispersal and recruitment in the degraded forests of Guam that correlated with the disappearance of birds (Caves et al. 2013, Rogers et al. 2017) and fruit bat (*Pteropus mariannus*) population declines (Wiles 1987, Wiles and Fujita 1992), as well as the removal of top-down control exerted by arthropod eating bird species. This eventually led to an explosion of the spider population and an increased spider web density 40 times greater than densities observed on nearby islands with undisturbed bird populations (Rogers et al. 2012). The accidental introduction and unmonitored growth of *Boiga irregularis* populations on Guam directly and indirectly resulted in great costs to the island in terms of biodiversity losses and economic growth, with costly measures put in place attempting to mitigate the associated damages to the island's public infrastructure (Rodda et al. 1999).

A similar situation to the invasion of *B. irregularis* on Guam is currently occurring with the establishment of Burmese python (*Python bivittatus*) populations in the Florida Everglades and the entirety of the Everglades National Park (ENP) (Snow et al. 2007). *Python bivittatus* is a large-bodied constrictor native to southeast Asia. Individuals of this species reach average

lengths of 3.7 m in the wild (Campden-Main 1970) and a maximum known length of 5.74 m (Barker et al. 2012). Similarly to Brown tree snakes, Burmese pythons prey on a variety of vertebrates, predominately appropriately-sized mammals and birds (Secor 2008), killing via constriction. The establishment of Burmese pythons as an invasive species in the region is attributed to individuals being inadvertently released during the 1980s as a knock-on effect of the thriving reptile pet trade (Willson et al. 2011). Since 2000 the population of this species has increased exponentially and resulted in an expanding geographic range that correlates with relatively low mammal encounter rates in areas of high python density (Djalili 2015). A variety of local taxa representing several diverse taxonomic groups, previously abundant and easily observed, have been documented in the diet of Burmese pythons within the ENP (Snow et al. 2007, Reed and Rodda 2009). The above observations along with spatial and temporal correlation of snake increases with mammal declines implicates the invasive Burmese python as the primary cause of severe declines in mammal abundances within the Florida everglades and ENP (Dorcas et al. 2012).

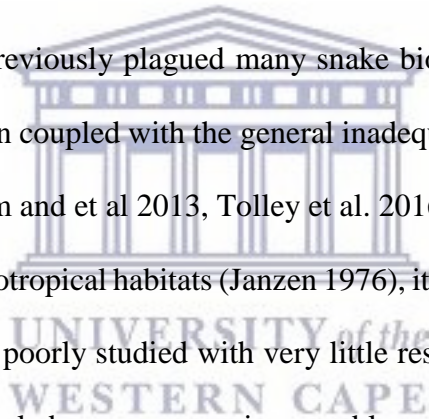


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These examples of *Boiga irregularis* and *Python bivittatus* show the remarkable ability of snakes to dominate environments as apex predators, albeit in an invasive context. These cases also provide clear evidence for the potentially severe impacts of snakes within ecosystems. It is worth noting however that impacts such as extirpation of local species, marked economic costs and community structure changes aren't particularly uncommon with invasive species (Sakai et al. 2001). Despite their potential as top predators within various ecosystems around the world, snakes also display characteristics that may lead to *a priori* underestimation of their impact on ecosystems. These include seemingly low population densities (Reading et al. 2010) and low consumption rates due to their low energy requirements as ectotherms and the ability to fast for long periods of time (Diller and Johnson 1988, Secor 2008). It is worth mentioning that snakes are a diverse group of organisms with a great variety of life history traits. Our

underestimation of their roles within ecosystems may be attributable to sampling difficulties coupled with a limited number of investigations into their community ecology. This however does not change the fact that the only major examples of their impacts on ecosystems are found in the context of invasive species studies creating doubts with regards to their potential as ecosystem regulating predators.

Despite the fact that most snake species occur in tropical areas, studies into their ecology and population dynamics are relatively scarce, particularly in areas such as South America, southeast Asia, Australia and Africa (Bonnet et al. 2002a, Böhm and et al 2013, Tolley et al. 2016). Reasons for the scarcity are likely due to the cryptic habits and elusive nature of these organisms as a whole, in conjunction with the associated low “academic payoff” when studying ectothermic vertebrates that previously plagued many snake biologists (Bonnet et al. 2002b, Mullin and Seigel 2009). When coupled with the general inadequacy of foundational diversity data for African reptiles (Böhm and et al 2013, Tolley et al. 2016) and lower suspected reptile biomass levels compared to neotropical habitats (Janzen 1976), it is predictable that the ecology of southern African species is poorly studied with very little research into their roles on their ecosystems. This lack of knowledge poses a serious problem when attempting to prioritize snake conservation efforts within a South African context.



Problem Statement

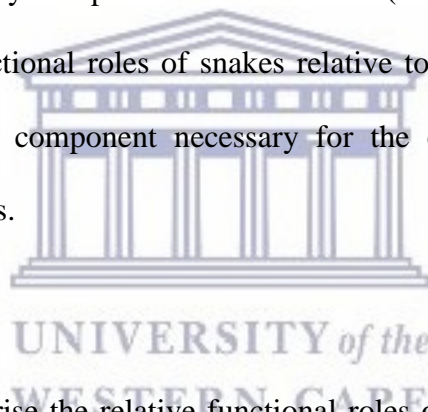
Globally, research into the functional ecology of snakes and their relationships with other vertebrate taxa is limited, with literature on African snakes in the field of population ecology being no exception (Bonnet et al. 2002a). This gap in our understanding regarding the importance of snakes in the face of global snake population declines (Reading et al. 2010) undermines our ability to predict the cascading effects their removal could have on ecosystems. Snakes and other terrestrial vertebrate species extirpations, and the associated diversity losses, could potentially be accompanied by losses in ecosystem functionality. By losing non redundant species and the functional traits they provide, we run the risk of losing important maintaining forces behind ecosystem processes and services (Hooper et al. 2012, Gascon et al. 2015). Research into the functional roles of snakes relative to, and in the context of, other vertebrates then is a crucial component necessary for the effective management of all ecosystems that include snakes.

Aims and objectives

This project aims to characterise the relative functional roles of snakes and other terrestrial tetrapod species within the Koeberg Nature Reserve. It will answer the question of whether or not snakes share functional traits with other vertebrates in a manner that might induce functional redundancy. Additionally, these findings would also answer the question of whether or not their removal is likely to result in functional losses within the ecosystem under study.

Specific objectives include:

- Identify the terrestrial tetrapod species across all tetrapod classes (mammals, birds, reptiles and amphibians) within the Koeberg Nature Reserve.



- Select and quantify appropriate functional traits from the literature for all selected species.
- Identify dietary and functional guilds within the Koeberg terrestrial tetrapod community
- Quantify the contribution of different tetrapod classes to community functional diversity
- Quantify the relationship between species richness and community functional diversity, within and between, dietary guilds, functional guilds and tetrapod classes.
- Investigate the level of functional redundancy exhibited by snakes.



Chapter 2: Methods

Study site

All sampling was conducted within the Koeberg Nature Reserve (Fig. 1), Western Cape, South Africa (33° 37'S, 18° 25'E). The reserve covers an area of approximately 3000 ha and is characterised by three main vegetation types (Cape Flats Dune Strandveld, Atlantis Sand Fynbos, and Cape Seashore Vegetation) occurring on calcareous sand, overlying metasediments of the Tygerberg Formation (Eskom Holdings SOC Limited 2014). The area follows a winter-rainfall regime with an approximate mean annual rainfall of 350 mm (Mucina, et al. 2006). Temperatures in warmer months' peak at approximately 30°C dropping to minimum temperatures of approximately 5°C in colder months', with average annual temperatures ranging between 15.9 – 18.1°C. The reserve has been included previously in broad scale projects such as SARCA (South African Reptile Conservation Assessment) and the associated publication (Bates et al. 2014) as well as both South African Bird Atlas projects (Harrison et al. 1997). The only major faunal studies within the reserve have focussed on the characteristics and life histories of various avifauna (Curtis et al. 2004, Naiwanga et al. 2004, Auer et al. 2007). Additional studies have investigated the effectiveness of biological control on the invasive *Acacia cyclops* (Mokotjomela and Hoffmann 2013), but any fine scale research into the reserve's faunal communities is limited to those conducted by the reserve's management unit (Eskom Holdings SOC Limited 2014).

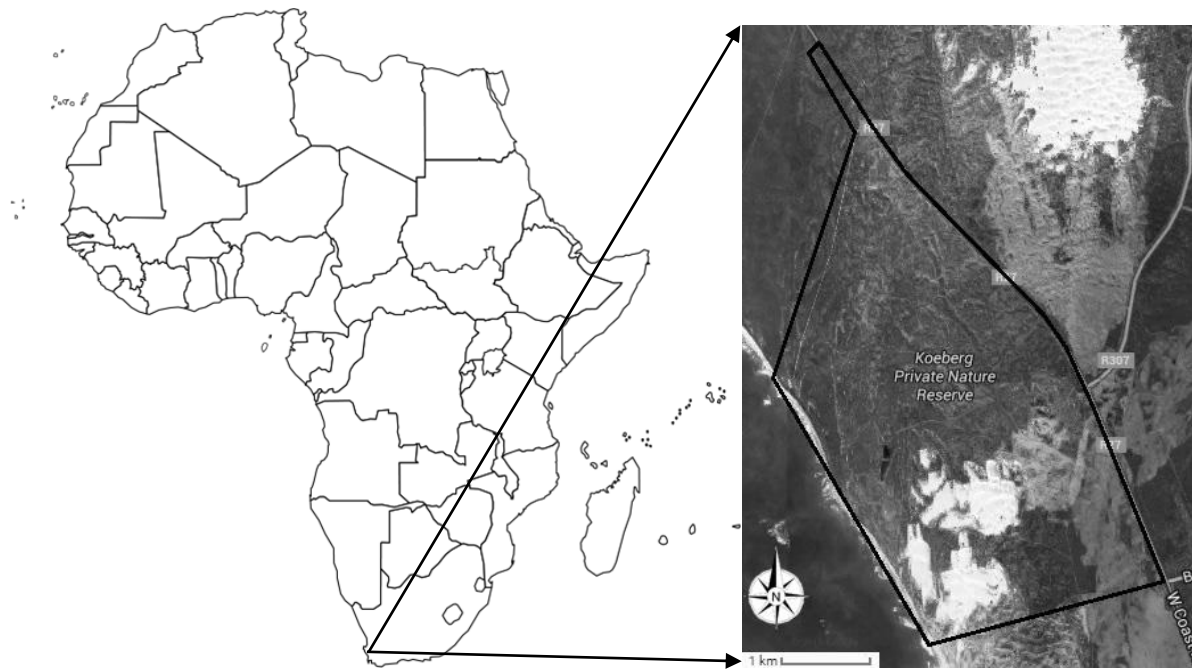


Figure 1 - Koeberg Private Nature Reserve bordered by the South African west coast and R27 (West Coast Road) with reserve boundaries indicated

Study design

A full tetrapod species list for the study site was necessary. I compiled this list using the methods detailed in the *sampling* section below. Thereafter I quantified the dietary traits of the terrestrial tetrapod community, using the literature, in order to identify and compare dietary guilds according to the *dietary data collection and guild characterisation* section below. I characterised the diets of each species to create a metric for the dietary functional trait. I selected additional functional traits and quantified them for each species. I described these traits and their relation to ecosystem processes within the *functional trait selection* section. Thereafter I entered the trait data into a functional trait matrix (referred to as the “all trait matrix”) and used it to identify and compare functional guilds within the reserve according to the methods outlined in the *functional trait data collection and functional guild characterisation* section below. Next, I quantified the community’s functional diversity which involved comparing the effects of taxonomic group and functional guild removals on

community functional diversity measures relative to each group's species richness. I achieved this using the methods detailed in the *quantifying functional diversity* section. These steps were all necessary in order to conduct a multi-trait functional guild and functional diversity analysis to test for functional redundancy within the terrestrial tetrapod community.

1) **Sampling**

Passive camera trapping

Six motion sensor camera traps (Cuddeback Model C2 – with white strobe flash modules) were placed in various locations around the study site in order to sample mammal species (identified species presented in results) and the GPS coordinates of each camera recorded. The cameras were left to survey over a period of two weeks (as per the suggestion of an experienced trapper within the reserve) that resulted in six individual two week surveys. Thereafter the cameras were relocated to new locations within the study site and the new GPS co-ordinates recorded. Cameras were placed mainly along roads and trails where the presence of animals, in the form of tracks, droppings and grazing on vegetation, was visible. This process was repeated over the course of six months (June 2016 – November 2016) and resulted in 60 individual camera trap surveys. The mean survey duration was 15.9 days with a duration range of eight days (max: 21 days, min: 13 days). The variation was due to time constraints and occasional site accessibility issues resulting in cameras not always being collected all at once every two weeks resulting in some surveys lasting longer. Camera trapping effort amounted to 954 camera days observing various locations within the reserve (Fig. 2). Limitations in terms of time and the number of cameras available prevented repeated sampling of the same sites. Therefore, in order to cover as many unique locations as possible, the minimum distance maintained between sampling sites was at least 50 metres. This distance was decided upon after considering the topography of the reserve and which areas were safely accessible.

All camera trap images were checked and all photographed tetrapod taxa were identified to species level. A rarefaction curve, using a method derived by Shinozaki (1963) and subsequently redescribed by Chiarucci et al. (2008), was plotted for the recorded species to observe the rate of species accumulation relative to sampling effort. This was done using the R' function "specaccum" to gauge whether or not any more camera trap sampling was necessary.



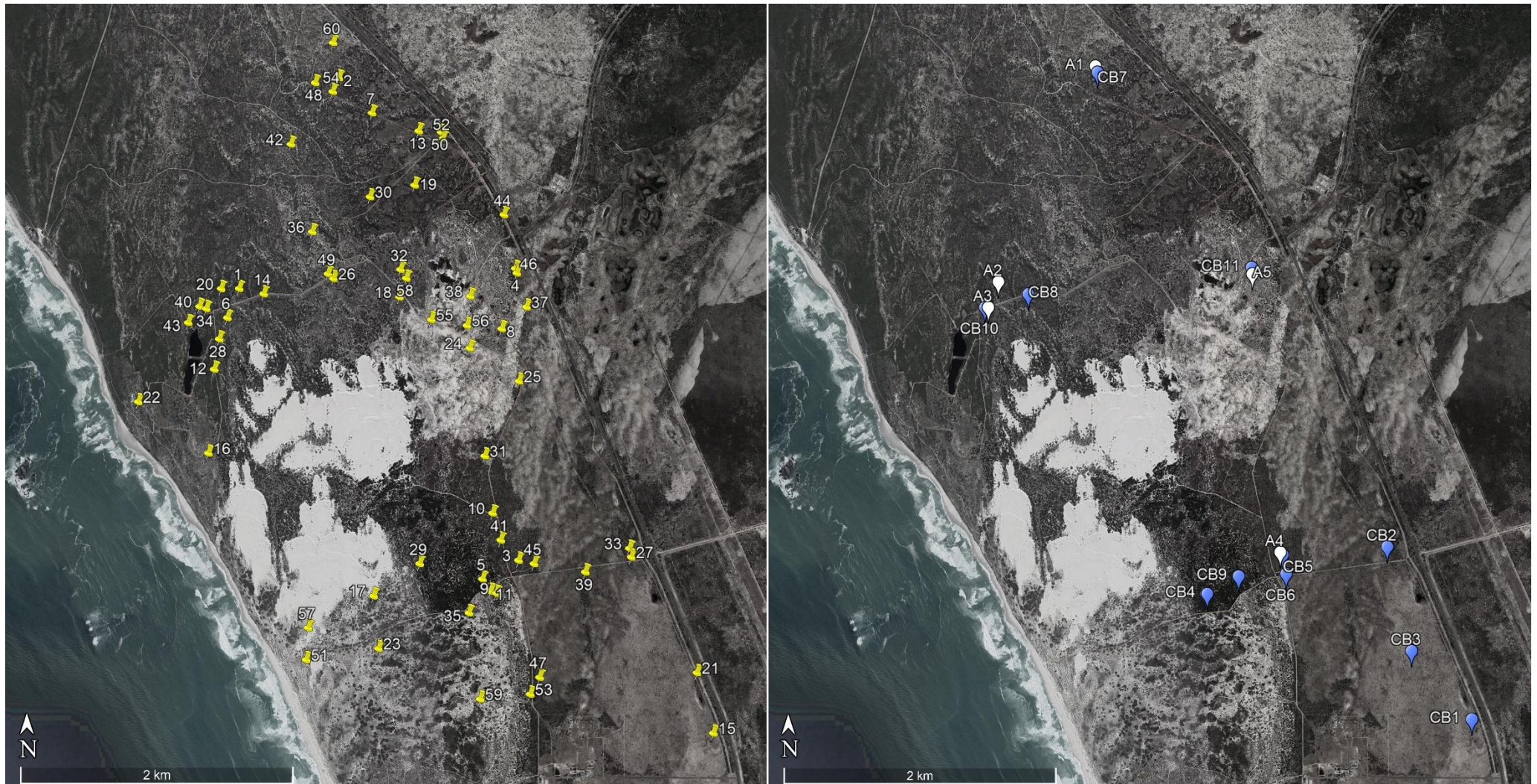


Figure 2 – Sampling locations for passive camera trapping surveys (left image) and coverboard (CB)/pitfall-funnel-trap arrays (A) (right image) within Koeberg Private Nature Reserve

Artificial cover object and active searching surveys

Artificial cover objects, also called cover-boards, were varnished, wooden boards measuring 600 mm x 600 mm x 19 mm. These were used to provide easily checkable artificial refuge to animals within the reserve. Ten cover-board grids each consisting of 25 cover boards arranged in a five by five pattern, with each grid dispersed over an area of approximately 100 m², were installed within the study site aimed at sampling the reptile community (Fig.2). Initially, 12 cover-board arrays were installed at designated sites within the reserve. These sites were stratified across the study site such that sampling included dune strandveld, *Acacia cyclops* invaded habitats as well as previously invaded but recently cleared *Acacia cyclops* sites. Unfortunately, during the installation process a section of the reserve burnt and destroyed the board arrays placed at two of the sites. This prompted the relocation of three of the remaining ten arrays to within the newly burnt sections of the reserve in order to add the ‘novel’ landscape (burnt dune strandveld) to the three habitat types already being sampled. This resulted in the cover-board sites allocated as follows: three dune strandveld, three burnt dune strandveld, two cleared of invasive vegetation and two invaded. These 250 boards were checked at least twice per month resulting in at least 18 sample checks for all sites over the course of 2016–2017.

Loosely structured active searching sessions were also conducted in conjunction with the cover-board checking trips. This involved random walking and driving along the dirt roads within the reserve whenever cover-board arrays were checked, searching for medium to large sized mammal and reptile taxa. Where possible, reptile specimens were caught, identified and released back into the reserve.

Pitfall and Funnel-trap arrays

Plastic sheet drift fence arrays in conjunction with plastic bucket pitfall and fine steel mesh funnel traps (Maritz et al. 2007) were installed within the reserve. Five arrays were installed

with each array consisting of two intersecting drift fences forming a 'plus' shape (Fig. 3). Each array was then outfitted with five pitfall traps (four at each point and one at the intersection of the fences) as well as two funnel traps on opposing sides along each branch of the array (eight funnel traps per array). Due to obstacles within the environment the length of the drift fences varied with an average length of 12.4 ± 4.89 m per array. The fences were 500 mm tall and were buried 200 mm deep to ensure animals were not able to crawl underneath. These five arrays were installed for two separate sampling periods, 3 April 2016 – 28 April 2016 and 15 September 2016 – 10 October 2016, and checked daily with any caught specimens identified and released. This equated to a pitfall trap sampling period of 52 days as well as a funnel-trap sampling period of 52 days aimed at small to medium sized herpetofauna as well as small mammal taxa.

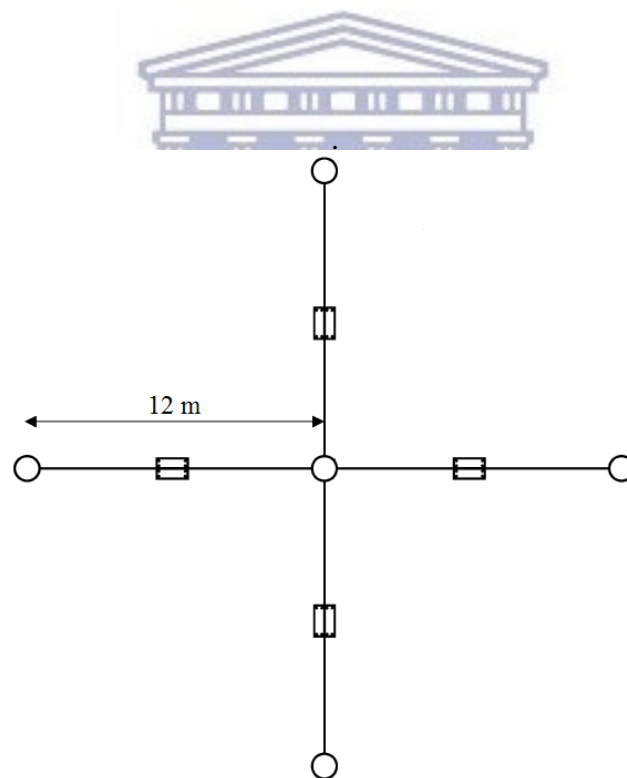
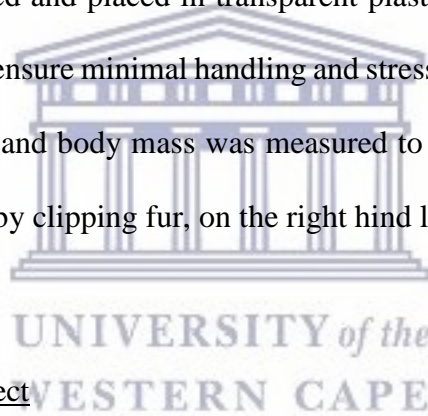


Figure 3 - Pitfall, funnel trap and drift fence array configuration with solid lines indicating fences, rectangles indicating funnel traps and circles indicating pitfall traps

Sherman trap sampling

Transect lines of 15 Sherman-type live-traps were set out at ten sites corresponding with the locations of the artificial cover object sites. The traps were placed approximately 10 m apart, resulting in a length of 70 m per transect line. Small mammals were trapped at each site during two seven-day field-sampling sessions (26th Apr – 03rd May 2017 and 06th Sep – 13 Sep 2017). Traps were baited in the afternoon (16:00 – 19:00) with a combination of peanut butter and oats. In the morning (08:00 – 11:00) traps were checked for small mammals and then closed for the duration of the day to prevent overheating and dehydration of animals during the daytime.

Trapped animals were removed and placed in transparent plastic bags (for ease of handling) and measured immediately to ensure minimal handling and stress to the animals. Animals were identified to the species level and body mass was measured to the nearest 0.1 g. The animal was then temporarily marked by clipping fur, on the right hind leg and released at the point of capture.



South African Bird Atlas Project

The avian component of the reserve's tetrapod community was obtained using species summary data for QDGC 3318CB from the South African Bird Atlas Project 1 (SABAP1) as well as species summary data for the SABAP2 database (sabap2.adu.org.za) pentads: 3335_1820 and 3335_1825. These were the designated areas covering the study site location for each atlas project and the summary lists provided for them were combined to create a single bird species list for the reserve.

After physical sampling was completed, the recorded species were compiled into one complete faunal list (Southwood 1996) along with the SABAP one and two species lists, chiropteran species whose geographic distribution ranges included the reserve area (Monadjem et al. 2010),

and the pre-existing species list for the tetrapod community (Eskom Holdings Limited 2011), provided by the Koeberg environmental conservation unit for the study site.

2) **Dietary data collection and guild characterisation**

The diets of each species were characterised based on various literature sources. These included Hockey et al. (2005) for birds, Monadjem et al. (2010) for bats, Skinner and Chimimba (2005) for the rest of the mammals, Branch (1998) for reptiles and Du Preez et al. (2009) as well as Channing (2001) for amphibians. Dietary items were assigned to 46 dietary categories (Table 1) created to summarize the variability in diet across different taxonomic groups. Ideally, the relative abundances of dietary components for the various species should have been taken into account. However, for most species, data on the relative abundances of dietary items are not available and so an alternative method was necessary for quantifying species diet. An incidence based dietary matrix was created using binary entries (1 indicated the presence of a food item/s from a specific category and 0 indicated the lack thereof) to indicate the presence of dietary items in each species diet. A dissimilarity matrix based on the dietary data was then calculated using Jaccard distance (Jaccard 1901) between the different species. The dissimilarity matrix was subjected to a hierarchical cluster analysis using Unweighted Pair Group Method with Arithmetic Mean (UPGMA) agglomeration (Sneath and Sokal 1973). The resultant dendrogram was used to identify broad scale dietary clusters resulting in ten dietary guilds within the terrestrial tetrapod community. The cophenetic correlation coefficient between the dissimilarity matrix and resultant dendrogram was calculated in order to test whether or not the dendrogram provided an accurate representation of the unmodelled pairwise distances between species (Sokal and Rohlf 1962, Rohlf and Fisehr 1968). These guilds were then described and the dietary guild of each species used as their entry within the “diet” column of the all trait matrix. This analysis was done using the “vegan” (Oksanen et al. 2018), “cluster” (Maechler et al. 2017) and “ggplot2” (Wickham 2009) packages in R.

Table 1 - Categories used for characterising dietary components of species within Koeberg terrestrial tetrapod community

Vegetation	Invertebrates	Vertebrates	Other
Bark	Insecta	Mammals (<0.1kg)	Bones
Twigs/Branches	Myriapods	Mammals (0.1-1kg)	Mushrooms
Grass	Arachnids	Mammals (1-10kg)	Algae
Leaves	Crustaceans	Mammals (>10kg)	Carrion
Stems/Shoots	Molluscs	Birds (<0.1kg)	Bees Wax/ Honeycomb/ Honey
Fruits	Tunicates	Birds (0.1-1kg)	Aeroplankton
Seeds	Worms	Birds (1-10kg)	
Roots/Bulbs	Polychaetes	Bird Eggs	
Flowers	Echinoderms	Reptiles (<0.1kg)	
Pollen	Sea Sponges	Reptiles (0.1-1kg)	
Nectar	Pycnogonids	Reptiles (1-10kg)	
Sap	Zooplankton	Reptiles (>10kg)	
Mosses		Reptile Eggs	
		Amphibians	
		Fish	

3) Functional trait selection

The proliferation of empirical studies into the classification of terrestrial plant functional types has resulted in the establishment of guidelines and protocols that facilitate appropriate trait selection (Cornelissen et al. 2003). While these guidelines only provide a foundation for plant functional type studies they nevertheless aid in the crucial task of justifying selected traits and defining the links to their associated ecosystem processes. Despite these guidelines having been available for the better part of the past two decades, similar guidelines for faunal species are scarce. Fortunately, the past decade has seen an increased focus on research attempting to provide guidelines for vertebrate species. Luck et al. (2012) proposed guidelines for the selection of vertebrate functional traits using functional traits for bird species as an example. Similarly Ortiz and Moreno (2017) provided a potential list of functional traits for mammals and reptiles, while Valencia-Aguilar et al. (2013) and Cortes-Gomez et al. (2016) did the same for amphibian taxa. While these lists provide functional traits that apply to within taxonomic group analyses, for across group taxonomic studies such as the current one, only ‘common

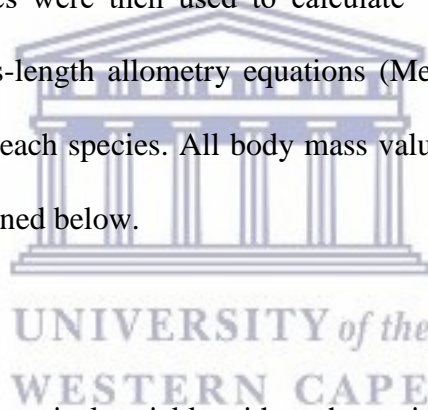
currency' traits applicable to all tetrapod classes under study are appropriate. Therefore, the lists provided in each of these studies were compared and only traits that were measurable across all four tetrapod classes were selected. This list was then narrowed down to include only traits quantifiable from the literature for all species under study. As a result, along with the dietary data used for identifying dietary guilds, four additional functional traits linked to morphology, resource use and behaviour were selected to characterise the functionality of species within the community. These traits were body mass, space use, time use and energy flow (detailed below).

Dietary breadth in bird, mammal, reptile, and amphibian species is linked to foraging behaviour, transfer of matter, use of food resources, pollination, and prey population control within ecosystems, indicating its important prospect as a functional trait (Luck et al. 2012, Cortes-Gomez et al. 2016, Ortiz and Moreno 2017). Body mass as an avian functional trait is linked to species metabolic rates, foraging behaviour and longevity, which may dictate the effects of species on ecosystem services (Luck et al. 2012). Body mass of mammal, reptilian and amphibian taxa links to trophic resources, energy expenditure, energy flow and nutrient recycling between trophic levels within the ecosystem (Cortes-Gomez et al. 2016, Ortiz and Moreno 2017). The same could be said for the functional trait energy flow as it describes species energy requirements and rate of resource use at a finer scale than estimations purely based on species body mass, by taking into account specific metabolic rates of individual species. The traits time-use and space-use dictate when and where species interactions will occur. These uses are linked to the process of resource use and the specific period and localities thereof within ecosystems (Luck et al. 2012, Cortes-Gomez et al. 2016, Ortiz and Moreno 2017). Additionally, selective use of resources by different species underlies the process of niche partitioning within ecosystems. This partitioning is linked to competition avoidance, as well as predator avoidance when those species occupy different trophic levels.

4) **Functional trait data collection and functional guild characterisation**

Body mass

Body mass was defined as a continuous variable representing the maximum mass (grams) for an individual of each species. For all species belonging to taxonomic groups exhibiting determinate growth (birds and mammals), maximum available recorded mass was quantified from the literature (Hockey et al. 2005, Monadjem et al. 2010, Skinner and Chimimba 2005). For those species displaying an indeterminate growth pattern (non-avian reptiles and amphibians) where only snout-to-vent length (SVL) values were available, the maximum available SVL for each species was recorded from the literature (Branch 1998, Channing 2001, Du Preez 2009). These values were then used to calculate ‘maximum masses’ using the appropriate family level mass-length allometry equations (Meiri 2010, Feldman and Meiri 2013, Santini et al. 2017) for each species. All body mass values were then log-transformed during the analysis phase outlined below.



Space-use

This trait was defined as a categorical variable with each species assigned to one of five tiers within the landscape. These tiers were aerial, arboreal, terrestrial, fossorial, and aquatic with each species assigned based on their dominant area use within the ecosystem according to literature (Branch 1998, Channing 2001, Hockey et al. 2005, Monadjem et al. 2010, Du Preez 2009, Skinner and Chimimba 2005, Stuart and Stuart 2005).

Time-use

Like space use, this trait was also a categorical variable assigned to each species representing their dominant activity times reported within literature (Branch 1998, Channing 2001, Hockey et al. 2005, Monadjem et al. 2010, Du Preez 2009, Skinner and Chimimba 2005, Stuart and

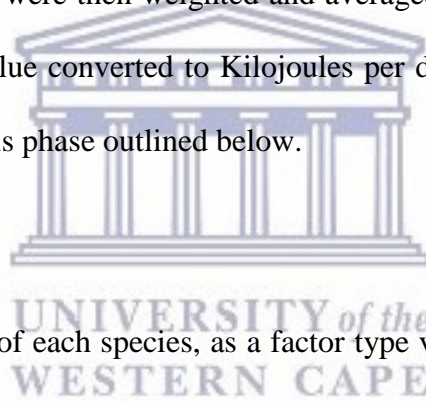
Stuart 2005). The categories were diurnal, crepuscular, nocturnal, and cathemeral (for species exhibiting no particular activity pattern).

Energy flow

The numerical trait 'energy flow' was a value representing the product of the masses of individual (grams) and estimated field metabolic rate for each species. Field metabolic rates, in kilojoules per day (Kj.d^{-1}), for bird, mammal and reptile taxa were calculated using appropriate mass-metabolic rate allometric equations (Nagy et al. 1999). Field metabolic rate values for amphibian taxa were estimated by first, using mass-oxygen consumption (ml.h^{-1}) allometric equations to calculate V_{O_2} (rest) and V_{O_2} (max) (Feder and Burggren 1992) for each species at 20°C. These values were then weighted and averaged for each species (80%/20%, rest/max) and the resultant value converted to Kilojoules per day. Thereafter they were log-transformed during the analysis phase outlined below.

Analysis

Along with the dietary guild, of each species, as a factor type variable, these four traits were entered into a functional trait matrix and used to create an all trait dissimilarity matrix using Gower distance (Gower 1971). This approach was adopted due to its suitability for handling mixed data types. The dissimilarity matrix was subjected to two different clustering methods, namely partitioning around medoids (PAM; Kaufman and Rousseeuw 1990) and hierarchical cluster analysis using UPGMA agglomeration (Sneath and Sokal 1973), and the solutions compared to test the validity of the resulting clustering solutions. The optimum number of functional guilds was assessed using silhouette plots (Rousseeuw 1987). This was done by finding the clustering solution for both PAM and the hierarchical method that displayed the greatest average silhouette width. Silhouette width is defined as a measure between -1 and 1 indicating how similar a species is to other species within its own cluster versus species within



the closest neighbouring cluster. A high average silhouette value indicates appropriate assignment of species. The resulting guilds were then characterised and compared between each clustering method for coherence in order to identify ‘unique’ functional guilds within the terrestrial tetrapod community. A functional dendrogram was constructed to display the results of the hierarchical clustering and the cophenetic correlation coefficient between the dendrogram and dissimilarity matrix calculated to gauge how accurately the dendrogram displayed the pairwise distances between species. The R packages used within the analysis were, “vegan” (Oksanen et al. 2018), “cluster” (Maechler et al. 2017), “ggplot2” (Wickham 2009) and “stats” (R Core Team 2017).

5) **Quantifying functional diversity**

To investigate the relationship between functional diversity and species richness within various taxonomic and functional groups within Koeberg Nature Reserve, a tree based measure of Functional Diversity (Petchey and Gaston 2002, 2006, Podani and Schmera 2006), was used. When using the tree based measure of FD, functional diversity is defined as the total branch length in a functional trait dendrogram connecting all species while excluding those unnecessary root segments not needed to connect them. This particular metric was used due to its ability to calculate community FD from functional dendrograms produced using cluster analysis. The total FD value for the dietary trait dendrogram, produced during the hierarchical cluster analysis was calculated, including all identified species. Thereafter, all species belonging to a single major terrestrial vertebrate class were removed from the dietary matrix, FD recalculated in their absence, and the group returned to the matrix. This was repeated for each class in order to simulate the loss of (and thereby contribution to) functional diversity resulting from the extirpation of the eight major taxonomic groups considered, namely, all birds, passerine birds, non-passerine birds, mammals, all reptiles, snakes, non-snake reptiles, and amphibians. The percent FD losses for each group were divided by their respective

percentage contributions to overall species richness to look for disproportionate losses of FD as a result of group extirpation. Thereafter, the FD losses were divided by each group's species richness to calculate mean loss per species within each group. The resultant dietary FD to species richness ratios were compared to observe the relative losses of functional diversity resulting from the loss of the different taxonomic groups. This process was then repeated for the same taxonomic groups using the functional trait matrix including data for all five functional traits. Thereafter, the analysis was iterated to simulate the loss of individual species. These values were converted to percentages and used to calculate the mean per species percent FD loss within the eight taxonomic groups to observe whether or not single species were driving each group's overall post removal FD loss.

The project's terrestrial focus naturally meant that the effects of removing all four terrestrial vertebrate classes on community functional diversity were tested. Additionally, being the main taxonomic focus of the project, separating the effects of snakes from non-snake reptiles was also necessary to answer the primary research questions. This prompted the investigation and subsequent separation of the order Passeriformes from non-passerine birds due to the former including over half of all extant bird species. Any further separation of species into finer sub groups was not absolutely necessary for achieving the objectives of the study.

The final step in the analysis was simulating the extirpation of each identified functional guild and to observe the resultant FD values. The same method, described above, was used with each functional guild being removed rather than the previously removed taxonomic groups. This was repeated until FD had been calculated after the removal and replacement of all 50 functional guilds. The resultant FD losses, as with the taxonomic group FD, were then divided by each functional guild's species richness and the resultant ratios used to compare relative FD losses between functional guilds.

Chapter 3: Results

1) Sampling

Passive camera trapping

The camera trapping yielded a total of 14 species across 60 individual surveys (Table 2). The rarefaction curve based on the survey count data (Fig. 4) indicated that a second camera trapping sampling period was not necessary due to the plateauing rate of new species observations and low likelihood of encountering novel species with increased camera surveys

Table 2 - Vertebrate species captured during passive camera trapping surveys within Koeberg Nature reserve

Species	Records	Surveys in which records appear
<i>Caracal caracal</i>	4	2, 46, 49
<i>Chersina angulata</i>	6	49, 54
<i>Chrysochloris asiatica</i>	1	33
<i>Connochaetes taurinus</i>	1	58
<i>Equus quagga</i>	16	13, 15, 19, 24, 36, 50, 51, 53
<i>Galerella pulverulenta</i>	32	6, 15, 17, 18, 19, 25, 27, 28, 30, 33, 35, 37, 39, 40, 43, 46, 47
<i>Genetta genetta</i>	4	14, 15, 31, 45
<i>Hystrix africaeaustralis</i>	6	1, 3, 34, 36, 40, 53
<i>Lepus saxatilis</i>	2	45, 53
<i>Oryx gazelle</i>	3	2, 36, 60
<i>Raphicerus campestris</i>	20	4, 8, 16, 19, 22, 51, 57, 58
<i>Rhodomys pumilio</i>	11	42, 46, 49, 59
<i>Sylvicapra grimmia</i>	43	2, 3, 4, 5, 7, 8, 11, 15, 18, 27, 29, 31, 33, 39, 40, 45, 47, 53, 56
<i>Taurotragus oryx</i>	31	1, 3, 4, 5, 6, 7, 9, 11, 12, 14, 15, 16, 18, 19, 21, 24, 27, 36, 39, 43, 48, 50, 58

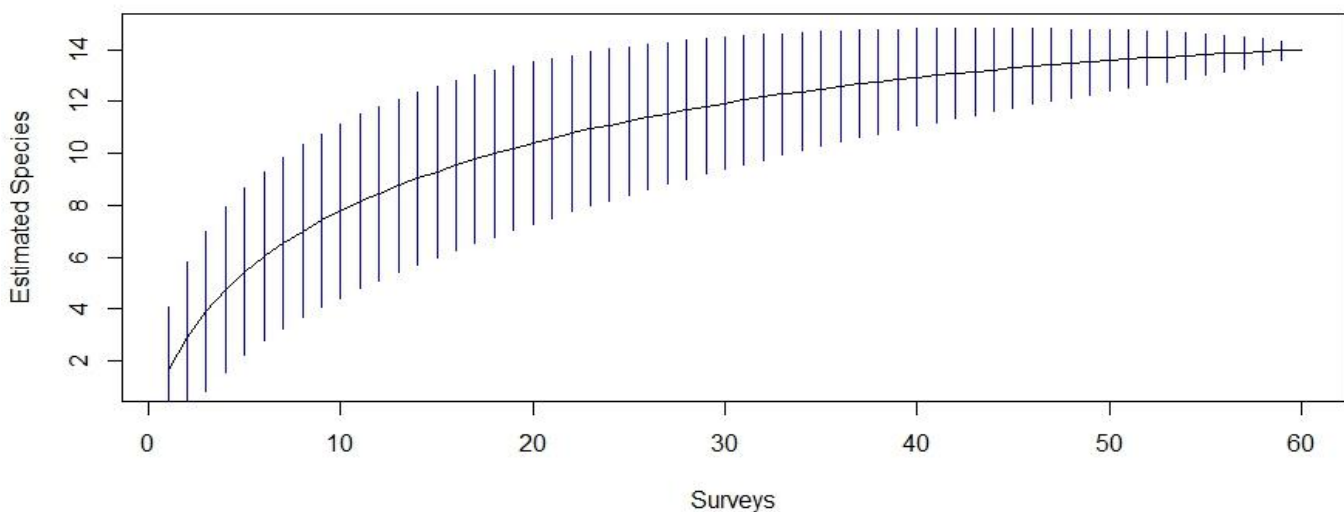


Figure 4 - Rarefaction curve displaying estimated species richness for each camera trapping survey based on species count data for actual surveys within Koeberg Nature Reserve

Artificial cover object arrays

As of April 2017, coverboard sampling yielded a total of 225 herpetofaunal records consisting of 13 species over the course of the 2016 – 2017 sampling period (Table 3). Of these records, 220 were reptiles comprising 13 species, of which six were snake taxa. The five remaining records represented the only amphibian taxa captured via this method, *Breviceps rosei*.

Table 3 - Species captured using artificial cover object surveys within Koeberg Nature reserve

	Family	Species	Total Captures
Snakes	Colubridae	<i>Dasypeltis scabra</i>	4
		<i>Homoroselaps lacteus</i>	1
	Lamprophiidae	<i>Psammophis crucifer</i>	19
		<i>Psammophis leightoni</i>	9
		<i>Psammophylax rhombeatus</i>	41
Unknown	<i>Unidentified snake species</i>	5	
Lizards	Gekkonidae	<i>Pachydactylus geitje</i>	12
	Lacertidae	<i>Meroles knoxii</i>	1
		<i>Acontias meleagris</i>	3
		<i>Scelotes bipes</i>	8
	Scincidae	<i>Trachylepis capensis</i>	106
		<i>Trachylepis homolocephala</i>	8
<i>Trachylepis variegata</i>		3	
Amphibians	Brevceptidae	<i>Breviceps rosei</i>	5

Pitfall and Funnel-trap arrays

The initial pitfall trap array sampling period yielded a total of 54 individual herpetofaunal captures from 16 species (12 reptile and four amphibian). The second period yielded slightly fewer herpetofaunal captures (47 individuals) and although no new amphibian species were captured, it added five new reptile species to the list (Table 4). The pitfall and funnel-trap arrays yielded a total of 71 reptile and 30 amphibian captures consisting of 17 and four species, respectively (Jacobs 2016).

Table 4 - Species captured during pitfall and funnel-trap array sampling across two survey periods within Koeberg Nature reserve

	Family	Species	Survey 1	Survey 2	Total captures	
Snakes	Typhlopidae	<i>Rhinotyphlops lalandei</i>	1	0	1	
	Lamprophiidae	<i>Lycodonomorphus inornatus</i>	1	0	1	
		<i>Psammophis crucifer</i>	3	6	9	
		<i>Psammophis leightoni</i>	1	0	1	
		<i>Psammophylax rhombeatus</i>	6	2	8	
	Colubridae	<i>Crotaphopeltis hotamboeia</i>	1	1	2	
	Elapidae	<i>Dasyplepis scabra</i>	0	6	6	
<i>Naja nivea</i>		0	1	1		
Lizards	Gekkonidae	<i>Pachydactylus austeni</i>	0	2	2	
		<i>Pachydactylus geitje</i>	1	0	1	
	Lacertidae	<i>Meroles knoxii</i>	1	0	1	
	Gerrhosauridae	<i>Tetradactylus seps</i>	0	1	1	
		<i>Scelotes bipes</i>	3	0	3	
		<i>Scelotes montispectus</i>	2	6	8	
		Scincidae	<i>Trachylepis capensis</i>	1	3	4
			<i>Trachylepis homalocephala</i>	0	9	9
<i>Trachylepis variegata</i>	7		6	13		
Amphibians	Brevipectidae	<i>Brevipectis rosei</i>	11	1	12	
	Pipidae	<i>Xenopus laevis</i>	3	0	3	
		<i>Strongylopus grayii</i>	2	0	2	
	Pyxicephalidae	<i>Tomopterna delalandii</i>	10	3	13	

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Sherman trap sampling

Sherman trap sampling yielded a total of 403 mammal captures covering five species. Four of these species belonged to the family Muridae with a single species, the Forest shrew (*Myosorex varius*) belonging to the Soricidae (Table 5).

Table 5 - Species captured using Sherman traps within Koeberg Nature reserve

Species	Total Captures
<i>Gerbilliscus afra</i>	43
<i>Gerbillurus paeba</i>	61
<i>Mus minutoides</i>	44
<i>Rhabdomys pumilio</i>	253
<i>Myosorex varius</i>	2
Total Captures	403

South African Bird Atlas Projects

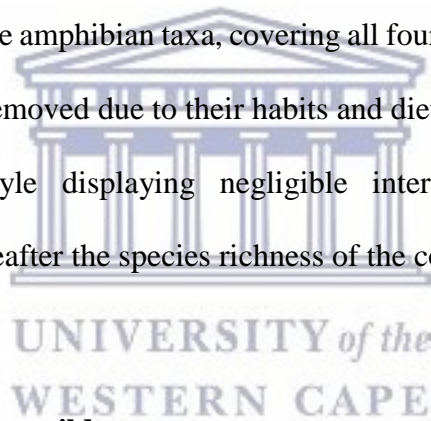
The SABAP1 QDGC 3318CB indicated a total of 216 species recorded across a cumulative total of 11366 cards (likely that different species were recorded on the same cards). The SABAP2 pentads 3335_1820 and 3335_1825 indicated 106 (from 500 cards) and 153 (from 1674 cards) species, respectively. A breakdown of the number of cards to date each species appears on is listed in Table 6 (supplementary material).

2) Tetrapod richness and diversity

Sampling along with existing records, including SABAP one and two records, yielded a combined list of 297 species for the study site tetrapod community. The list covered 231 bird, 39 mammal, 25 reptile, and five amphibian taxa, covering all four tetrapod groups. Thirty-three recorded avian species were removed due to their habits and dietary composition suggesting a predominantly marine lifestyle displaying negligible interactions with the terrestrial community under study. Thereafter the species richness of the community under study shrunk to 265 species (Fig. 5)

3) Characterising dietary guilds

Hierarchical cluster analysis of the dietary data identified ten broad dietary guilds within the Koeberg tetrapod community (Table 7). The cophenetic correlation coefficient between the dietary dissimilarity matrix and resultant dendrogram (Fig. 6) was high (0.81) indicating that the dendrogram provided an accurate representation of the unmodelled pairwise distances between species.



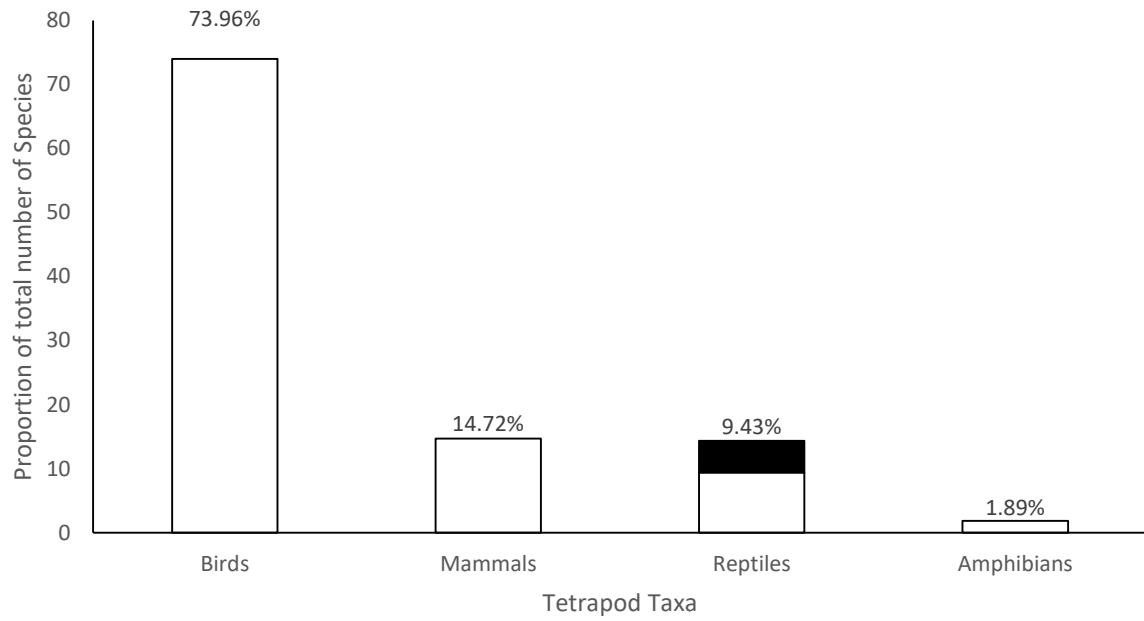


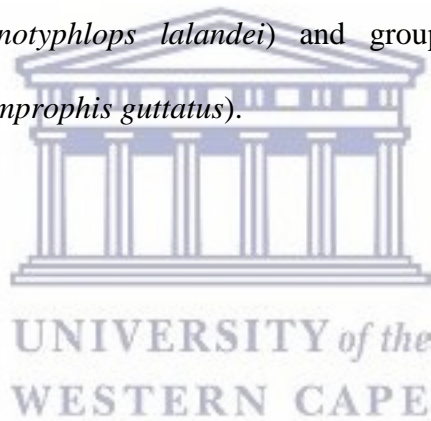
Figure 5 - Proportions of species (post marine bird removal) representing terrestrial tetrapod groups for sampled community at Koeberg Nature reserve with snake species indicated by solid black section



Table 7 – UPGMA hierarchical clustering dietary guild details for terrestrial tetrapod community at the Koeberg Private Nature Reserve (percentages indicate proportion of total guild species)

Guild	Species	Birds	Mammals	Reptiles	Amphibians	Main diet details
1	80	63 (78.8%)	16 (20%)	1 (1.2%)	0	Plant material (mainly fruit) along with insects and other invertebrates
2	50	48 (96%)	1 (2%)	0	1 (2%)	Invertebrates, fish and amphibians
3	1	1 (100%)	0	0	0	Fish, crustacean and avian prey, also carrion
4	1	1 (100%)	0	0	0	Fish and amphibian prey
5	54	37 (68.5%)	9 (16.7%)	8 (14.8%)	0	Invertebrate and vertebrate (small, medium, sometimes large) prey items
6	70	44 (62.9%)	10 (14.3%)	12 (17.1%)	4 (5.7%)	Insect prey
7	5	2 (40%)	0	3 (60%)	0	Small reptiles
8	2	0	2 (100%)	0	0	Grass
9	1	0	1 (100%)	0	0	Fruit
10	1	0	0	1 (100%)	0	Bird eggs

Most bird taxa clustered together within four groups, of which one was almost entirely bird species. Mammal taxa were present within six groups. Reptiles were clustered within five groups and amphibians were split between two with *Xenopus laevis* being one of two non-bird species belonging to guild 2, the other was the Forest shrew (*Myosorex varius*). Four of the ten clusters formed unique single species groups with group 3 containing only the great white pelican (*Pelecanus onocrotalus*), group 4 the African darter (*Anhinga rufa*), group 9 the Egyptian rousette (*Rousettus aegyptiacus*) and group 10 the rhombic egg-eater (*Dasypeltis scabra*). The remaining 12 snake species apart from *Dasypeltis scabra* fell within group 5 (*Dispholidus typus*, *Naja nivea*, *Psammophis leightoni*, *Crotaphopeltis hotamboeia*, *Psammophis notostictus*, *Pseudaspis cana*, *Lycodonomorphus inornatus* and *Psammophylax rhombeatus*), group 6 (*Rhinotyphlops lalandei*) and group 7 (*Psammophis crucifer*, *Homoroselaps lacteus* and *Lamprophis guttatus*).



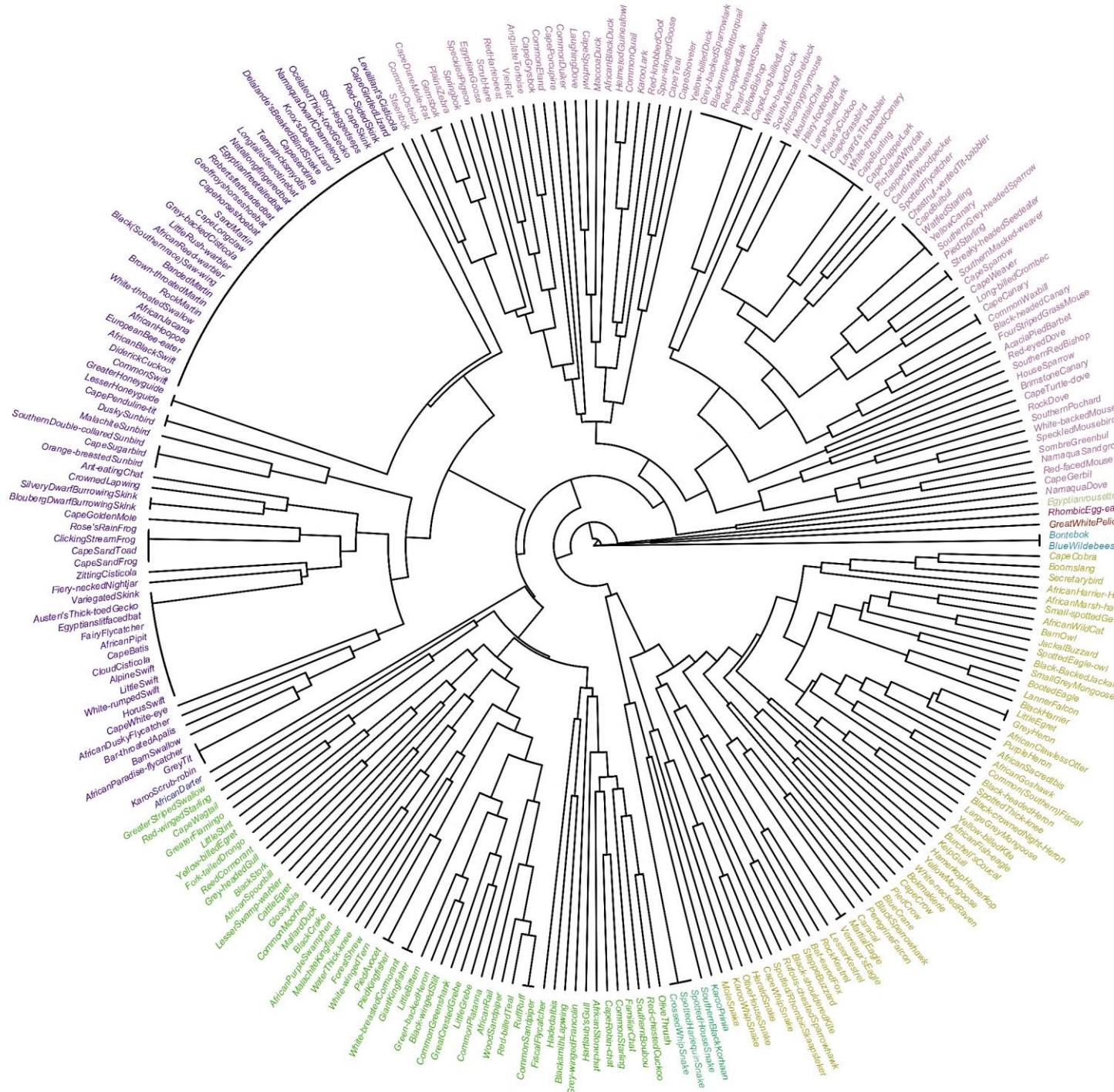
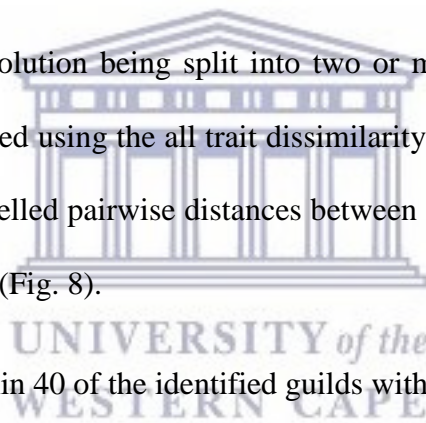


Figure 6 - UPGMA hierarchical functional dendrogram displaying terrestrial tetrapod dietary guilds within the Koeberg Private Nature Reserve

4) Characterising functional guilds

Partitioning Around Medoids (PAM) clustering was applied to the full functional trait matrix. The clustering grouped the community into an optimum number of 54 functional guilds with an average silhouette width of 0.704 indicating a good structure to the clusters (Fig. 7a). The results of the hierarchical clustering strongly mimicked those produced by PAM with an average silhouette width of 0.74 for a 54-group clustering solution (Fig. 7b). The greater silhouette width for the hierarchical clustering solution indicated an even stronger clustering structure than that of the PAM clustering. Comparing the clusters produced by these solutions revealed an identical cluster match of 83% (45 out of 54 guilds were identical) indicating the robustness of the attained guilds. Variation between the clustering solutions resulted from single guilds in a particular solution being split into two or more groups in the other. The functional dendrogram produced using the all trait dissimilarity matrix provided a reasonably accurate display of the unmodelled pairwise distances between species based on a cophenetic correlation coefficient of 0.71 (Fig. 8).

Bird species were present within 40 of the identified guilds with 15 guilds being multi-species guilds containing exclusively avian taxa. Of the guilds containing bird species 16 formed functionally unique, single species guilds. Mammals were present in 14 guilds with three guilds being mammal only multi-species guilds. Three mammal species formed separate, functionally unique guilds with the remaining species grouped together with species belonging to other vertebrate classes. Amphibians were present within four guilds, with two being unique single species guilds. Reptiles were present within 12 guilds of which four were functionally unique single species guilds. In total the cluster analysis revealed 25 unique single species guilds within the terrestrial tetrapod community (Table 8). The only testudine species within the community, Angulate tortoise (*Chersina angulate*), was placed into guild 16. This made it the only reptile species within an almost entirely bird guild, the exceptions being itself and a single mammal species, the Vlei rat (*Otomys irroratus*). A summary of the major characteristics of



each functional guild is provided (Table 9) and the species composition of each guild produced by hierarchical cluster analysis provided as supplementary material (Table 10).

Table 8 - Species composition for all single species functional guilds within Koeberg Private Nature reserve terrestrial tetrapod community. Based on UPGMA hierarchical clustering solution

Taxonomic Group	Guild Number	Common Name	Species
Birds	5	African darter	<i>Anhinga rufa</i>
	9	African jacana	<i>Actophilornis africanus</i>
	19	Black saw-wing	<i>Psalidoprocne pristopectera holomelaena</i>
	21	Black-crowned night heron	<i>Nycticorax nycticorax</i>
	22	Blacksmith lapwing	<i>Vanellus armatus</i>
	34	Fiery-necked nightjar	<i>Caprimulgus pectoralis</i>
	36	Fork-tailed drongo	<i>Dicrurus adsimilis</i>
	39	Great white pelican	<i>Pelecanus onocrotalus</i>
	40	Grey heron	<i>Ardea cinerea</i>
	44	Purple heron	<i>Ardea purpurea</i>
	45	Red-billed teal	<i>Anas erythrorhyncha</i>
	47	Rock martin	<i>Ptyonoprogne fuligula</i>
	49	Spotted flycatcher	<i>Muscicapa striata</i>
	52	Water thick-knee	<i>Burhinus vermiculatus</i>
	53	White-backed duck	<i>Thalassornis leuconotus</i>
54	Yellow-billed duck	<i>Anas undulata</i>	
Mammals	25	Cape dune mole-rat	<i>Bathyergus suillus</i>
	33	Egyptian rousette	<i>Rousettus aegyptiacus</i>
	35	Forest shrew	<i>Myosorex varius</i>
Amphibians	29	Clicking stream frog	<i>Strongylopus grayii</i>
	31	Common platanna	<i>Xenopus laevis</i>
Snakes	42	Mole snake	<i>Pseudaspis cana</i>
	46	Rhombic egg-eater	<i>Dasypeltis scabra</i>
	50	Spotted harlequin snake	<i>Homoroselaps lacteus</i>
	51	Spotted house snake	<i>Lamprophis guttatus</i>

Snakes were present within nine of the identified functional guilds with four of those guilds containing a single species each, making snakes the only reptile species forming single species guilds. The nine remaining snake species were grouped together with members of other vertebrate classes. Boomslang (*Dispholidus typus*) was grouped together with two bird species, namely the African fish eagle (*Haliaeetus vocifer*) and African goshawk (*Accipiter tachiro*) within guild 6. The most speciose guild that snakes appeared in was guild 7 that included the Cape cobra (*Naja nivea*), Cape whip snake (*Psammophis leightoni*), Karoo whip snake

(*Psammophis notostictus*) and Rhombic skaapesteker (*Psammophylax rhombeatus*) along with nine bird and three other mammal species. Guild 15 contained the Herald (*Crotaphopeltis hotamboeia*) and Olive house snake (*Lycodonomorphus inornatus*) as well as the African wildcat (*Felis lybica cafra*), Small-spotted genet (*Genetta genetta*) and Spotted thick-knee (*Burhinus capensis*). Delalande’s beaked blind snake (*Rhinotyphlops lalandei*) was the sole snake species within its guild, 23, being grouped together with the Blouberg dwarf burrowing skink (*Scelotes montispectus*), Silvery dwarf burrowing skink (*Scelotes bipes*), Cape golden mole (*Chrysochloris asiatica*) and Rose’s rain frog (*Breviceps rosei*). This was also true for the Crossed whip snake (*Psammophis crucifer*) within guild 32 being grouped with two other bird species, Karoo prinia (*Prinia maculosa*) and Southern black korhaan (*Afrotis afra*).

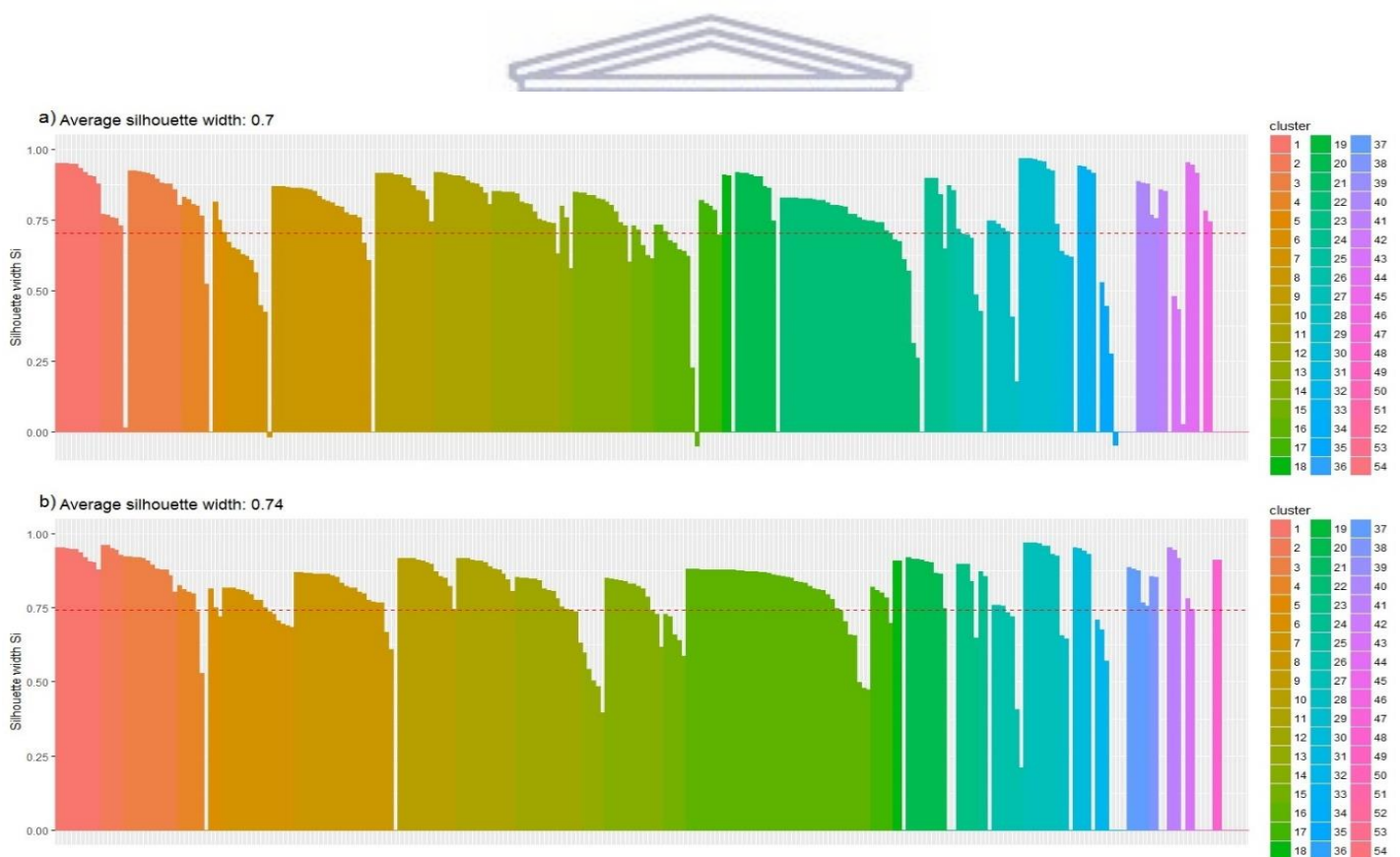


Figure 7 - Silhouette plots displaying strength of clustering solutions for a) Partitioning Around Medoids and b) Hierarchical clustering using UPGMA agglomeration for functional guilds inside Koeberg Nature Reserve. The range of colours represents the 54 identified functional guilds with the dotted line indicating the average silhouette width across all clusters. The closer the average silhouette width is to +1, the more accurate the assignment of species to their respective guilds for that clustering solution.

Table 9 – 54 functional guild description for tetrapod community in Koeberg Private Nature Reserve. Based on UPGMA hierarchical clustering solution

Guild	Number of species	Birds	Mammals	Reptiles	Amphibians	Mean Log Mass	Mean Log Energy Flow	Description	Matches Pam Cluster
1	10	10	0	0	0	1.612	3.729	Diurnal, Arboreal, Diet Category 1	Yes
2	5	5	0	0	0	2.954	5.986	Diurnal, Aquatic, Diet Category 1	No
3	12	12	0	0	0	1.475	3.792	Diurnal, Aerial, Diet Category 6	Yes
4	6	2	4	0	0	3.637	7.113	Cathemeral, Terrestrial, Diet Category 5	Yes
5	1	1	0	0	0	3.259	6.499	Diurnal, Aquatic, Diet Category 4	Yes
6	3	2	0	1	0	2.998	5.672	Diurnal, Arboreal, Diet Category 5	Yes
7	16	9	3	4	0	2.805	5.396	Diurnal, Terrestrial, Diet Category 5	No
8	22	15	0	7	0	1.342	2.795	Diurnal, Terrestrial, Diet Category 6	Yes
9	1	1	0	0	0	2.431	5.214	Diurnal, Aquatic, Diet Category 6	Yes
10	13	13	0	0	0	2.903	5.900	Diurnal, Aerial, Diet Category 5	Yes
11	13	13	0	0	0	1.303	3.207	Diurnal, Arboreal, Diet Category 6	Yes
12	15	15	0	0	0	2.739	5.678	Diurnal, Aquatic, Diet Category 2	Yes
13	5	0	5	0	0	2.522	5.251	Nocturnal, Terrestrial, Diet Category 1	No
14	13	13	0	0	0	1.934	4.248	Diurnal, Terrestrial, Diet Category 2	Yes
15	5	1	2	2	0	2.890	5.351	Nocturnal, Terrestrial, Diet Category 5	Yes
16	41	39	1	1	0	1.783	3.964	Diurnal, Terrestrial, Diet Category 1	No
17	5	0	1	2	2	0.890	1.106	Nocturnal, Terrestrial, Diet Category 6	Yes
18	2	2	0	0	0	2.912	5.916	Nocturnal, Aerial, Diet Category 5	Yes
19	1	1	0	0	0	1.097	2.860	Crepuscular, Aerial, Diet Category 6	Yes
20	9	9	0	0	0	2.467	5.215	Cathemeral, Aquatic, Diet Category 2	Yes
21	1	1	0	0	0	2.903	5.901	Nocturnal, Aquatic, Diet Category 5	Yes
22	1	1	0	0	0	2.354	5.077	Cathemeral, Fossorial, Diet Category 2	Yes
23	5	0	1	3	1	1.019	1.384	Cathemeral, Fossorial, Diet Category 6	Yes
24	2	0	2	0	0	5.029	9.536	Diurnal, Terrestrial, Diet Category 8	Yes
25	1	0	1	0	0	3.100	6.467	Cathemeral, Fossorial, Diet Category 1	Yes
26	7	1	6	0	0	4.084	7.902	Cathemeral, Terrestrial, Diet Category 1	Yes
27	8	0	8	0	0	1.219	2.861	Nocturnal, Aerial, Diet Category 6	Yes
28	2	2	0	0	0	2.955	5.989	Crepuscular, Terrestrial, Diet Category 1	Yes
29	1	0	0	0	1	1.432	1.777	Cathemeral, Terrestrial, Diet Category 6	Yes
30	4	1	3	0	0	5.325	10.041	Diurnal, Terrestrial, Diet Category 1	Yes
31	1	0	0	0	1	2.593	4.024	Nocturnal, Aquatic, Diet Category 2	Yes
32	3	2	0	1	0	1.929	3.817	Diurnal, Terrestrial, Diet Category 7	No

33	1	0	1	0	0	2.217	4.540	Nocturnal, Aboreal, Diet Category 9	Yes
34	1	1	0	0	0	1.820	4.080	Crepuscular, Arboreal, Diet Category 6	Yes
35	1	0	1	0	0	1.301	2.930	Nocturnal, Fossorial, Diet Category 2	Yes
36	1	1	0	0	0	1.740	3.941	Crepuscular, Aerial, Diet Category 2	Yes
37	5	5	0	0	0	1.946	4.291	Diurnal, Arboreal, Diet Category 2	Yes
38	2	2	0	0	0	1.776	4.038	Diurnal, Aerial, Diet Category 2	Yes
39	1	1	0	0	0	4.176	8.358	Diurnal, Aquatic, Diet Category 3	Yes
40	1	1	0	0	0	3.316	6.595	Cathemeral, Aquatic, Diet Category 5	No
41	3	3	0	0	0	2.886	5.957	Diurnal, Aquatic, Diet Category 5	Yes
42	1	0	0	1	0	2.687	4.368	Diurnal, Fossorial, Diet Category 5	Yes
43	2	2	0	0	0	3.355	6.660	Crepuscular, Aerial, Diet Category 5	Yes
44	1	1	0	0	0	3.086	6.208	Crepuscular, Aquatic, Diet Category 5	Yes
45	1	1	0	0	0	2.980	6.031	Crepuscular, Aquatic, Diet Category 2	Yes
46	1	0	0	1	0	2.377	3.782	Nocturnal, Terrestrial, Diet Category 10	Yes
47	1	1	0	0	0	1.207	3.045	Cathemeral, Aerial, Diet Category 6	Yes
48	2	2	0	0	0	3.205	6.409	Cathemeral, Aquatic, Diet Category 1	No
49	1	1	0	0	0	1.318	3.231	Diurnal, Aerial, Diet Category 1	Yes
50	1	0	0	1	0	1.951	2.978	Cathemeral, Fossorial, Diet Category 7	Yes
51	1	0	0	1	0	1.922	2.922	Nocturnal, Terrestrial, Diet Category 7	No
52	1	1	0	0	0	2.648	5.598	Cathemeral, Terrestrial, Diet Category 2	Yes
53	1	1	0	0	0	2.898	5.892	Crepuscular, Aquatic, Diet Category 1	Yes
54	1	1	0	0	0	3.117	6.261	Nocturnal, Aquatic, Diet Category 1	No

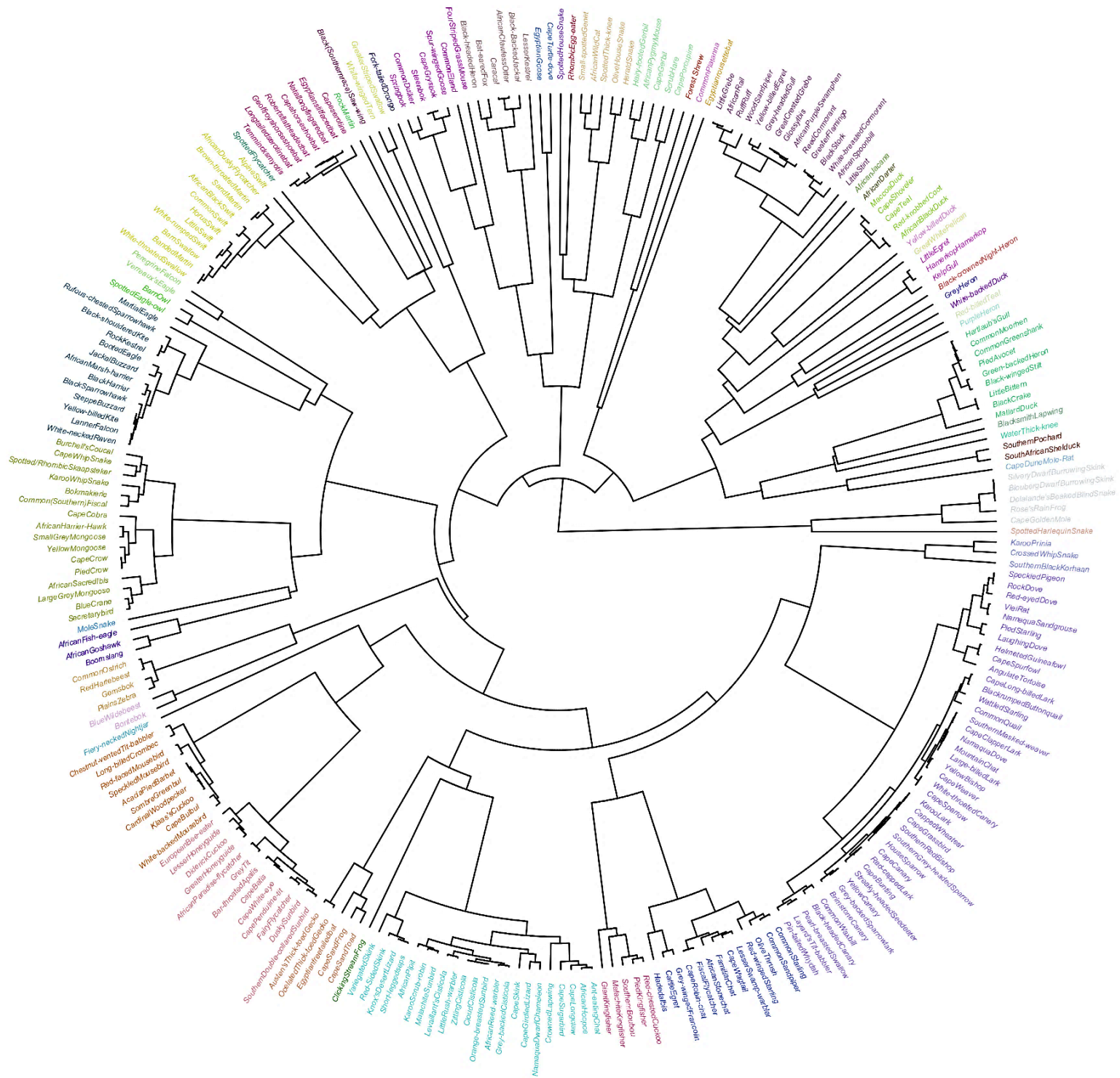


Figure 8 - UPGMA hierarchical functional dendrogram displaying terrestrial tetrapod functional guilds within the Koeberg Private Nature Reserve

5) Quantifying functional diversity

Effect of group removals on dietary functional diversity (FD)

Dietary FD tended to decrease as taxonomic groups were removed from the community. Removal of birds as a group represented the greatest loss of dietary FD (71.88%) followed by the removal of non-passerines (47.3%), passerines (21.74%), mammals (13.58%), reptiles (7.3%), snakes (6.6%), amphibians (0.91%) and non-snake reptiles (0.74%). However, when these FD losses were divided by each group's species contribution to overall species richness, snakes as a group displayed the greatest loss of relative FD with non-passerines as a group displaying the second greatest value (Fig. 9). This indicates that snake species may display a disproportionate relative contribution to community dietary FD and losing the entire group may result in a significant loss of FD. Naturally, these results were mimicked by the mean per species values with snakes once again displaying the greatest dietary FD loss value post entire group removals (Fig. 10).

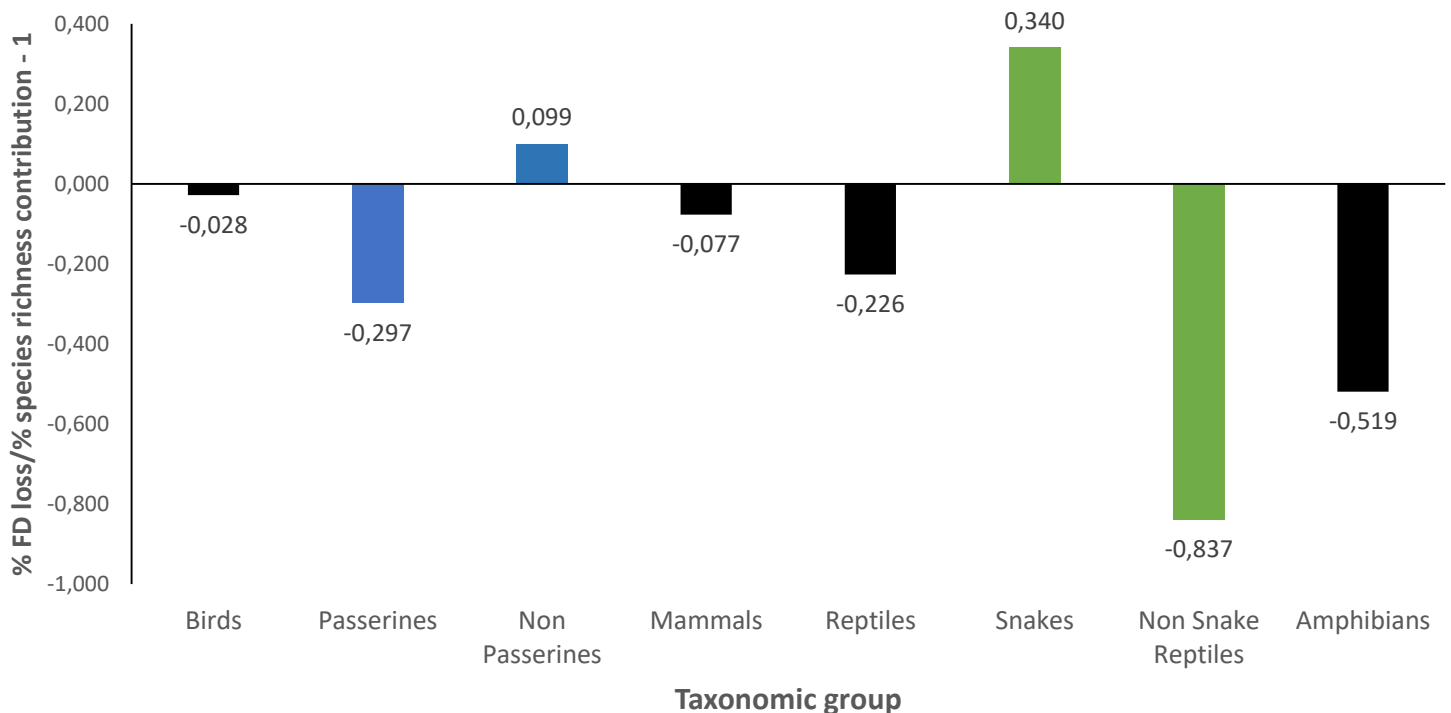


Figure 9 - Dietary FD loss post taxonomic group removal divided by each group's contribution to overall species richness minus 1 between vertebrate classes in Koeberg terrestrial tetrapod community. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions

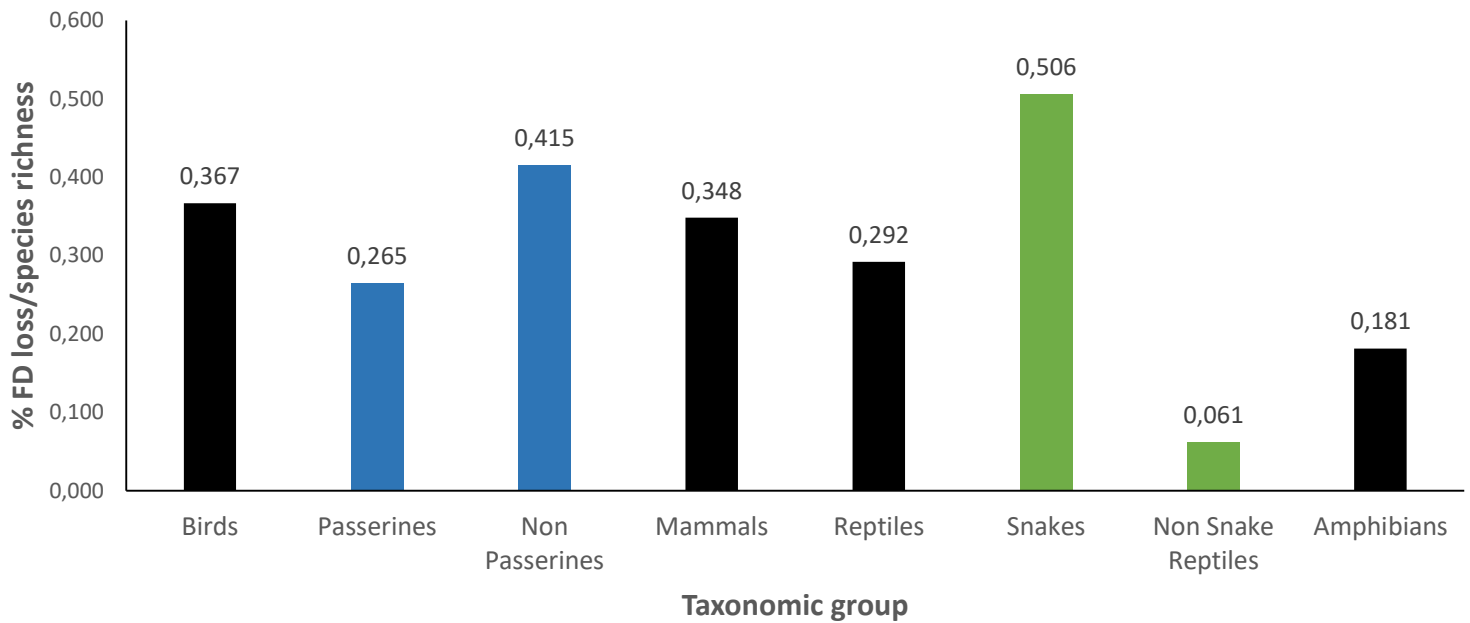


Figure 10 – Mean per species dietary FD loss post entire taxonomic group removal for Koeberg terrestrial tetrapod community. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions

Effect of single species removals on dietary functional diversity (FD)

Single species removals displayed varied effects on dietary FD with the majority of removals resulting in an FD decrease while removing others increased community FD. The latter result was likely due to those species occupying less extreme positions in the modified multidimensional trait space resulting in the remaining species falling farther apart and resulting in a longer tree (Podani and Schmera 2006). FD changes for single species removals within each of the analysed taxonomic groups revealed that as a group, snakes displayed the greatest mean FD loss per species followed by non-passerines, mammals, birds, reptiles, passerines, amphibians and finally, non-snake reptiles displaying a slightly lower mean per species loss (Fig. 11). The standard deviations for per species FD losses within groups displayed values greater than the mean within six of the eight taxonomic groups, indicating values were more spread out than clustered. Spreads in values of this nature indicated that the effects of species on a group's contribution to dietary FD varied. This was likely due to,

within groups, specific species driving the perceived contribution of taxonomic groups to community dietary FD. For snakes this was true for *Dasypeltis scabra*, *Psammophylax rhombeatus*, *Pseudaspis cana* and *Psammophis notostictus* with the summed individual dietary FD loss values of these four species resulting in a greater loss of dietary FD than the rest of the snake species individual FD loss values combined.

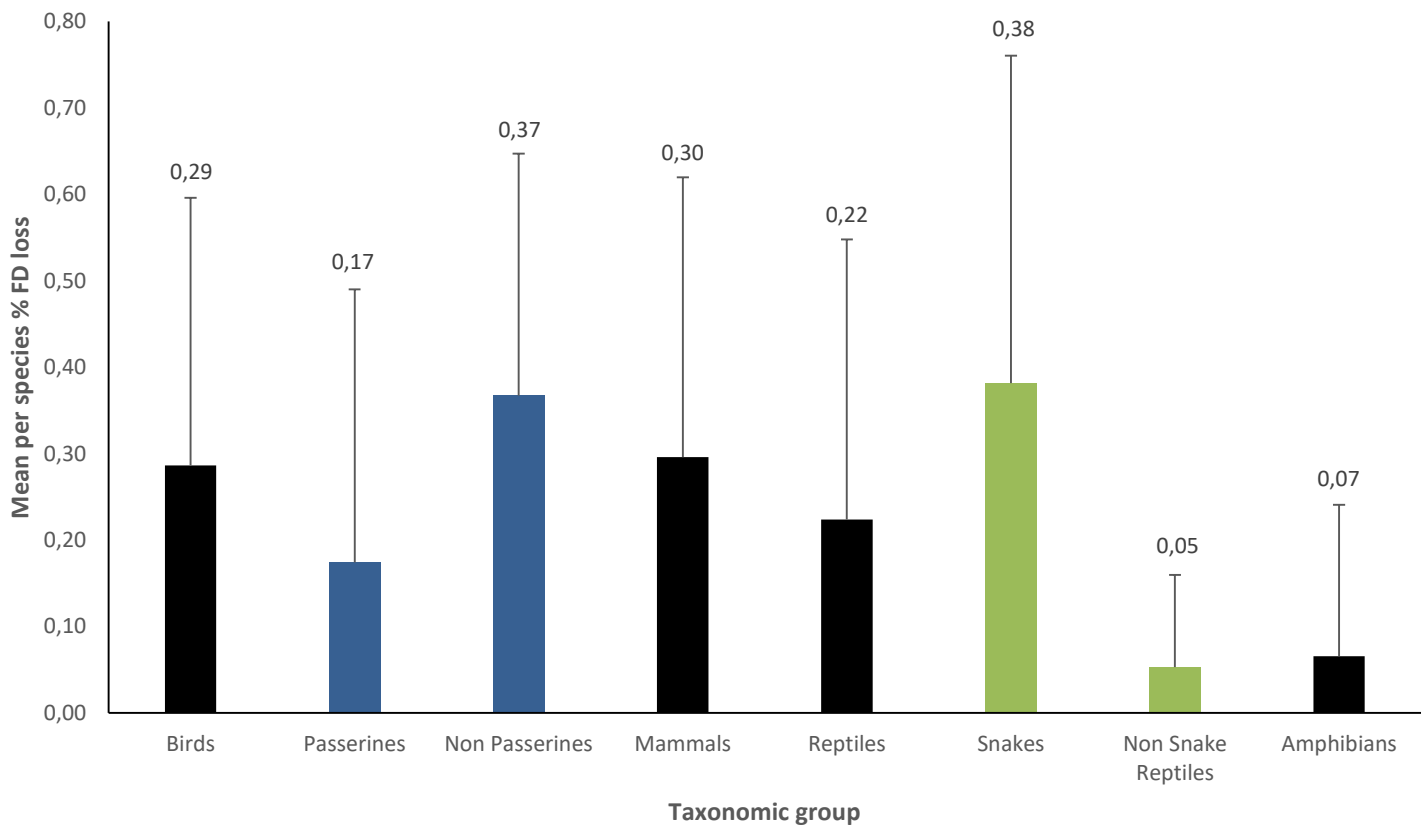


Figure 11 - Mean per species dietary FD loss post single species removals on dietary FD for terrestrial tetrapod groups within Koeberg Nature Reserve. Error bars represent standard deviation of per species FD loss values. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions

Effect of group removals on all trait functional diversity (FD)

As with the dietary analysis, community FD tended to decrease as taxonomic groups were removed. The removal of birds as a group resulted in the greatest loss of FD (53.78%) followed by non-passerines (36.25%), mammals (12.15%), passerines (9.37%), snakes (6.63%), all reptiles (6.10%), amphibians (2.94%) and non-snake reptiles whose removal resulted in a -0.51% gain in FD (through the effect of changing the number of branches is the functional trait dendrogram – see methods). Relative to their contribution to community species richness, amphibians displayed the greatest FD loss followed by snakes (Fig. 12). The FD loss to species richness contribution ratio for every other taxonomic group was less than one indicating some degree of functional redundancy within those groups and a disproportionate loss of FD displayed by amphibians and snakes. This indicates that amphibians and, similarly to dietary FD, snakes as a group may display a disproportionate relative contribution to general community FD and losing the entire group may result in a major loss of FD. These results were mimicked by the mean per species values with snakes once again displaying a relatively high FD loss value post entire group removals (Fig. 13).

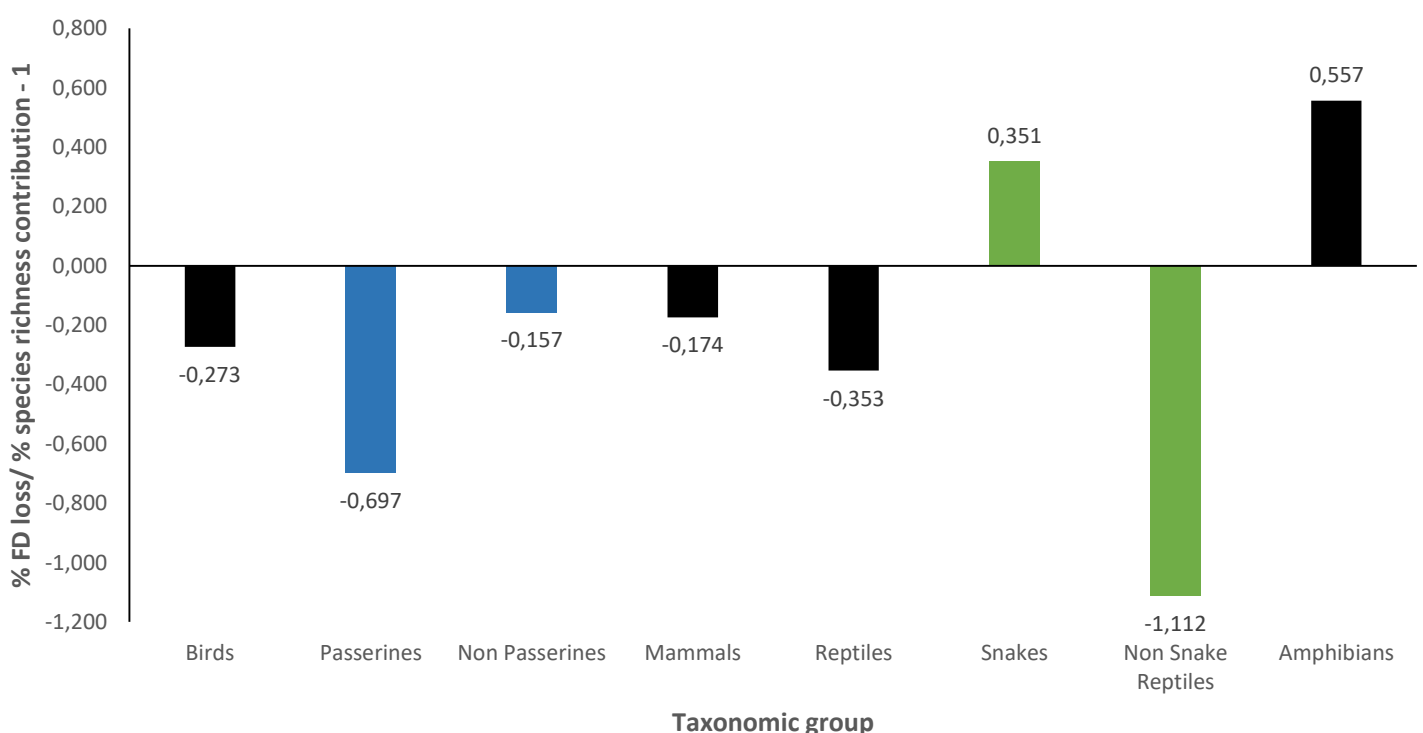


Figure 12 - All trait FD loss post taxonomic group removal divided by each group's contribution to overall species richness minus 1 between vertebrate classes in Koeberg terrestrial tetrapod community. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions

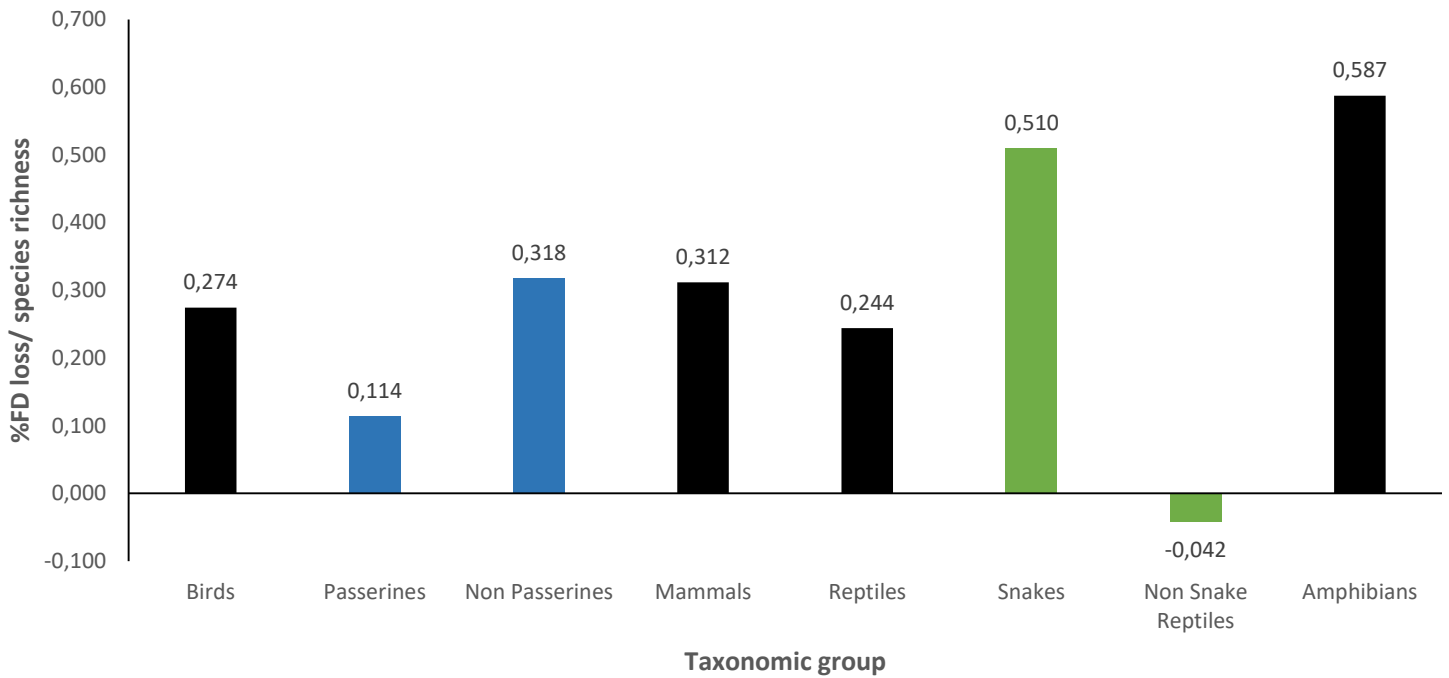


Figure 13 - Mean per species FD loss post entire taxonomic group removal for Koeberg terrestrial tetrapod community. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions.

Effect of single species removals on all trait functional diversity (FD)

Removal of single species once again had variable results with the majority of removals resulting in decreased FD while individual removals of 75 species resulted in increased community FD. The effects of removing single species for all analysed taxonomic groups (Fig. 14) resulted in amphibians and snakes displaying the greatest mean FD losses per species, followed by reptiles, mammals, non-passerines, birds, passerines and non-snake reptiles. The standard deviations for per species FD losses within groups displayed values greater than the mean within all eight groups. These standard deviation values suggested that specific species drive the perceived contribution of taxonomic groups to community FD rather than all members of each taxonomic group. For snakes this was true for *Dasypeltis scabra*, *Homoroselaps lacteus*, *Lamprophis guttatus* and *Pseudaspis cana* with the summed individual FD loss values of these four species resulting in a greater loss of FD than the rest of the snake species individual FD loss values combined. Additionally, as previously mentioned, these four species

were also the only reptile species to form unique single species guilds further supporting their functional uniqueness within this community.

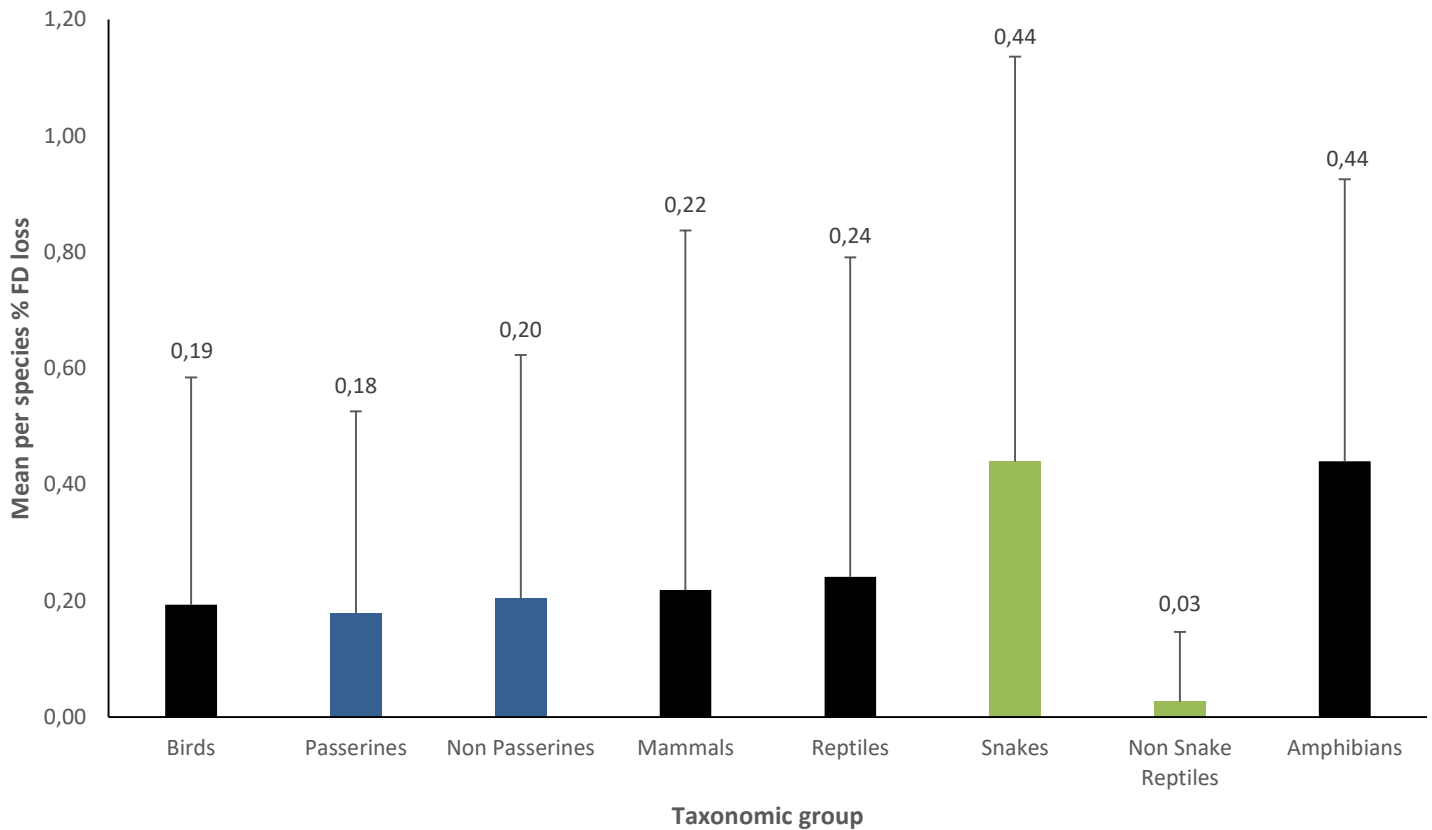


Figure 14 - Mean per species FD loss post single species removals on FD for terrestrial tetrapod groups within Koeberg Nature Reserve. Error bars represent standard deviation of per species FD loss values. Black bars represent vertebrate classes and coloured bars represent relevant subdivisions

Of the 54 identified guilds, 19 displayed FD loss to species richness contribution ratios indicating a higher species richness contribution than FD contribution (any value less than 0 on Fig. 15). This indicates that within those guilds a major overlapping of functional traits between species exists, thus increasing the likelihood of finding functionally redundant species within. Of these 19 guilds two contain snake species (guild 7 and 23). The overlapping of traits between those species and their fellow guild mates suggests their extirpation would result in negligible amounts of functionality loss to the ecosystem. As for those species belonging to guilds displaying only slightly positive ratios, albeit to a lesser degree, an overlapping of traits

still exists with rarer traits provided by specific species. This suggests that there may be a few functionally redundant species within. Only within single species guilds and guilds displaying more positive ratios than those close to 0 can we be certain that functionally redundant species would be a rarity or non-existent.



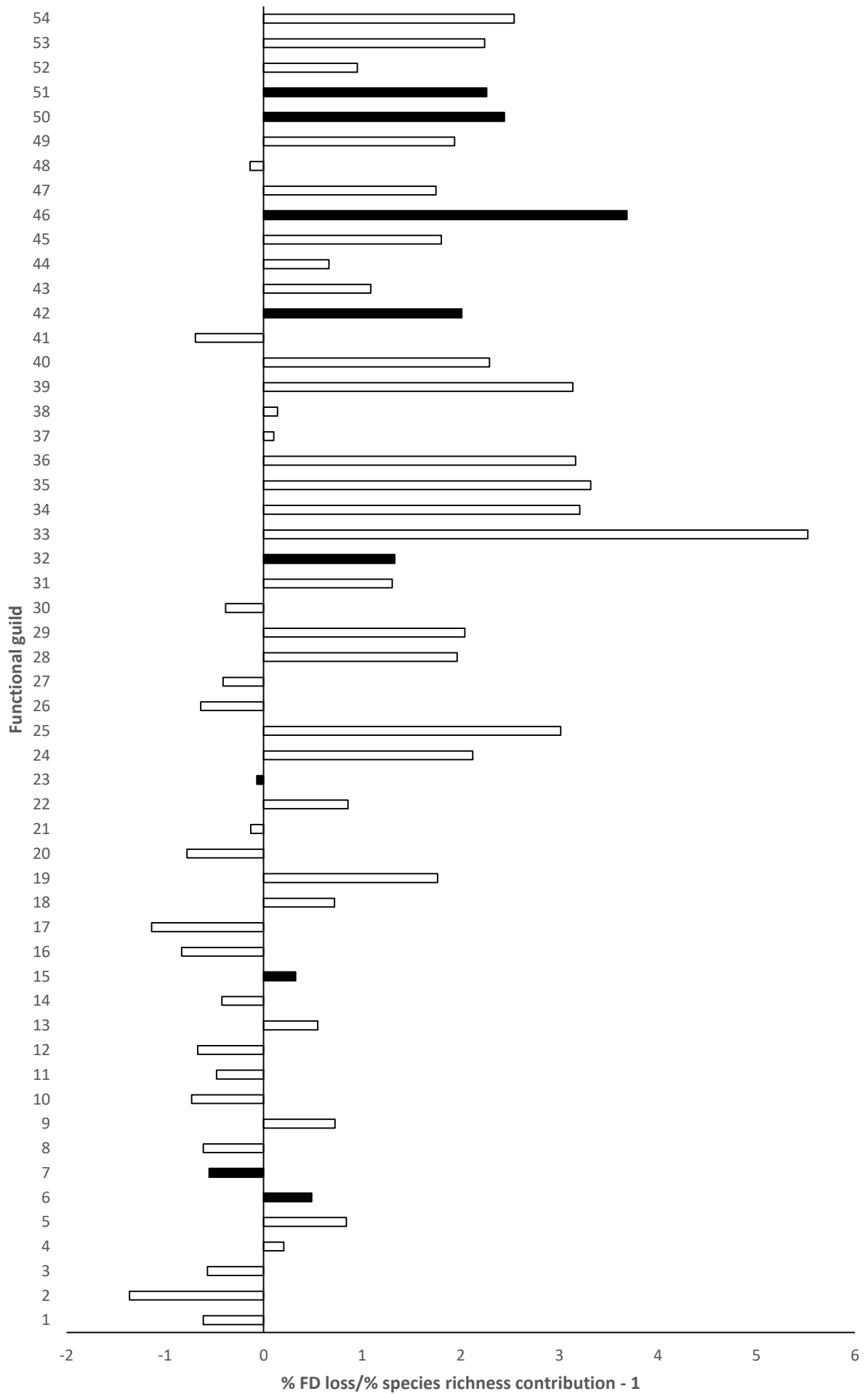


Figure 15 - Comparison between all trait FD loss post functional guild removal divided by each guilds contribution to species richness for the Koeberg terrestrial tetrapod community. Black bars indicate the guilds in which snake species are present

Chapter 4: Discussion

Major findings

The results of the cluster analyses provide ambivalent support for the functional uniqueness of snakes as a group within the Koeberg Private Nature reserve's tetrapod community. The identification of both dietary and functional guilds saw some snake species grouped within speciose guilds while others were grouped within guilds containing few or single species. In terms of dietary guilds *Dasypeltis scabra* formed the only single species reptile guild and only exclusively egg eating species in the entire community. The identified functional guilds placed four snake species (*Pseudaspis cana*, *Dasypeltis scabra*, *Homoroselaps lacteus* and *Lamprophis guttatus*) within single species guilds that seem to occupy unique functional positions within the community. The remaining snake species were placed into guilds of low to medium richness levels. These guilds tended to contain predator species from other taxonomic groups displaying similar traits as the snake species, indicating their low to moderate levels of functional redundancy with their guild mates.

The relationship between species richness and functional diversity within and between taxonomic groups indicated that losing snakes, as a group, would result in disproportionate losses of dietary and functional diversity. However, the likelihood of losing entire taxonomic groups when the different species within those groups display different functional traits is unlikely. This prompted the investigation of individual species effects on functional diversity. This analysis found that single species, rather than the group as a whole, were responsible for the seemingly significant contribution to functional diversity made by snakes within the community. This was true for both dietary and functional diversity. In descending order, the loss of *Dasypeltis scabra*, *Homoroselaps lacteus*, *Lamprophis guttatus* and *Pseudaspis cana* resulted in the highest functional diversity loss values for any individual species of snake.

Considering that these four species also fell into single species guilds, it is clear that they occupy unique functional positions within the community and cannot be replaced if extirpated. The relationship between functional diversity and species richness for most of the guilds including snakes indicates that losing snakes would result in a slightly disproportionate loss of functional diversity. It is likely that within less speciose guilds, including those containing snakes, extirpation of one or more species could drastically change the level of functional redundancy and thereby the functional importance of those guilds.

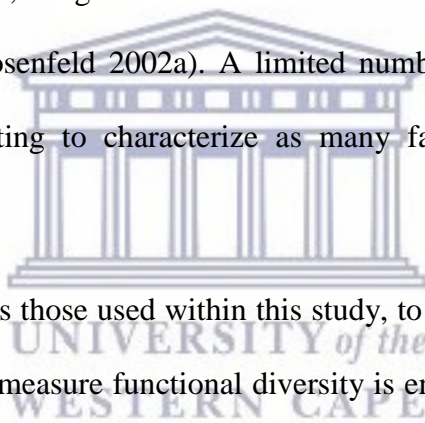
The findings of the single species analyses also highlight the impact species identity has on the functional importance of the guild they are grouped within. Although functional guilds are based on the idea that species within them exhibit similar traits, it does not necessarily mean that those species perform the same roles as their guild mates. The formation of guilds is based on the traits used to characterise species. Due to the colossal challenge of characterising the myriad of traits exhibited by species, despite being the same functional type, the functional importance of the finer more explicit differences between species are underestimated. Tackling this challenge would require an increased focus on the identity and life history of faunal species in general in order to better characterise their functioning within ecosystems.

Overall, the results of this study suggest that snakes within the Koeberg Nature reserve exhibit low to moderate levels of functional redundancy. Certain species occupy clearly unique positions within the terrestrial tetrapod community and losing those species would likely result in significant losses of ecosystem functionality. In contrast, the effects of losing other functionally redundant species would in all likelihood be buffered by the shared traits of their guild-mates.

Limitations

Trait selection is of utmost importance in studies making use of traits to represent species involvement or contribution towards ecosystem processes (Naeem and Wright 2003). The need to identify ‘common currency’ traits while still ensuring that those traits accurately represent the effects all study species play on ecosystem processes poses a considerable challenge. Confidence in selected traits would require further research into the actual effects of species traits on ecosystem functionality (Petchey et al. 2009). As a result, the number of traits used in this study was limited to five due to difficulties in establishing appropriate traits with readily available data for each species. When assessing functional redundancy of species, the fewer the number of traits considered, the greater the likelihood of misleadingly classifying species as functionally redundant (Rosenfeld 2002a). A limited number of traits is an unfortunate limitation in a study attempting to characterize as many facets of terrestrial vertebrate functionality as possible.

The ability of analyses, such as those used within this study, to accurately identify functional guilds within ecosystems and measure functional diversity is entirely dependent on available trait data for species within the community under study. The associated challenges of obtaining such data limits predictive power due to each drawn conclusion being essentially a temporal snapshot of the state of a community at that time (Jaksic 1981, Hooper et al. 2005). The lack of long-term data on the study community’s species composition and resource availability changes over time is problematic. The general dearth of such data results in investigators being limited to making conservation decisions prioritizing non-redundant species on short term assessments. This has the potential to be troublesome since sudden changes in the state of the community may alter the state of previously identified guilds and species redundancy.

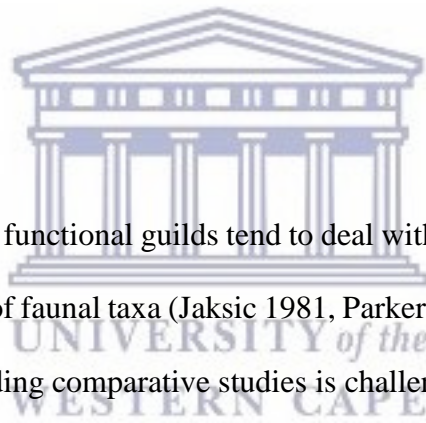


Despite understanding that the degree to which species influence ecological processes is strongly tied to its abundance within a community (Grime 1998), the effect species abundance has on the ecological influence of presented functional traits is not well understood. Time limitations during the sampling period of this project prevented the acquisition of abundance data for all species within the community. This lack of data prevented us from using functional diversity measures that took into account the abundance of each species. Analyses taking into account species abundance tend to provide more complex and detailed insight into the influence of functional traits on species functional importance (Stuart-Smith et al. 2013). Abundance data would have been a valuable addition to the functional diversity component of this project's analysis and would have contributed to our understanding of the effects of species abundances on ecosystems.

Comparison to other studies

Most studies of ecological and functional guilds tend to deal with either floral taxa or narrowly defined taxonomic groupings of faunal taxa (Jaksic 1981, Parker et al. 2001, Blaum et al. 2011, Sundstrom et al. 2012), so finding comparative studies is challenging. While there are studies, like this one, that characterise and compare ecological guilds based on trait similarities between groups of species such as birds, mammals, reptiles, and invertebrates (Brown et al. 1979, Jaksic et al. 1996, Bremner et al. 2003, González-Salazar et al. 2014) they tend to focus on less speciose communities or specific species assemblages. These assemblages tend to be determined *a priori* for a community under study resulting in studies with narrow taxonomic scope.

In terms of taxonomic scope, the identification of trophic guilds across all four vertebrate classes in Sierra Nevada by Parker et al (2001) was most similar to this study. Similar dietary guilds to those identified within this study were characterized and comparisons were made of



each guild's relative contribution to total species richness. Their use of ecological groupings focused on a comparison between communities in order to highlight the importance of scaling in characterising vertebrate communities. Despite the major differences between their study and this one, it nonetheless remains one of few across all vertebrate classes, guild comparisons. Another study measured levels of functional redundancy within bird assemblages in Great Britain over a period of approximately 20 years (Petchey et al. 2007). This was done using a previous iteration of the same measure of functional redundancy used in our study (Petchey and Gaston 2002), albeit with fewer quantified functional traits. No functional redundancy was discovered within the investigated assemblages with fluctuations in functional diversity almost exactly matching the proportions of changes in species richness. Despite using fewer functional traits when conducting the analysis, it provides an example of an ideal long-term dataset. Research using long-term data sets has the potential to contribute towards formulating general laws for communities rather than purely revealing conclusions relevant for that moment in time only. The limited taxonomic scope however, in terms of vertebrate classes investigated, limits the comparability of their findings to ours. These limitations present within these studies could likely be attributed to the intensive time and financial costs associated with data collection and analysis at various spatial scales. These costs, along with a lack of standard methodology for faunal studies of this nature (Blondel 2003), create challenges for functional ecology investigators.

Those existing studies that have focussed on empirical application and comparisons of functional diversity measures have focussed on a variety of organisms including mixed plant species (Walker and Langridge 2002, Petchey et al. 2004), detritivorous arthropods (Heemsbergen 2004), mammalian predators (Blackburn et al. 2005) amphibians (Ernst et al. 2006) as well as a wealth of research on birds (Tschardtke 2008, Sundstrom et al. 2012, Edwards et al. 2013). Although these findings provide valuable insight into the specific

relationships between functional diversity, disturbance, species invasions and traits, their limited scope may be problematic. Looking at assemblages rather than entire communities presents a challenge when attempting to formulate standardized methods and empirically supported generalizations about ecosystem functionality and processes.

Importance and implications of findings

This study presents one of the rare investigations into the functional redundancy of snakes relative to taxa belonging to the other terrestrial vertebrate classes. Additionally, this study also incorporates various emphasized aspects of previous functional ecology research. Criteria such as careful trait selection, community level rather than assemblage investigation, statistically supported functional guild identification, as well as functional diversity analysis to aid in identifying redundancy. Based on the above I believe that this study constitutes a preliminary framework for empirical functional redundancy analyses of not just snake communities but multi-taxa vertebrate communities as well.

As mentioned previously, the suggestion that certain species are very functionally similar to their guild mates also brings up questions of competitive interactions and possible resource partitioning within the environment. Certain snake species such as the Psammophines, for example, were almost exclusively grouped into the same guild suggesting similar use of resources within the environment. If these closely related species display similar functional roles within the ecosystem, the fact that they have not yet excluded each other suggests partitioning on a finer scale than the traits investigated in this study (e.g. fine-scale differential space use, variable foraging times, etc.). On the other hand, there are guilds containing species belonging to very different lineages such as the grouping of a functionally important snake species *Dispholidus typus*, and two raptor species, *Haliaeetus vocifer* and *Accipiter tachiro*.

Findings such as these indicate the importance of studies into the finer functional traits exhibited by species in general.

The prospect that certain species within a given community could be fulfilling unique functional roles has the potential to lend focus to ecological research and conservation efforts involving those species. Ecological research highlighting the functional roles species fulfil combined with statistical support for their proposed importance strengthens propositions and arguments in favour of maintaining their presence in ecosystems. This study highlights the possible functional importance certain snake species play within the community under study. Of these the most obviously important, *Dasypeltis scabra*, seemingly provides traits (particularly diet-wise) that other species do not. It is likely that the rate of predation on bird eggs by *Dasypeltis* species is greatly underestimated with multiple studies providing evidence suggesting that *D. scabra* is an important predator on eggs of various bird species (Bates and Little 2013). Prior knowledge of their activities in Koeberg Nature Reserve highlights their role as one of the dominant bird nest predators within this particular community (Naiwanga et al. 2004). The separation of *D. scabra* into its own specific feeding and functional guild seems appropriate then considering the existing literature highlighting its status as an important, specialist predator of bird eggs in various communities. The functional importance highlighted within this study along with existing records of predation suggest that *D. scabra* is likely to be consuming eggs at a higher rate than their fellow, more generalist, vertebrate species that include eggs in their diets. This and possible future ecological research, spurred on by the functional uniqueness highlighted in this study, may lead to bigger conclusions regarding their role in controlling bird populations within the reserve. A similar scenario could also be true for species such as *Naja nivea*. The ecology and dietary habits of this species has received more attention than that of *Dasypeltis scabra* (Shine et al. 2007, Layloo et al. 2017). While this knowledge is invaluable when focusing on the role of snakes in ecosystems, our results suggest

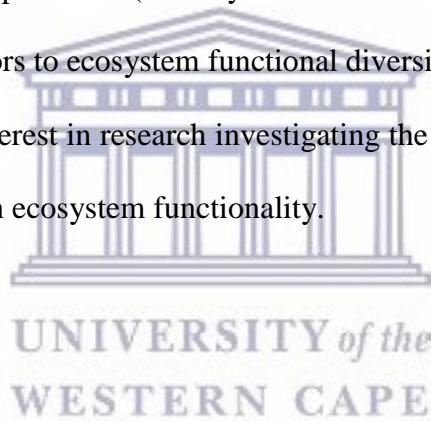
their functional importance is less significant compared to other, less studied, snake species within this ecosystem. By developing analyses such as those used within this study, it improves our ability to identify those species deserving of an increase in focus on their ecology due to their greater contribution to ecosystem functioning.

Conclusion and suggestions for future research

The true value of this project lies in its potential applications in conservation management. Quantifying the level of functional redundancy within biological communities provides us with the ability to better allocate limited resources to those species most significantly contributing to the maintenance of ecosystem functionality. Functional redundancy analyses should not be used in isolation when conducting Biodiversity-Ecosystem Functioning investigations. The ongoing debate regarding the applicability, optimisation and invention of various functional diversity measures, while important, has created issues in functional diversity research. Previously, it had us running the risk of placing too much focus on the measures themselves rather than the slightly more important matter of trait selection (Petchey et al. 2009). Fortunately, the rise in faunal functional diversity studies over the past few decades has drawn attention to the various functional traits of species as well as the specific links between those traits and ecosystem processes. Additionally, the study also highlights lack of focus that research into the functional traits of animals has received relative to plant taxa. Readily available data on various functional traits for many animal species is scarce and of the available trait data, even less can be compared across vertebrate taxonomic groups due to the major differences in physiology and life histories between those groups. Something akin to the “TRY Plant Trait Database” (<https://www.try-db.org/>) for animals would be crucial for increasing the amount of studies making use of animal functional traits. A tool of this nature would greatly improve ease of access to fine scale functional trait data beyond the accuracy of data used within this study however further research would definitely be needed to establish additional

traits for comparing across groups. Once a deeper understanding of the effect various traits have on ecosystem functioning has been achieved, our ability to compare across groups would improve. Less obviously comparable physical traits for species from different groups may become comparable as further research sheds light on the similarities of their functional effects. This is crucial for gaining a more holistic understanding of the functional importance of animals within ecosystems.

The need for research focussing on diversity changes over time within small scale ecosystems as well as the characterisation of the functional relationships within will always be a necessity for correctly measuring functional diversity. By acknowledging the importance of functional diversity in driving ecosystem processes (Petchey and Gaston 2002) we hope to place value on snakes as important contributors to ecosystem functional diversity. This is done with the hope that it will generate further interest in research investigating the potentially significant impact these cryptic creatures have on ecosystem functionality.



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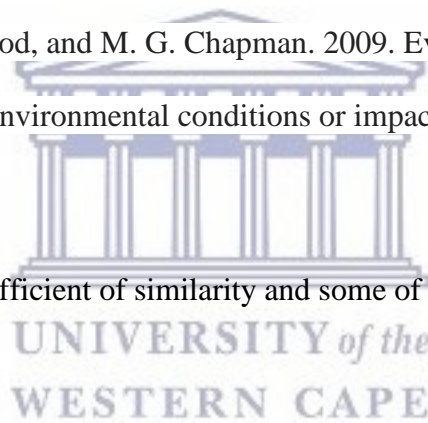
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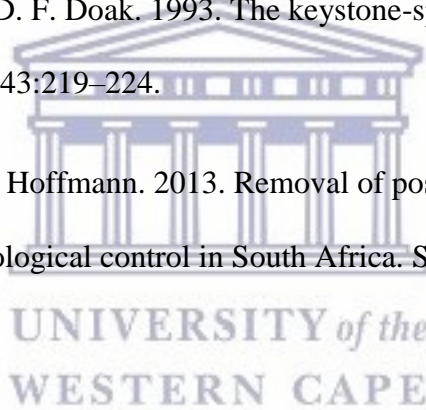
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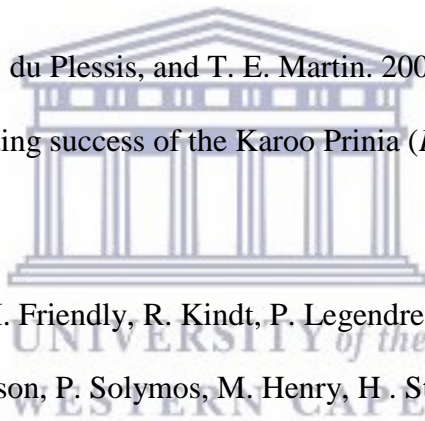
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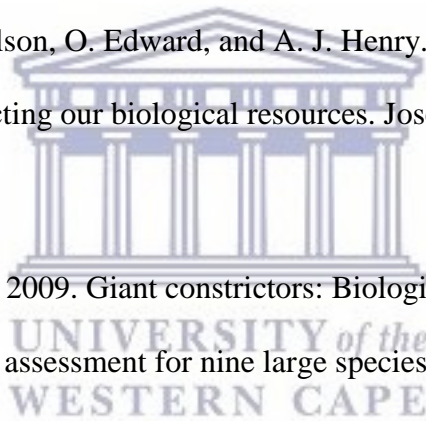
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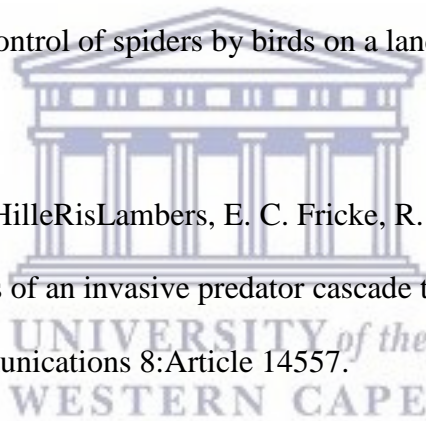
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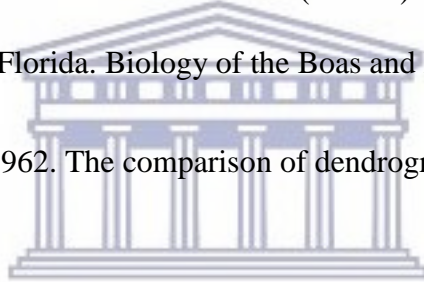


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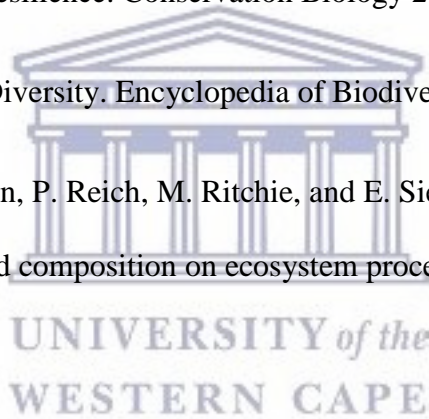
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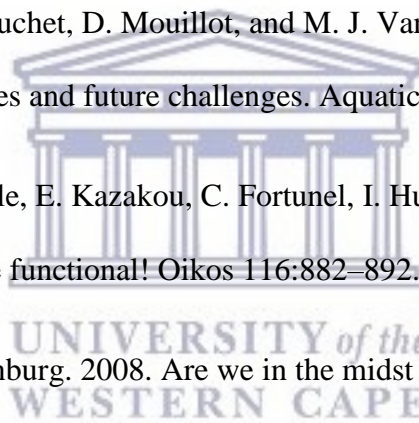
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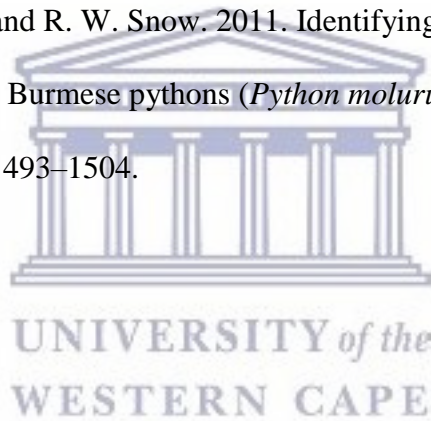
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Supplementary Material**Table 6** - Per species card appearance (pre marine bird removal) breakdown for all relevant bird species reported in South African Bird Atlas Projects 1 and 2

Common name	Number of cards species appeared on			Total Cards
	SABAP 1 (3318CB QDGC)	SABAP 2 (pendat 3335_1820)	SABAP 2 (pendat 3335_1825)	
Acacia Pied Barbet	100	0	2	102
African Black Duck	2	0	2	4
African Black Oystercatcher	126	10		136
African Black Swift	60	1	5	66
African Darter	31	9	5	45
African Dusky Flycatcher	1	0	0	1
African Fish-Eagle	13	1	9	23
African Goshawk	0	0	2	2
African Harrier-Hawk	2	0	0	2
African Hoopoe	46	0	3	49
African Jacana	1	0	0	1
African Marsh-Harrier	9	1	7	17
African Penguin	16	0	0	16
African Pipit	45	0	10	55
African Purple Swamphen	26	0	3	29
African Rail	10	0	0	10
African Reed-Warbler	11	0	2	13
African Sacred Ibis	55	6	16	77
African Snipe	30	0	0	30
African Spoonbill	35	1	4	40
African Stonechat	31	0	2	33
Alpine Swift	46	1	6	53
Antarctic Tern	5	0	0	5
Ant-eating Chat	7	0	0	7
Arctic Tern	17	0	0	17
Banded Martin	16	6	8	30
Bank Cormorant	19	0	1	20
Barn Owl	5	0	0	5
Barn Swallow	77	3	10	90
Bar-tailed Godwit	2	0	0	2
Bar-throated Apalis	41	13	23	77
Black Crake	27	2	0	29
Black Harrier	11	3	11	25
Black Korhaan	53	0	0	53
Black Sparrowhawk	0	0	1	1
Black Stork	4	0	0	4
Black-crowned Night-Heron	30	0	4	34
Black-headed Canary	0	0	1	1
Black-headed Heron	93	4	14	111
Black-necked Grebe	5	0	1	6
Black-rumped Buttonquail	1	0	0	1
Black-shouldered Kite	218	5	18	241
Blacksmith Lapwing	171	2	32	205
Black-winged Stilt	38	1	7	46
Blue Crane	8	0	1	9



Bokmakierie	173	10	26	209
Booted Eagle	0	0	2	2
Brimstone Canary	12	0	11	23
Brown-throated Martin	115	10	18	143
Burchell's Coucal	9	0	0	9
Cape Batis	2	1	6	9
Cape Bulbul	208	13	32	253
Cape Bunting	116	12	17	145
Cape Canary	54	0	14	68
Cape Cormorant	129	11	11	151
Cape Crow	2	0	0	2
Cape Gannet	45	2	2	49
Cape Grassbird	13	9	15	37
Cape Longclaw	30	0	2	32
Cape Penduline-Tit	16	1	1	18
Cape Robin-Chat	157	13	33	203
Cape Shoveler	80	0	9	89
Cape Sparrow	198	7	27	232
Cape Spurfowl	178	9	29	216
Cape Sugarbird	23	0	1	24
Cape Teal	19	0	0	19
Cape Turtle Dove	221	9	28	258
Cape Wagtail	215	9	28	252
Cape Weaver	168	10	27	205
Cape White-eye	93	11	28	132
Cape Long-billed Lark	0	1	1	2
Capped Wheatear	79	0	18	97
Cardinal Woodpecker	2	0	0	2
Caspian Tern	1	2	2	5
Cattle Egret	157	0	7	164
Chestnut-vented Tit- Babbler	45	8	23	76
Clapper Lark	19	0	1	20
Cloud Cisticola	12	0	1	13
Common Fiscal	206	6	24	236
Common Greenshank	22	0	2	24
Common Moorhen	80	4	8	92
Common Ostrich	86	0	1	87
Common Quail	8	0	0	8
Common Ringed Plover	31	0	0	31
Common Sandpiper	10	0	0	10
Common Starling	209	6	32	247
Common Swift	3	0	0	3
Common Tern	74	1	0	75
Common Waxbill	58	8	15	81
Crowned Cormorant	111	3	2	116
Crowned Lapwing	166	0	13	179
Curlew Sandpiper	56	0	0	56
Dideric Cuckoo	3	0	1	4
Dusky Sunbird	1	0	0	1
Egyptian Goose	91	6	26	123
European Bee-eater	33	1	6	40
Fairy Flycatcher	1	0	0	1
Familiar Chat	3	0	1	4
Fiery-necked Nightjar	6	0	1	7



Fiscal Flycatcher	73	1	11	85
Giant Kingfisher	21	0	1	22
Glossy Ibis	22	0	6	28
Great Crested Grebe	7	0	4	11
Great White Pelican	23	6	14	43
Greater Flamingo	3	1	0	4
Greater Honeyguide	0	0	1	1
Greater Sheathbill	3	0	0	3
Greater Striped-Swallow	10	2	15	27
Green-backed Heron	0	0	1	1
Grey Heron	62	6	13	81
Grey Plover	4	0	0	4
Grey Tit	3	1	0	4
Grey-backed Cisticola	92	12	26	130
Grey-backed Sparrowlark	1	0	0	1
Grey-headed Gull	21	0	3	24
Grey-winged Francolin	60	0	1	61
Hadedda Ibis	37	2	15	54
Hamerkop	14	0	0	14
Hartlaub's Gull	215	9	25	249
Helmeted Guineafowl	128	0	21	149
Horus Swift	1	0	0	1
House Sparrow	105	1	8	114
Jackal Buzzard	7	3	11	21
Karoo Lark	18	0	0	18
Karoo Prinia	0	13	34	47
Karoo Scrub-Robin	151	12	25	188
Kelp Gull	219	13	27	259
Kentish Plover	1	0	0	1
Kittlitz's Plover	105	0	0	105
Klaas's Cuckoo	15	1	4	20
Lanner Falcon	5	0	0	5
Large-billed Lark	38	0	2	40
Laughing Dove	218	1	16	235
Layard's Tit-Babbler	25	0	0	25
Le Vaillant's Cisticola	71	1	12	84
Lesser Honeyguide	0	0	1	1
Lesser Kestrel	1	0	0	1
Lesser Swamp- Warbler	68	8	8	84
Little Bittern	3	0	0	3
Little Egret	79	0	3	82
Little Grebe	78	4	10	92
Little Rush-Warbler	19	2	4	25
Little Stint	32	0	0	32
Little Swift	104	3	18	125
Long-billed Crombec	45	7	15	67
Longbilled Lark	2	0	0	2
Maccoa Duck	42	0	0	42
Malachite Kingfisher	35	0	5	40
Malachite Sunbird	125	9	16	150
Marsh Sandpiper	6	0	0	6
Martial Eagle	1	0	0	1
Mountain Chat	1	0	0	1
Namaqua Dove	80	1	6	87
Namaqua Sandgrouse	2	0	0	2



Olive Thrush	5	0	2	7
Orange-breasted Sunbird	0	0	1	1
Parasitic Jaeger	3	0	0	3
Pearl-breasted Swallow	51	6	10	67
Peregrine Falcon	0	1	2	3
Pied Avocet	15	0	0	15
Pied Crow	200	12	31	243
Pied Kingfisher	43	1	2	46
Pied Starling	158	10	27	195
Pin-tailed Whydah	40	1	6	47
Purple Heron	4	2	3	9
Red Knot	5	0	0	5
Red-billed Teal	73	0	8	81
Red-capped Lark	58	0	10	68
Red-chested Cuckoo	2	0	0	2
Red-eyed Dove	98	2	25	125
Red-faced Mousebird	43	4	13	60
Red-knobbed Coot	107	2	9	118
Red-winged Starling	14	0	17	31
Reed Cormorant	80	8	16	104
Rock Dove	33	1	3	37
Rock Kestrel	31	4	23	58
Rock Martin	51	4	12	67
Ruddy Turnstone	76	0	0	76
Ruff	15	0	0	15
Sabine's Gull	1	0	0	1
Sand Martin	1	0	0	1
Sanderling	60	0	0	60
Sandwich Tern	80	0	0	80
Secretarybird	1	0	0	1
Shy Albatross	1	0	0	1
Sombre Greenbul	1	0	0	1
Sooty Shearwater	6	0	0	6
South African Shelduck	52	3	3	58
Southern Boubou	8	5	12	25
Southern Double-collared Sunbird	140	11	30	181
Southern Fulmar	1	0	0	1
Southern Giant-Petrel	1	0	0	1
Southern Masked-Weaver	36	1	11	48
Southern Pochard	15	0	2	17
Southern Red Bishop	78	1	11	90
SouthernBlack Korhaan	0	1	1	2
Speckled Mousebird	22	2	6	30
Speckled Pigeon	143	3	29	175
Spotted Eagle-Owl	42	0	0	42
Spotted Flycatcher	5	0	0	5
Spotted Prinia	146	0	0	146
Spotted Thick-knee	34	1	16	51
Spur-winged Goose	69	1	12	82
Steppe Buzzard	83	1	10	94
Streaky-headed Seedeater	7	0	0	7
Subantarctic Skua	1	0	0	1
Swift Tern	53	4	4	61
Three-banded Plover	90	0	8	98



Verreaux's Eagle	2	0	0	2
Water Thick-knee	1	1	1	3
Wattled Starling	37	0	0	37
Whiskered Tern	1	0	0	1
White-backed Duck	6	0	2	8
White-backed Mousebird	97	8	26	131
White-breasted Cormorant	113	8	11	132
Whitechinned Petrel	7	0	0	7
White-fronted Plover	142	2	0	144
White-necked Raven	0	2	1	3
White-rumped Swift	25	2	9	36
White-throated Canary	93	1	9	103
White-throated Swallow	54	2	11	67
White-winged Tern	12	0	0	12
Wood Sandpiper	36	0	3	39
Yellow Bishop	125	1	15	141
Yellow Canary	182	5	23	210
Yellow-billed Duck	90	3	13	106
Yellow-billed Egret	12	0	7	19
Yellow-billed Kite	45	2	9	56
Zitting Cisticola	10	0	0	10



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Table 10 - Species composition for 54 guild hierarchical clustering solution using UPGMA agglomeration

Species	Guild	Species	Guild	Species	Guild	Species	Guild
Acacia pied barbet	1	African clawless otter	4	African hoopoe	8	African marsh-harrier	10
Cape bulbul		Bat-eared fox		African pipit		Black harrier	
Cardinal woodpecker		Black-backed jackal		African reed-warbler		Black-shouldered kite	
Chestnut-vented tit-babbler		Black-headed heron		Ant-eating chat		Black sparrowhawk	
Klaas's cuckoo		Caracal	Cape girdled lizard	Booted eagle			
Long-billed crombec		Lesser kestrel	Cape longclaw	Jackal buzzard			
Red-faced mousebird		African darter	Cape skink	Lanner falcon			
Sombre greenbul		African fish-eagle	Cape sugarbird	Martial eagle			
Speckled mousebird		African goshawk	Cloud cisticola	Rock kestrel			
White-backed mousebird		Boomslang	Crowned lapwing	Rufous-chested sparrowhawk			
African black duck	2	African harrier-hawk	7	Grey-backed cisticola	9	Steppe buzzard	11
Cape shoveler		African sacred ibis		Karoo scrub-robin		White-necked raven	
Cape teal		Blue crane		Knox's desert lizard		Yellow-billed kite	
Maccoa duck		Bokmakierie		Levaillant's cisticola		African paradise-flycatcher	
Red-knobbed coot		Burchell's coucal		Little rush-warbler		Bar-throated apalis	
African black swift	3	Cape cobra	9	Malachite sunbird	9	Cape batis	11
African dusky flycatcher		Cape crow		Namaqua dwarf chameleon		Cape penduline-tit	
Alpine swift		Cape whip snake		Orange-breasted sunbird		Cape white-eye	
Banded martin		Common (Southern) fiscal		Red-sided skink		Diderick cuckoo	
Barn swallow		Karoo whip snake		Short-legged seps		Dusky sunbird	
Brown-throated martin		Large grey mongoose		Variiegated skink		European bee-eater	
Common swift		Pied crow		Zitting cisticola		Fairy flycatcher	
Horus swift		Secretarybird		African jacana		Greater honeyguide	
Little swift		Small grey mongoose				Grey tit	
Sand martin		Spotted skaapsteker				Lesser honeyguide	
White-rumped swift	Yellow mongoose		Southern double-collared sunbird				
White-throated swallow							

Species	Guild	Species	Guild	Species	Guild	Species	Guild
African purple swamphen	12	African wild cat	15	Pied starling	16	Black-crowned night-Heron	21
African rail		Herald snake		Pin-tailed whydah		Blacksmith lapwing	22
African spoonbill		Olive house snake		Red-capped lark		Blouberg dwarf burrowing skink	23
Black stork		Small-spotted genet		Red-eyed dove		Cape golden mole	
Glossy ibis		Spotted thick-knee	Rock dove	Delalande's beaked blind snake			
Great crested grebe		Angulate tortoise	Southern grey-headed sparrow	Rose's rain frog		24	
Greater flamingo		Black-headed canary	Southern masked-weaver	Silvery dwarf burrowing skink			
Grey-headed gull		Blackrumped buttonquail	Southern red bishop	Blue wildebeest		25	
Little grebe		Brimstone canary	Speckled pigeon	Bontebok		26	
Little stint		Cape bunting	Streaky-headed seedeater	Cape dune mole-rat			
Reed cormorant		Cape canary	Vlei rat	Cape grysbok		27	
Ruff		Cape clapper lark	Wattled starling	Common duiker			
White-breasted cormorant		Cape grassbird	White-throated canary	Common eland			
Wood sandpiper		Cape long-billed lark	Yellow bishop	Four-striped grass mouse		28	
Yellow-billed egret		Cape sparrow	Yellow canary	Springbok		29	
African pygmy mouse		Cape spurfowl	Austen's thick-toed gecko	Spur-winged goose			
Cape gerbil		Cape weaver	Cape sand frog	Steenbok	30		
Cape porcupine	Capped wheatear	Cape sand toad	Cape horseshoe bat				
Hairy-footed gerbil	Common quail	Egyptian free-tailed bat	Cape serotine				
Scrub hare	Common waxbill	Ocelated thick-toed gecko	Egyptian slit-faced bat	31			
African stonechat	Grey-backed sparrowlark	Barn owl	Geoffroy's horseshoe bat				
Cape robin-chat	Helmeted guineafowl	Spotted eagle-owl	Longtailed serotine bat	32			
Cape wagtail	House sparrow	Black (Southernrace) saw-wing	Natal long-fingered bat				
Cattle egret	Karoo lark	Black crane	Robert's flat-headed bat	33			
Common sandpiper	Large-billed lark	Black-winged stilt	Temminck's myotis				
Common starling	Laughing dove	Common greenshank	Cape turtle-dove	28			
Familiar chat	Layard's tit-babbler	Common moorhen	Egyptian goose	29			
Fiscal flycatcher	Mountain chat	Green-backed heron	Clicking stream frog				
Grey-winged francolin	Namaqua dove	Hartlaub's gull	Common ostrich	30			
Hadedda ibis	Namaqua sandgrouse	Little bittern	Gemsbok				
Lesser swamp-warbler	Pearl-breasted swallow	Mallard duck	Plains zebra				
Olive thrush		Pied avocet	Red hartebeest				
Red-winged starling							

Species	Guild	Species	Guild
Common platanna	31	Hamerkop	
Crossed whip snake		Kelp gull	41
Karoo prinia	32	Little egret	
Southern black korhaan		Mole snake	42
Egyptian rousette bat	33	Peregrine falcon	43
Fiery-necked nightjar	34	Verreaux's eagle	
Forest shrew	35	Purple heron	44
Fork-tailed drongo	36	Red-billed teal	45
Giant kingfisher		Rhombic egg-eater	46
Malachite kingfisher		Rock martin	47
Pied kingfisher	37	South african shelduck	48
Red-chested cuckoo		Southern pochard	
Southern boubou		Spotted flycatcher	49
Greater striped swallow	38	Spotted harlequin snake	50
White-winged tern		Spotted house snake	51
Great white pelican	39	Water thick-knee	52
Grey heron	40	White-backed duck	53
		Yellow-billed duck	54

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